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The ecology of lowland rainforest bird community in Papua New Guinea

Ph.D. Thesis

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ANNOTATION

The thesis addresses several aspects of ecology of lowland rainforest avifauna in Papua New Guinea. It describes spatial and temporal distributional patterns of abundance and diversity of bird community and different feeding guilds. More specifically, spatial patterns were explored in relation to topography, tree species composition, forest structure including vertical forest strata and inter-specific associations. The thesis also focuses on nest survival in continuous and fragmented forest, particularly in relation to nest predation.

DECLARATION [IN CZECH]

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Kryštof Chmel

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LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

The thesis is based on the following papers:

Fine-scale spatial patterns in bird community from a tropical rainforest: topography matters.

Chmel K., Riegert J., Paul L., Fibich P., Leps J., Molem K., Weiblen G. & Novotný V. manuscript

Kryštof Chmel participated in experiment preparation and data collection in the field, and was responsible for data assembly, partially for statistical analysis and for writing the manuscript.

Vertical stratification of an avian community in New Guinean tropical rainforest.

Chmel K., Riegert J., Paul L. & Novotný V. (2016): Population Ecology 58: 535-547 (IF = 1.865)

Kryštof Chmel participated in experiment preparation and data collection in the field, and was responsible for data assembly, for statistical analysis and for writing the manuscript.

Predation on artificial and natural nests in the lowland rainforest of Papua New Guinea.

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TABLE OF CONTENTS

CHAPTER I	General introduction	**1**
CHAPTER II	Fine-scale spatial patterns in bird community from a tropical rainforest: topography matters	**21**
CHAPTER III	Vertical stratification of an avian community in New Guinean tropical rainforest	**61**
CHAPTER IV	Predation on artificial and natural nests in the lowland rainforest of Papua New Guinea	**93**
CHAPTER V	Summary of results	**119**

CHAPTER I

General introduction

New Guinea is after the ice-capped Greenland the world's second largest island in the world, covering 785,753 km^2 of land. From west to east the island is intersected by the magnificent mountain range that exceeds altitude of mountain ranges in neighbouring Malay Archipelago, Melanesia or Australia. The highest peak Puncak Jaya reaches 4 884 m a.s.l. New Guinea and Australia are divided by a shallow sea and throughout the geological history they formed one connected land mass for several times. New Guinea sits on the edge of the Australian tectonic plate where long-continued interaction with the Pacific plate has been built the island during the last 40 m.y. (Dow 1977; Audley-Charles 1991). Due to shared geological history Australia and New Guinea bird lineages have predominantly a common origin. For instance, the ancestral area of the major passerine bird radiation of core Corvoidea with more than 700 species is located here (Jønsson et al. 2011). Despite the common origin substantial proportion of New Guinean bird taxa are not found anywhere else. There are several reasons for this. New Guinean topography is very complex with many biogeographical barriers that contributed to the local speciation (Deiner et al. 2011). Further, the divergent environmental conditions of New Guinea and neighbouring Australia stand behind the distinct differences in avifaunas. New Guinea is characterized by a tropical-humid climate and presence of high mountains. It supports the pacific richest humid forest avifauna, while Australia is a low country with mostly dry and temperate climate hosting the Pacific's richest savanna and dry zone avifauna (Beehler and Pratt 2016).

Difference in avifaunas and species composition of other vertebrate communities between Southeast Asia (including Malay Archipelago) and New Guinea is striking and more profound than in case of New Guinea and Australia. Wallace (1869) was the first investigator who described the biographical difference between Sundaic and Sahul region. When he was travelling from western islands of Malay Archipelago to New Guinea, he suddenly observed a sharp discontinuity separating Oriental vertebrate fauna and distinctly different fauna in New Guinea, which was most similar to one known from Australia. For instance, bulbuls, pheasants or woodpeckers are common on islands of Sumatra, Java and Borneo as well as on Asian mainland, while they are entirely absent in New Guinea. Instead megapodes, birds of paradise, bowerbirds, and honeyeaters are among the typical birds in

New Guinea and Australia (Pratt 1982). These differences must have been even more surprising considering that climate and vegetation are very similar in Malay Archipelago and New Guinea. Wallace (1869) therefore proposed that during the time of a lower sea level the island of New Guinea was in conjunction with Australia and similarly Malay Archipelago sits on the continental shelf of mainland Asia, therefore it formed continual land mass. Conversely, between Asia and New Guinea the sea was always deep thus the land bridge has been never formed here and the marine barrier prevented exchange of faunas. Wallace's conclusions explaining historical zoogeography of these two regions have been widely accepted and the transition zone is known as Wallace's line (Huxley 1868; Darlington 1957; Pratt 1982; Barber et al. 2000). However, number of disputes and alternatives of Wallace‘s line position and concept has been proposed, due to the presence of mixed biotas from the Sundaic and Sahul regions on Sulawesi, the Mollucas and Lesser Sunda Islands, that are situated on New Guinean side of Wallace‘s line (reviewed in Clode and O'Brien 2001). Mayr (1944) proposed a line of faunal balance where the fauna was evenly distributed between Asian and Australian species. Simpson (1977) argued that there should be no single line at all, but rather the transition zone that comprises of mentioned islands where the zoogeographic zones overlap - commonly termed Wallacea.

New Guinea is often geographically included in Melanesia – the region of islands in the South West Pacific. Most of the Melanesian islands are volcanic and arose from the sea, therefore all birds had to arrive from other islands. New Guinea is believed to be the major source area for such colonisations with relatively small numbers colonising directly from Australia or Polynesia (Mayr and Diamond 2001). It has been documented that number of species and saturation of Melanesian island avifaunas depends on island size and distance from New Guinea (MacArthur and Wilson 1963). Melanesia, including New Guinea, is where the foundations for models of the island and historical biogeography were laid (Mayr 1942; MacArthur and Wilson 1963; Diamond 1973).

Politically, the island of New Guinea is bisected by two countries. On western half of New Guinea island is West Papua, Indonesia, formerly Irian Jaya and on the eastern half is the the mainland portion of Papua New Guinea (PNG). Besides the mainland PNG (470,500 km2), where our research projects were situated, this country also encompasses over 600 small islands and archipelagos in western Melanesia. Mainland of PNG itself houses more than 465 bird species (Tvardiková 2013).

«✒ New Guinean avifauna ✒»

Mayr (1941) was first who published a complex species account of New Guinea region. He made remarkable achievement, regarding that the region was very poorly explored at the time, and his list comprised of 649 species. According to the most current checklist (Beehler and Pratt 2016) on avifauna of New Guinea and closely adjacent satellite islands the region hosts 769 bird species (101 families, 330 genera and 1 331 forms). Additional 120 species were recognised in nearly a century. However, it needs to be clarified that a substantial proportion of species "added" by Beehler and Pratt (2016) are based on recognition of phenotypically varying populations that were previously treated as a single species. Though it is not impossible to describe new species in New Guinea even in 21st century: expedition to Foja Mountains in Western New Guinea discovered new species of Smoky Honeyeater (*Melipotes carolae*) in 2005 (Beehler et al. 2007).

Beehler and Pratt's (2016) checklist defines 630 species as breeding land birds, 46 as seabirds, 60 as Palearctic migrants and 33 as Australian migrants. More than half of the breeding species (56.5%, N = 356) are endemic to the area. High rate of endemism in New Guinean birds is also supported by the presence of 81 endemic genera and seven endemic families. Hereafter I used taxonomic attribution according to Beehler and Pratt (2016). Endemic families are all part of the Passeriformes order and are characteristic by having a few members or being monotypic: Cnemophilidae (number of species = 3), Melanocharitidae (11), Paramythiidae (3), Rhagologidae (1), Eulacestomatidae (1), Ifritidae (1), Melampittidae (2). Among the near endemic families are the iconic birds of paradise (Paradisaeidae) or Cassowaries (Casuaridae). We recognise 41 species of birds of paradise and from 37 species that occur in the New Guinea region, 35 species are endemic. Cassowaries share one species (*Casuarius* casuarius) with Northern Australia, while other two family members are endemic to New Guinea (*C. bennetti* and *C. unappendiculatus*). Other families with large proportion of endemic species (exceeding 70%) are as follows:

Centropodidae (number of endemic species = 3, number of species occurring in New Guinea = 4), Aegothelidae (6, 7), Psittrichasidae (1, 1), Ptilonorhynchidae (12, 13), Climacteridae (1, 1), Maluridae (6,6), Meliphagidae (47, 65), Acanthazidae (14, 20), Orthonychidae (1, 1), Psophodidae (1, 1), Cinclosomatidae (5, 5), Oreoicidae (2, 2), Pachycephalidae (15, 20), Petroicidae (20, 26).

In terms of biogeographical composition of bird lineages most of the occurring families exhibit world-wide distribution (*N* = 39), 27 families are confined to the Old World, 18 families are found only in Australasia and species of eight families range from Asia to Australasia. Species of two families are introduced to New Guinea (Pycnonotidae and Passeridae). Different situation can be found passerines (Passeriformes) that contain half of the all occurring families (*N* = 49). Large proportion of families is either restricted to Australasia (*N* = 15) or are distributed throughout the Old World (*N* =15). Only six families exhibit world-wide distribution and four range from Asia to Australasia. Two of the latter families have an ancestrals in Australia-New Guinea (Artamidae, Pachycephalidae), while members of the Diceaidae and Rhipiduridae families colonized New Guinea from Asia (Nyári et al. 2009a, b, Jønsson et al. 2010, 2017).

« New Guinea bird regions »

New Guinea can be divided into a several ornithogeographic zones that are primarily given by the complex topography of the region. Mainland of New Guinea is represented by the large lowland rainforest areas (44% of the land lies below 100 m asl), as well as the high mountain areas (27% of the land lies between 1000 to 4500 m a.s.l.). Mountains of New Guinea consist of Central Range plus additional 19 outlying ranges (Diamond 1985). Local bird communities are to a large extent dependent on altitude (Tvardiková 2013), and the differences between mountain and lowland avifaunas can be clearly defined. In this sense the New Guinea behaves as an island archipelago, since its mountain ranges and lowlands are isolated from each other by a "sea" of uninhabitable habitats: by mountains for lowlands birds and by lowlands for mountain birds (Diamond 1973). New Guinea has therefore a substantial number of bird regions that are important in terms of a high local endemism. Moreover, some of them are listed among the critical regions of the world for the conservation of restricted-range bird species: Endemic Bird Areas (EBAs), declared by the Bird Life International, Stattersfield et al. 1998). New Guinea has nine EBAs, this number outreach some of the much larger continents: Australia has, for instance, only seven EBAs.

Four EBAs are confined to lowlands. Three lowland EBAs contains avifaunas of rainforests with disjunctive evolutionary history (West, North and South Papuan lowlands). Their boundaries follow the distribution of three endemic species of crowned pigeons: *Goura cristata* in the west, *Goura victoria* in the north and *Goura sheepmakeri* in the south. Other lowland EBA (Trans-Fly) represents coastal region of savannas, wetlands, and monsoon forests. Although we can find several endemics in the latter region (*Megalurus albolimbatus, Lonchura nevermanni and Lonchura stygia*) it also shares a large proportion of species with Australia both due to habitat similarities and a short distance between Australia and Trans-Fly region. Highlands of New Guinea are divided into four EBAs: West, Central and North Papuan mountains plus Aledebert and Huon Ranges. Geelvink Islands EBA comprise of adjacent islands of Biak, Supiori, Numfor and Meos Num.

« **Lowland rainforest avifauna** »

Lowland rainforests bird communities are among the richest within the world. This applies also to New Guinea, where lowland rainforest hosts the richest bird community among the New Guinean habitats. Along the altitudinal gradient, species richness of forest birds decreases nearly linearly. On Mt. Wilhelm altitudinal gradient number of recorded bird species decreased from 113 at 200 m a.s.l. to 37 bird species at the tree line (Tvardiková 2013). Around 230 species are known to occur in New Guinean lowland rainforests. Numbers of species recorded per one site differ among conducted surveys. It depends particularly on covered area and length of survey period. I personally accumulated observations of 135 species during the seven months that I spent at study site in Wanang Conservation Area (covered area ≈ 500 ha) in northern New Guinea, Madang Province. Considering only standardised survey from the same area that was carried out in the 50 ha forest plot (141 observation hours) the number drops to 93 recorded species. In nearly a doubled time period (225 observation hours) Pearson (1977) recorded only 83 species in northern New Guinea, East

Sepik Province. Driscoll and Kikkawa (1989) covered a larger area composed of mosaic of terrace, swamp and hill forests (including regrowth patches) and documented presence of 147 species in mosaic of terrace, swamp and hill forest in Trans-Gogol area in Madang Province. Bell (1982) carried intensive survey in a small forest plot (2.5 ha) in southern New Guinea, Central Province and during the period of two years (725 observation hours) he observed remarkable 165 species. However, seven species are not associated with the rainforest habitat. Still, 158 species is a very high number for a forest study plot of particular size. Beehler et al. (1995) explored forest bird community at larger spatial scale (c. 10 km^2) also in southern lowlands (Gulf Province) and they recorded 184 species (143 forest dwelling species). This suggests that species richness of rainforest avifauna of southern lowlands is higher than in the northern lowland rain forest.

In Global perspective, New Guinean lowland rainforests host fewer species than rainforests of large continents. The most species rich bird communities of lowland rainforest are found in New World, where one can encounter more than 240 species at one site (Terborgh et al. 1990). Pearson (1977) carried out standardised pantropical comparison of lowland rainforest bird communities and documented highest species richness on study sites in South America (Ecuador = 159 species, Peru = 131, Bolivia = 124), followed by Africa (Gabon = 112) and Borneo (108), while the study site in New Guinea had the least number bird species (83). This decreasing trend can be explained by differences in regional historical events and by the island effect: extinction rate is higher on islands than on mainland (MacArthur and Wilson 1963). Climate conditions and other abiotic factors that determine distribution of rainforest varied throughout the geological history and tropical regions. Therefore, regions that undergone more favourable historical influences now have rainforest biota of higher species richness (Ricklefs 2004; Graham et al. 2006; Hoorn et al. 2010). Borneo is slightly smaller (by 8%) island than New Guinea. According to the island effect it should host less species. On contrary, it hosts a richer bird species community than New Guinea. However, Borneo likely received faunal contributions from Greater and Lesser Sundas, together with Malaysian Peninsula that were connected by land bridges during eustatic lowering of sea level during the Late Quaternary (Fairbanks 1989). Their contribution to species number of Borneo were likely greater than that of the relatively species poorer rainforest avifauna of the Australian continent to New Guinea (Driscoll and Kikkawa 1989), when the land bridge occurred between the latter land masses (Voris 2000).

Lower number of species that occur in New Guinea may be caused by more ubiquitous distribution of species than in richer tropical regions and lower rarity of species. Rare species tend to use specialized hunting techniques, rely on rare food resources, or utilize large home ranges. Large home ranges are common among tropical birds, possibly because of patchily distributed food supplies (Karr 1976) and thus detectability of these species is very low. Pearson (1977) was able to record 70% of regional lowland rainforest avifauna in northern New Guinea after 225 hours of observation, while in Ecuador, Peru, Gabon and Borneo he observed smaller percentages from available species pool during more observation hours. In New Guinea Bell (1982) was able to record over 93% of the lowland rainforest species known regionally in a 2 ha plot, which confirms that New Guinean birds tend to be less rare than in other tropical regions (South America or Africa).

Families such as Accipitridae, Columbidae, Psittacidae, Cuculidae, Halcyonidae, Meliphagidae, Acanthizidae, Rhipiduridae, Monarchidae are among the most species rich families in New Guinean lowland rainforest. Pigeons and doves (Columbidae) of New Guinea actually reached the greatest diversity worldwide (Kissling et al. 2009) and some lowland localities inhabit more than 20 species (Beehler et al. 1995; Pratt and Beehler 2014). Iconic birds of paradise or bowerbirds occur mostly in hills and mountains whereas fewer species occur in lowlands. In lowlands of mainland New Guinea we can find three species of genus *Manucodia* (socially monogamous birds of paradise in which sexes look alike), Brown Sicklebill (*Drepanornis bruijnii*), two rifle birds (*Ptiloris magnificus* and *P. intercedens*), Twelve-wired Bird of Paradise (*Seleucidis melanoleucus*), King Bird of Paradise (*Cicinnurus regius*) and three species of genus *Paradisaea* (*P. apoda, P. minor* and *P. raggiana*). However, due to disjunctive distributional ranges usually less than six species co-occur at one forest site (Bell 1982a; Driscoll and Kikkawa 1989; Beehler et al. 1995). Bowerbirds are confined to mountains even more strictly. White-eared Catbird (*Ailuroedus buccoides*), a monogamous bowerbird which lacks the habit of building bowers, is the only species inhabiting lowland rainforest. Although another two species of bowerbirds (*Chlamydera* *cerviniventris and C. lauterbachi*) occur in lowlands, they avoid rainforest interior and inhabit open habitats (grasslands and scrubs).

« Composition of trophic guilds »

The insectivory is the most abundant and species rich feeding class in New Guinean lowland rainforests (Chmel et al. 2016). The majority of insectivorous species belong to the following families: Cuculidae, Halcyonidae, Alcedinidae, Acanthizidae, Pachycephalidae and Monarchidae. Frugivorous birds of New Guinean lowland rainforest are in terms of species richness associated in the second most common trophic guild. The majority of obligate frugivores are represented by the family Columbidae. Other typical frugivores belong to families that contain only few (Casuaridae, Cacatuidae or Psittacidae) or even single species (Cuculidae, Bucerotidae). Obligate frugivores are, therefore, purely represented by non-passerines. There are various facultative frugivores among passerines that also exploit other food resources, mostly insect (e.g. Ptilonorhynchidae, Melanocharitidae, Oriolidae, Paradisaeidae and Sturnidae). Frugivory combined with insectivory together within a feeding class composed of birds that replenish insects with nectar are the most common strategies among omnivorous birds of lowland rainforest (Chmel et al. 2016). Species feeding on insect and nectar are primarily represented by honeyeaters (Meliphagidae), which substitute sunbirds (Nectariniidae), the typical nectar feeders of the Old World. New Guinea with only three species is on the border of sunbirds distributional range. Lastly, the endemic family Melanocharitidae encompass partly insectivorous and partly nectarivorous longbills with three species that inhabit lowland rainforest. Other clearly defined omnivorous guild consists of birds that feed on fruits and nectar. This strategy is confined merely to lories and lorikeets (Psittacidae). They often consume nectar together with pollen and entire flowers. Several birds have many different components of diet (or is not well understood) and therefore it is hard to classify them further than omnivores. For instance, pygmy parrots (genus *Micropsitta*) were reported to forage on lichen, fungi, small seeds and also insects (Pratt and Beehler 2014). The friarbirds from family Meliphagidae (e.g. *Philemon meyeri, P. bucceroides*) can feed on combination of fruits, nectar and insects too. Above that the latter has been reported to predate bird nests (del Hoyo et al. 2016). Carnivorous birds that feed on vertebrates represent relatively species rich group of larger birds. Their abundance detectability is however usually very low (Beehler et al. 1995). Hawks (Accipitridae) make up the large proportion of carnivorous birds with 12 species that can occur in lowland rainforest including the enormous forest raptor: New Guinea Harpy-Eagle (*Harpyopsis novaeguineae*). Large kingfishers (Halcyonidae) may also take small vertebrate prey. Furthermore, some species of bitterns and herons (Ardeidae) or cormorants (Phalacrocoracidae) prey upon fish in small forest streams, thus adding to the list of forest carnivores.

Lastly, several aspects in composition of trophic guilds are specific for New Guinean rainforest. In New Guinea we find the worldwide greatest diversity of frugivorous birds after South America (Kissling et al. 2009). Most of the frugivores are confined to canopy (Chmel et al. 2016). This pattern is similar to bird communities in Southeast Asia, while African and Neotropical frugivores are relatively common also in understorey (Karr 1980). Regarding insectivory, we don't find ant-following birds in New Guinea. These specialized insectivores are known from Africa and South America only. Further, New Guinea has similarly to Southeast Asia low diversity of terrestrial insectivores, which are more common in African and Neotropical rainforests (Karr 1980). Nectarivorous birds of New Guinea and Australia (honeyeaters and lorikeets) are less phenotypically and ecologically specialized (i.e. birds have non-specific feeding relationships with their food plants) than Neotropical (hummingbirds) and African (sunbirds) nectarivorous birds (Fleming and Muchhala 2008; Zanata et al. 2017).

« Spatial distribution of rainforest birds »

Many studies have documented that species do not occur randomly across the space suggesting that environmental filtering is a dominant mechanism in the assembly of many ecological communities (Diamond 1973; Levey 1988; Goetz et al. 2007; John et al. 2007; Jabot et al. 2008). Spatial variation in abundance of food resources and distribution of preferred microhabitats within rainforest therefore affects distribution of local birds. A typical example connecting both factors is tree fall gaps. These natural forest openings contribute to the structural heterogeneity of the forest and influence composition and richness of the bird community (Schemske and Brokaw 1981). The tree fall gaps create unique microhabitats and simultaneously thus influence an abundance of food resources. In Costa Rica, an understory fruit bearing trees were more abundant in gaps, which was reflected in abundance of frugivorous birds (Levey 1990). Distribution of microhabitats together with food availability may be further defined by various characteristics: e.g. elevation, slope steepness, edaphic properties, distance to the water or by stratification of forest vegetation (Smith 1973; Lee and Marsden 2008; Keppel et al. 2011; Pomara et al. 2012).

In addition, associations between species may play an important role in shaping spatial patterns of rainforest bird community. In Puerto Rico, Saracco et al. (2004) observed a positive correlation between abundance of frugivorous birds and availability of fruits. The frugivory was, however, more localized than fruit abundance. This was due to interspecific facilitation, which explained the differences in bird foraging locations. Interspecific aggression contributed to the segregation patterns in these rainforest birds. This also enhances the local species diversity, insomuch as the competing pairs of species, often congenerics with similar ecologies, exhibit low co-occurrence, but are able to coexist in one rainforest area (Graves and Gotelli 1993). Competition within and between species is therefore reflected by the patchy distribution that is typical for large proportion of forest-dwelling birds. Consequently, bird communities of tropical forests are typically dominated by rarity (Thiollay 1994). However, the community organisation can differ between tropical regions, whilst some rainforests exhibit distinctly a lower proportion of rare species than others (e.g. Panama and New Guinea vs. Amazonia with a very high proportion of rare species; Pearson 1977; Robinson et al. 2000). We can expect that the distribution of species in regions with increased species occurrence will be less patchy. Positive associations between species may conversely contribute to aggregation of species. One common example in tropical rainforests, including New Guinea (Bell 1983), are mixed-species foraging flocks. Flocking enhances foraging efficiency and reduce the risk of predation (Buskirk 1976; Powell 1985; Goodale and Kotagama 2006; Magrath et al. 2015).

«✒ Vertical stratification of rainforest ✒»

Tropical rainforest represents a suitable environment for research on vertical stratification of various taxa. Perhaps every biologist is familiar with illustrations depicting composition of vegetation layers from ground trough the canopy to emergent trees that tower over the rainforest (e.g. Whitmore 1984; Kricher 2011). Although the described number of layers differs between literature resources, mainly because the transition between layers is continuous, it is indisputable that we can observe a zonation or gradient of biotic (floristic composition, leaf area, biomass density etc., e.g. Pearson 1977; McWilliam et al. 1993; Clark et al. 2011) and abiotic (temperature, wind speed, light intensity or humidity, e.g. Yoda 1974; Smith et al. 1992; Chmel et al. 2016) parameters across the vertical rainforest profiles. Great vertical heterogeneity of tropical rainforest maintains a high diversity of different microhabitats with specific biotic and abiotic conditions. Different assemblages, communities of organisms may be adapted to these varying conditions which results in their stratification. Thus, habitats with greater vertical heterogeneity hosts also animal communities of greater diversity (MacArthur and MacArthur 1961).

«✒ Methods for surveying vertical stratification of birds ✒»

The most commonly used methods for surveying vertical distribution are visual counts: (1) transects or (2) point counts, where heights of observed birds are estimated by the researcher from the forest floor (Colquhoun and Morley 1943; Pearson 1971; Dickson and Noble 1978; Bell 1982b). These survey methods are based on the direct observation of birds with estimated height of the feeding/moving bird. A great disadvantage of this approach is, especially in the tropical rainforest, that canopy birds may be underestimated due to the presence of dense vegetation. Moreover, the estimation of vertical position of birds from the ground is rather inaccurate and the error increases with distance from the observer. To avoid this methodological bias, Walther (2003) used a canopy crane to study the vertical distribution of birds. Canopy crane provides an opportunity to survey birds within the desired strata and on top of that the crane construction works as a good reference for estimating height at which the bird was observed. Walther (2003) confirmed that large proportion of birds that were observed in canopy would have been impossible to observe from the ground. Canopy walkways or watch towers provide another options how to get access to the canopy and sample the desired taxa in higher forest strata (Driscoll and Kikkawa 1989; Stokes et al. 1995; Schulze et al. 2001). The main disadvantage of canopy cranes, platforms or walkways is that these methods do not support a great spatial replication, whereas they cannot be easily transported to a new sampling site and they allow sampling to over a limited area. Mist netting is another widely used method for an assessment of forest bird communities, however, it has been mostly used at the ground level (e.g. Beehler et al. 1995; Blake and Loiselle 2001). This method is popular especially in regions where avifauna is not thoroughly explored or when researches are not familiar with local avifauna. Handling captured birds allows precise identification of species, to collect morphological data or genetic and other material. Nevertheless, only few researches has installed mist nets to the canopy to survey birds of higher forest strata (Humphrey et al. 1968; Meyers and Pardieck 1993; Derlindati and Caziani 2005; Vecchi and Alves 2015), probably because it is technically relatively difficult method that requires hours of preparations before the mist nets are set and ready for use. However, when the mist nets are installed across forest strata, they will provide precise data on vertical distribution of birds.

«✒ Population dynamics and nest predation ✒»

The tropical rainforests host much greater number of species than temperate habitats, however, the total density of species can be very similar to temperate habitats (Willis 1974; Thiollay 1990). As mentioned above, species are typically rare in tropics and their density is therefore substantially low. The total biomass of birds, however, can be considerably greater in tropical forests because of the occurrence of many more large species (Loiselle and Blake 1992). Tropical bird communities are viewed as relatively stable systems, where most species are expected to be long-lived and sedentary (Skutch 1985; Stutchbury and Morton 2001). Although some researches have pointed out that this does not necessarily apply to all species in the community (Karr and Freemark 1983; Karr 1990), in general, tropical birds have indeed higher adult survival than comparable temperate zone birds (reviewed in Stutchbury and Morton 2001). With a high adult survival we would expect that bird populations will exhibit increased fecundity and density. However, tropical birds have different life history traits compared to temperate zone birds: high nest predation together with small clutch sizes (reviewed in Stutchbury and Morton 2001) limit the potential densities of tropical birds.

Predation is generally the major cause of nest failure in birds (Ricklefs 1969; Martin 1992) and therefore it greatly influences population dynamics of birds, having even more profound impact on rainforest birds that suffer from higher nest predation compared to natural forest in temperate zones (Martin 1996; Robinson et al. 2000b; Remes et al. 2012). It has to be taken into account, that latitudinal trends in nest predation can be hugely influenced by broad variation in nest predation across different study sites, nest types or degree of habitat degradation (Robinson et al. 2000b; Noske et al. 2008; Spanhove et al. 2009; Brawn et al. 2011). The latter has been mostly explored in relation to forest fragmentation, whereas natural forests are globally becoming degraded and fragmented at an increasing rate (Wright 2005). Further, nest predation is considered to be one of the agents causing diversity loss in fragmented habitas (Willis 1974; Andren and Angelstam 1988). However, there is a large inconsistency in evidence that habitat fragmentation impacts nest survival of resident birds. Some reporting increased nest predation in rainforest fragments (e.g. Willis 1974; Newmark and Stanley 2011), while others have reported that fragmentation relaxed nest predation (Maina and Jackson 2003; Visco and Sherry 2015). This disparity suggests the nest predation rate in forest fragments substantially vary depending on the local composition of nest predators.

«✒ Objectives of the thesis ✒»

In this thesis I firstly focused on spatial patterns of bird community in lowland rainforest of Papua New Guinea. My main aim was to explore what are the environmental drivers of distribution of rainforest birds. In Chapter II I tested whether topography, habitat structure or floristic composition influence distribution of bird species and their abundance at fine spatial scale in 50 ha forest dynamic plot. I paid special attention to the distributional patterns of insectivorous and frugivorous birds. Additionally, I explored interspecific associations and their possible contributions to observed spatial patterns of local bird community.

Chapter III is also devoted to spatial analysis. However here I explored the structure of rainforest bird community along vertical forest strata. My aim was to answer the following questions: Are rainforest bird species vertically stratified?; Can we observe vertical gradient in distribution of abundance and diversity?; and Do birds exhibit different vertical patterns in respect to their trophic requirements?

The other part of my thesis (Chapter IV) examines nest predation and nest survival of birds breeding in the rainforest understory. My aim was to fill gaps in pantropical patterns of nest predation rate and nest predator composition. New Guinea still supports large quantity of pristine lowland rainforests, however composition of nest predators and the pressure they represent to breeding birds remained unknown. In addition, I explored how nest predation affects birds in fragmented rainforest and whether on going deforestation will likely lead to increased or decreased nest predation.

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CHAPTER II

Fine-scale spatial patterns in a tropical forest bird community: topography matters.

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manuscript

Abstract

The spatial distribution of birds in forests is determined by a range of factors, including topography, microclimate, physical structure and floristic composition of vegetation, and the distribution of prey, predators and competitors. We suggest that the relative importance of individual environmental factors structuring bird communities can be profitably tested on small spatial scales, where their effect can be separated from the importance of dispersal limitation and regional species pools.

The global network of 50 ha forest dynamics plots, with detailed information on topography and vegetation, represents an ideal yet so far under-exploited setting for such studies. We surveyed the avian community within the Wanang 50 ha forest dynamic plot in lowland rainforest of Papua New Guinea by distance point counts.

From the total explained variability in bird communities, topography (i.e. elevation, slope steepness and terrain convexity) alone explained 45%, forest structure (stem density and basal area of smaller and larger trees) explained 20% and tree species composition 27%; the remaining 8% were shared effects, mostly of topography and tree species composition. The abundance of frugivorous birds increased and that of insectivorous birds decreased during forest succession. Most pair-wise species associations were random or positive while negative associations were rare. This implies that inter-specific competition had a negligible effect on patterns of avian species distribution.

Our results demonstrate that even at small spatial scales, bird communities in tropical forests are structured partly in response to environmental factors, particularly terrain topography and vegetation structure. These may in turn determine resource availability or predation risk, the factors awaiting further study on small spatial scales in tropical forests.

Introduction

The composition and diversity of bird communities are influenced primarily by the type and structural complexity of their habitat (MacArthur and MacArthur 1961, Terborgh 1985, Jankowski et al. 2013), together with the regional species pools (van Dorp and Opdam 1987, Pearman 2002) generated by historical processes (Karr 1982, Ricklefs 1987). Typically, habitats with increased environmental heterogeneity host more species of birds (Rosenzweig 1995, Tews et al. 2004). The high heterogeneity typical for tropical rainforests is maintained by the presence of various plant life forms, tall canopies, immense tree species richness and successional dynamics of the vegetation in response to disturbance (Kricher 2011). Spatial distribution of diverse bird communities occupying tropical forests is driven by species-specific microhabitat use and interspecific interactions (Terborgh 1985, Robinson and Terborgh 1995, Heikkinen et al. 2007).

Microhabitats can be defined by terrain, physical structure of the vegetation, and/or species composition of the vegetation. These factors are interconnected as many rainforest plant species show preferences for microtopographic features such as slopes or ridges (e.g. Valencia et al. 2004, Jones et al. 2008) and the physical structure of vegetation depends to large extent on its species composition. Originally, it was widely accepted that vegetation structure and habitat heterogeneity are of principal importance for habitat occupancy by avian species (e.g. MacArthur and MacArthur 1961, Hildén 1965, Anderson and Shugart Jr. 1974, James and Wamer 1982). However, since Wiens and Rotenberry (1981) discovered strong correlations between avian and plant community composition, the importance of floristics has been recognised. In tropical rainforests both floristics and vegetation structure are likely to affect the bird community, although the significance of each of these parameters may vary regionally and with spatial scale (Schemske and Brokaw 1981, Pearman 2002, Hasui et al. 2007, Kissling et al. 2008, Lee and Marsden 2008, Pomara et al. 2012, Jankowski et al. 2013).

The individual influence of environmental factors can be disentangled by particularly detailed studies recording the topography and the floristic and structural variation of vegetation over contiguous plots where bird distribution is also recorded in detail. The CTFS (The Center for

Tropical Forest Science) 50 ha plots represent the best datasets available for such studies, as these detail fine-scale topography and vegetation composition within tropical rainforests, but we have so far been lacking a similarly detailed dataset concerning bird communities (Anderson-Teixeira et al. 2015).

Interspecific interactions may also influence the structure and composition of bird communities (Diamond 1975), resulting in co-occurrence or segregation of certain species combinations. Species that co-occur may mutually benefit from one another's presence, this may be through, for instance, participation in mixed flocks, which increases their foraging rate and allows reduced vigilance (Terborgh 1990, Sridhar et al. 2009). Conversely, competitive exclusion (MacArthur and Levins 1967) will create negative spatial associations between species. However, these patterns could be also generated by environmental filtering when pairs of species converge or diverge in their micro-habitat requirements. It is therefore important to study and interpret coexistence patterns in conjunction with an analysis of environmental variables.

In this paper we focused on spatial patterns of avian communities at fine scales within the 50 ha lowland tropical forest plot in Papua New Guinea. We explored whether abundance, diversity and species composition of birds was associated with forest structure, tree composition and/or terrain topography. Since trophic guilds may differ in response to habitat characteristics (Pearman 2002, Gray et al. 2007) we also studied the association of frugivorous and insectivorous birds with the environmental characteristics separately. Finally, we analysed species co-occurrence and its involvement in the spatial distribution of avian species.

Methods

Study site

This research was conducted in a pristine lowland rainforest in the centre of Wanang Conservation Area, Madang Province, Papua New Guinea (5° 6'49"S; 145° 2'19"E). We surveyed the avian community on a fine geographic scale within the Wanang 50 ha forest dynamics plot (Supporting information Appendix 1, Fig. S1). The plot is part of the global network of plots dedicated to the study of tropical and temperate forest function and diversity, managed by the Center for Tropical Forest Science and Forest Global Earth Observatories (CTFS-ForestGEO). The Wanang plot comprises ~288,000 stems with DBH ≥ 1cm from ~550 species and with ~211 tons per ha of live aboveground plant biomass (Anderson-Teixeira et al. 2015, Vincent et al. 2015). The terrain in the 50 ha plot is rugged, with a central ridge reaching up to 190 m a.s.l., while valley bottoms filled with small streams, decrease to 80 m a.s.l. (Fig. S2). The mean annual rainfall is ~3,400 mm, with a mild dry season from July to September and mean monthly air temperature ~26°C (Anderson-Teixeira et al. 2015).

Survey methods

We used a distant point count method to sample the avian community. The counts were repeated, being carried out five times at 169 regularly distributed points across the 50 ha forest plot, spaced 56.6 m apart (Fig. S3). We recorded the position of each bird seen or heard during a 10 min period within a 40 m radius around each point (see example in Fig. S4), resulting in complete coverage of the 50 ha plot. Daily measurements of rainfall were collected at the Swire research station situated within 500 m of the study plot.

Five complete surveys (one survey = 169 point counts) were carried out during three years, covering both rainy and dry seasons (1: Aug 26 – Nov 26, 2013; 2: May 20 - Jun 8, 2014; 3: Jul 8 – Jul 28, 2014; 4: Feb 10 - Mar 6, 2015; 5: Aug 24 – Sep 25, 2015). One observer was able to complete 13 points during one morning (6:00 – 10:30). We changed the order of sampled points among surveys to avoid counting birds repeatedly at the same points during similar morning hours.

We used the software ImageJ 1.48v to digitise the spatial position of each observed bird. Firstly we created a template with the positions of the point counts within the 50 ha plot and the 40 m radiuses around each point. The template was assigned with coordinates corresponding to the 50 ha plot (x = 0 - 1000, y = 0 - 500). The recorded position of birds was then projected from the field data sheet onto the corresponding point number on the template. In this way we obtained the real plot coordinates for each observation. We assigned individual birds to plot quadrats using their field coordinates. Quadrats (size = 20 x 20 m, *N* = 1250) were used as data units for further analyses. In order to cover the whole plot, the sampling points were spaced out in a dense grid. This resulted in slight overlapping of the 40 m point count sampling radiuses. However, the overlap was constant over the plot and covered all but 50 quadrats on the lower edge of the 50 ha plot (row 25, Fig. S3). Therefore, the sampling effort was approximately constant between the plot quadrats.

Bird species were divided into trophic guilds (Table S2) according to information on the main diet components obtained from del Hoyo et al. (2016) and Sam et al. (2017). Granivores were merged with frugivorous birds. Species feeding on insects (e.g. Alcedinidae) but also occasionally on small vertebrates were classified as insectivorous. We were unable to distinguish *Meliphaga spp.* It is possible to distinguish these very similar congenerics on close inspection, but we were unable to do so during the point count surveys. During mist-netting in the same area in 2015 and 2016 we recorded the presence of two species: *Meliphaga analoga* (*N* = 102) and *M. aruensis* (*N* = 79). From the number of captured individuals we can deduce that *M. analoga* was slightly more abundant.

Statistical analyses

Diversity, abundance and species composition of the plants and birds used in the statistical analysis refer to individual plot quadrats. Diversity of birds was characterised by the Shannon diversity index (Shannon 1948). Changes in the abundance and diversity of the avian community across 1- subsequent surveys and, 2- due to environmental variables, were analysed by Generalized Linear Models (GLM) using a Poisson error with a log link function (abundance) and a Gaussian (diversity) distribution of dependent variables. A Chi-square test was used to determine the model significance. We tested the relationship between the mean daily rainfall recorded during each survey and mean bird abundance and diversity by computing Spearman's rank correlation.

The following environmental characteristics of quadrats were used in the subsequent statistical analyses: elevation [m a.s.l.], terrain convexity, slope [°], log-basal area of trees between 1 to 10 cm ($BA_{1\text{-}10}$) and above 30 cm (BA_{30}) diameter at breast height (DBH), presence/absence of large trees

(DBH>30cm), gap phase (see below), abundance of trees and diversity of trees (Shannon index). Topographic variables were obtained from Vincent (2015). In that study, elevation readings were taken at each grid point to determine indices of mean elevation, slope, and convexity per quadrat, using the approach of Harms et al. (2001). Mean elevation was defined as the average elevation of the four corners of each quadrat. Slope was calculated as the average slope of four planes created by connecting three corners of each quadrat at a time. Convexity was calculated as the mean elevation of the focal quadrat minus the average elevation of all directly adjacent quadrats. Gap phase (GP) is an index of forest regeneration (Feeley et al. 2007) calculated as: $GP = \ln(BA_{30} + 1) - \ln(BA_{1\text{-}10} + 1)$. GP is based on the assumption that quadrats more recently disturbed will be dominated by small stems (low GP) whereas quadrats without recent disturbance will have increased presence of large trees (high GP).

A variation partitioning approach using Canonical Correspondence Analysis (CCA) with conditional effect (software Canoco 5: Ter Braak and Smilauer 2012) was applied to analyse the effects of environmental factors on the distribution of communities of bird species. The abundance of bird species in each quadrat was summed over five surveys ($N = 85$, only species with more than five observations were included) and was used as a response variable. The CCA test excluded samples (quadrats) with zero bird abundance ($N = 12$). We used three groups of environmental explanatory variables: 1) topography (elevation, convexity and slope); 2) forest structure (abundance of trees with DBH≥1cm, log-basal area of trees with DBH from 1 to 10 cm and above 30 cm); and 3) tree species composition (scores from first, second and third canonical axes derived by Detrended Correspondence Analysis (DCA) from a tree species distribution matrix, Fig. S5). Further, with the same dataset, we used a GLM in Canoco 5 to obtain estimates and the corresponding significance of the effects of topographic variables (elevation, terrain convexity and slope) on abundances of individual bird species.

The effect of environmental variables on the abundance of frugivorous and insectivorous birds was tested by a GLM model with Poisson distribution of dependent variables. Using this model we also tested whether the density of trees producing attractive fruits affected the abundance of frugivorous birds. For this, we selected 29 tree species ($N =$

38 784, Table S1) that represented potentially important tree species for frugivorous birds, based on the knowledge of the indigenous rainforest owners recruited as our field assistants. As a proxy for the density of the selected trees, we used the log-basal area inside individual quadrats summed up across species.

The probabilistic model of species co-occurrence was computed with package Cooccur, created by Griffith et al. (2016). The model calculates the expected frequency of co-occurrence between each pair of species based on the distribution of one species being independent of the second one. The expected frequency was further compared with the observed frequency (here represented by presence/absence of species inside plot quadrats) and the model returned the probability that a lower or higher value of co-occurrence (negative or positive association) could have been obtained by chance. 1085 species pair combinations were analysed after setting a threshold that included only species pairs with expected co-occurrences ≥ 1. Since temporal effects may play role in species co-occurrence, observations from different surveys were treated independently.

To test overall associations of bird species in the quadrats, we applied variance ratio v/N index (Pielou 1972) with a statistical test developed by Schluter (1984), where $v/N > 1$ (or $v/N < 1$) indicates that the species covary positively (or negatively) in their presence/absence. All statistical tests including plot creation were, unless stated otherwise, carried out in software R 4.3.0.

Results

In total we recorded 93 species with a mean abundance of 1697.0 (s.d. = 400.8) individual birds inside the whole 50 ha plot (Table S2 and Supporting information Appendix 2). The majority, 53 species, were relatively rare and occupied less than 5% of the plot quadrats when summed over all five surveys.

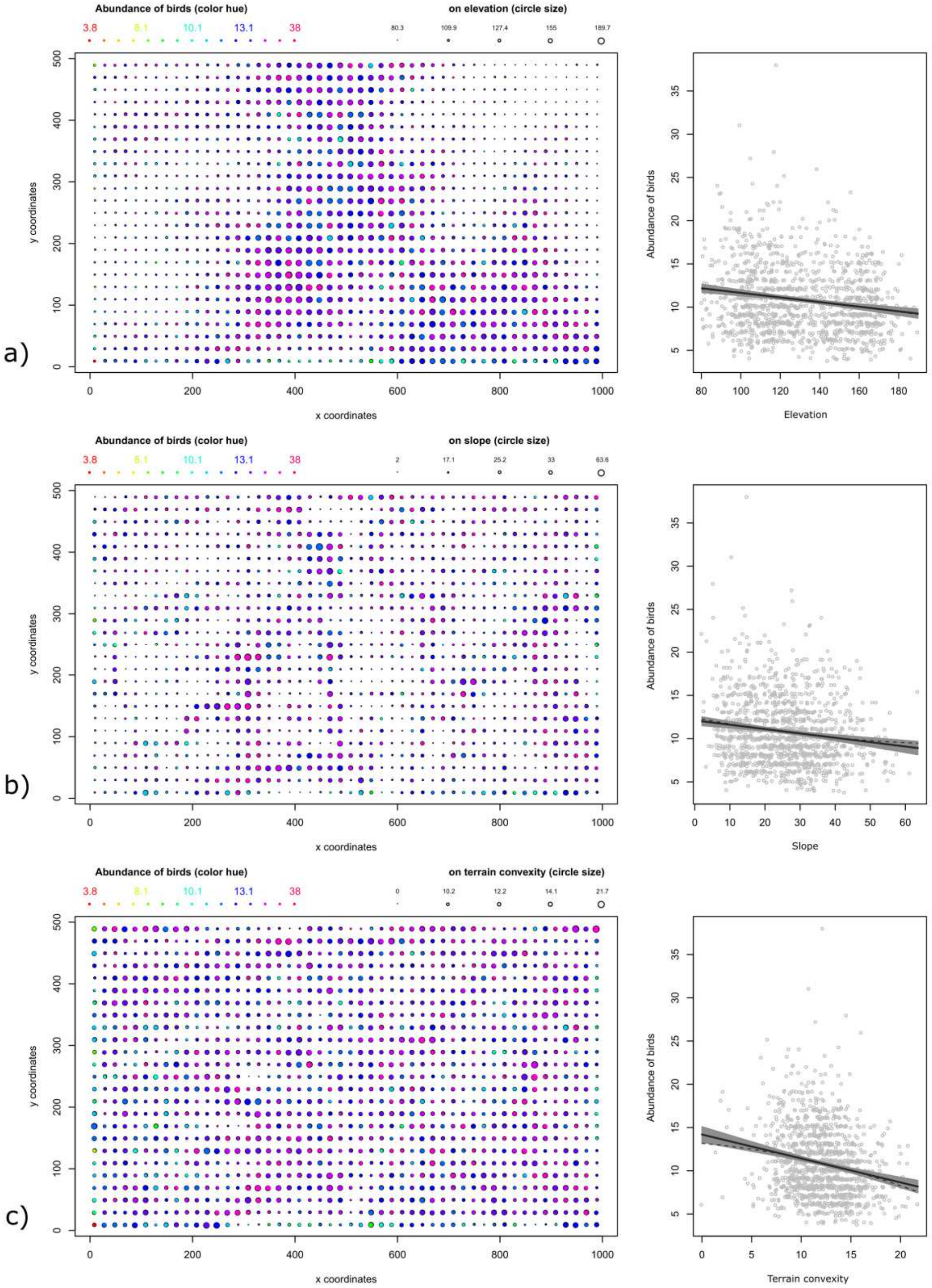

Figure 1. The distribution of bird abundance (a-c) within the 50 ha forest plot (left blocks) and their linear (solid line with shaded area representing standard error) and quadratic (dashed line) response (right blocks) to changes in environmental features of the plot: elevation (a), slope (b) and convexity (c) of the terrain. Colour hue of the circles within the left-hand side figures indicate to abundance of birds in each of the plot quadrats (20 × 20 m) and the size of the circle refers to the value of the environmental variables.

Only eight species exceeded 20% occupancy: *Carterornis chrysomela* (prevalence in quadrats: 22.1%, mean number of individuals over the five surveys ± s.d.: 65.8 ± 16.6), *Colluricincla megarhyncha* (23.9%, 70.4 ± 19.1), *Tanysiptera galatea* (24.2%, 72.0 ± 22.2), *Ptilinopus pulchellus* (25.4%, 74.4 ± 32.8), *Toxorhamphus novaeguineae* (25.6%, 74.6 ± 47.0), *Poecilodryas hypoleuca* (33.2%, 114.8 ± 20.2), *Pitohui kirhocephalus* (35.1%, 117.8 ± 39.1), *Meliphaga* spp. (39.3%, 128.4 ± 30.9). These most abundant species represented 42% of all individuals in the plot and belonged to various trophic strategies: small (*Symposiachrus guttula, P. hypoleuca*) and medium-sized (*C. megarhyncha, T. galatea)* insectivores, frugivorous *P. pulchellus,* omnivorous *T. novaeguineae,* insectivoro-nectarivorous *Meliphaga spp.* and frugivoro-insectivore *P. kirhocephalus.* All these species except *T. galatea* and *C. megarhyncha* are endemic to New Guinea (Table S2).

Insectivores represented nearly half of all recorded birds (40 species) and occupied the largest proportion of the 50 ha plot (Table 1). The second most common trophic guild, with 23 species, were frugivores. Frugivoro-insectivores (13 species) and insectivoro-nectarivores (6 species) were most abundant among omnivores, species that exploit a greater variety food resources (Table 1).

Table 1. Species richness, prevalence (% of occupied quadrats) and mean total abundance (± s.d.) of the entire community and different avian trophic guilds: CA – carnivores, FR – frugivores, FRIN – frugivoro-insectivores, FRNE – frugivoro-nectarivores, IN – insectivores, INNE – insectivoro-nectarivores, OM – omnivorous birds with more than two types of food resources. Species richness and prevalence were computed cumulatively, while abundance was averaged over five subsequent surveys.

Trophic Guild	Species richness	Prevalence [%]	Mean abundance (± s.d.)
CA	3	1.0	2.6 (±1.8)
FR	23	70.2	330.0 (±126.8)
FRIN	13	56.3	292.4 (±84.5)
FRNE	4	7.7	19.6 (±13.9)
IN	40	88.3	718.0 (±158.5)
INNE	6	64.7	271.2 (±66.5)
OM	4	21.9	62.8 (±11.3)
Community	93	99.0	1696.6 (±400.8)

Abundance and diversity significantly changed between consequent surveys (abundance: GLM, df = 4, explained variation = 4.2 %, $P < 0.001$; diversity: GLM, df = 4, explained variation = 4.2 %, $P < 0.001$). During surveys with low rainfall, birds were on average more abundant and their diversity was higher (Spearman's correlation; abundance: N = 5, r = -0.9, P = 0.037; diversity: N = 5, r = -1.0, $P < 0.001$, Fig. S6). Individual quadrats, serving as data points, represented relatively small samples of bird communities, even after five repeated surveys. This is why the abundance and diversity of birds was closely correlated between quadrats (Spearman's correlation, N = 1250, r = 0.99, $P < 0.001$), and as such, we hereafter analyse only the effects of environmental variables on abundance.

Abundance of birds was significantly influenced by topography (elevation, slope and convexity, Table 2). Highest abundances were found in quadrats with lower elevation, on more gentle slopes and in valleys with a concave ground profile rather than on ridges (Fig. 1). None of the forest structural parameters had a significant effect on the abundance of birds (Table 2).

A variation partitioning test revealed that topography (elevation, slope, convexity) of the plot quadrats explained a significant proportion of the spatial variation in birds community composition (Fig. 2). The distribution of tree species explained indicative proportion of variation, while forest structure did not influence the distribution of avian species inside the plot (Fig. 2). Further, the relatively high proportion of shared variation between topography and the distribution of tree species (Fig. 2) implies that the distribution of tree species is also influenced by topography. Among the topographic variables, elevation played the most important role (Table S3), since 26 species (30.6%) showed a significant preference ($P < 0.01$) for either lower elevations (19 species) or raised ridges (seven species). Also slope steepness (14.1%, N = 12) and convexity of the terrain (10.6%, N = 9) significantly affected the distribution of some species (Table S3). All these species showed a negative response to slope steepness and the majority of them exhibited a preference for a terrain with a concave profile (N = 7).

Table 2. The effect of environmental variables on the abundance of all birds and on the abundance of frugivorous and insectivorous birds separately (GLM analyses with Poisson distribution: *N* = 1250, z = test value).

Environmental variables	Estimate	Standard Error	z	*P*
Total abundance of birds				
Elevation	-0.002	0.001	-4.828	**<0,001**
Slope	-0.031	0.004	-7.453	**<0,001**
Convexity	-0.006	0.001	-5.655	**<0,001**
BA_{1-10}	-0.07	0.038	-1.856	0.063
BA_{30}	0.002	0.005	0.441	0.659
$Trees_{>30}$	-0.029	0.044	-0.667	0.505
GP	-0.001	0.012	-0.055	0.956
H_{trees}	0.081	0.053	1.515	0.137
N_{trees}	-0.001	0.001	-0.201	0.841
Abundance of frugivorous birds				
Elevation	-0.002	0.001	-2.175	**0.030**
Slope	-0.011	0.002	-4.646	**<0.001**
Convexity	-0.001	0.001	-4.601	**<0.001**
BA_{1-10}	-0.061	0.08	-0.758	0.448
BA_{30}	0.018	0.011	1.526	0.127
$Trees_{>30}$	0.061	0.098	0.627	0.531
GP	0.055	0.027	2.066	**0.039**
BA_{fr}	0.026	0.028	0.921	0.357
H_{trees}	-0.022	0.115	-0.190	0.849
Abundance of insectivorous birds				
Elevation	-0.007	0.001	-9.629	**<0.001**
Slope	-0.009	0.001	-5.776	**<0.001**
Convexity	-0.057	0.006	-10.253	**<0.001**
BA_{1-10}	0.036	0.057	0.624	0.533
$BA_{>30}$	-0.008	0.007	-1.150	0.250
$Trees_{>30}$	-0.127	0.061	-2.069	**0.039**
GP	-0.037	0.018	-2.121	**0.034**
H_{trees}	0.043	0.076	0.565	0.572

BA_{1-10} = log-basal area of trees with DBH 1-10 cm, BA_{30} = log-basal area of trees with DBH above 30 cm, GP = gap phase, $Trees_{>30}$ = presence/absence of large trees (DBH above 30cm), H_{trees} = Diversity of trees expressed by Shannon's diversity index, Ntrees = number of trees in quadrats

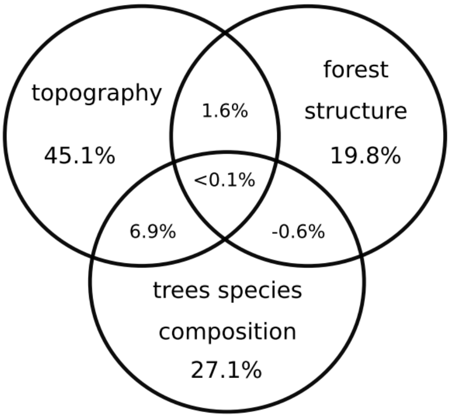

Figure 2. The proportion of explained variation in species composition of bird communities (based on a species matrix with abundances) by three groups of environmental variables (85 species with at least five observations are included, with variation partitioning carried out by Canonical Correspondence Analysis, total variation = 13.92, total explained variation = 1.3%). Topography consisted of elevation, slope and convexity of the terrain. Tree species composition refers to the spatial distribution of tree species along three ordination axes (Detrended Correspondence Analysis). Forest structure is represented by the abundance of individual trees, log-basal area of trees up to 10 cm and above 30 cm DBH. Numerical values indicate the proportional contribution of individual estimated variables and their shared fractions to the total explained variation. The results of significance tests for the groups of environmental variables are as follows: topography (F = 2.3, P = 0.001), tree species composition (F = 1.4, P = 0.052), forest structure (F = 1.0, P = 0.344).

The abundance of frugivorous birds was significantly higher in quadrats where the gap phase reached advanced values (mature stands with marked proportion of large trees, Fig. 3a). We did not confirm our expectation that the density (basal area) of tree species which produce attractive fruits would affect the abundance of frugivorous birds. No other parameters of forest structure influenced the distribution of frugivorous birds (Table 2). Insectivorous birds responded to variation in the gap phase. Conversely to frugivores, their abundance was higher in quadrats with an increased proportion of young to old trees (Fig. 3b, Table 2). Moreover, insectivores were more abundant in forest patches lacking the presence of large trees (Fig. 4, Table 2). Topography significantly influenced the distribution of both frugivorous and insectivorous birds (Table 2). Likewise, in the case of the total abundance of birds, frugivores and insectivores responded negatively to elevation, slope and convexity (Table 2).

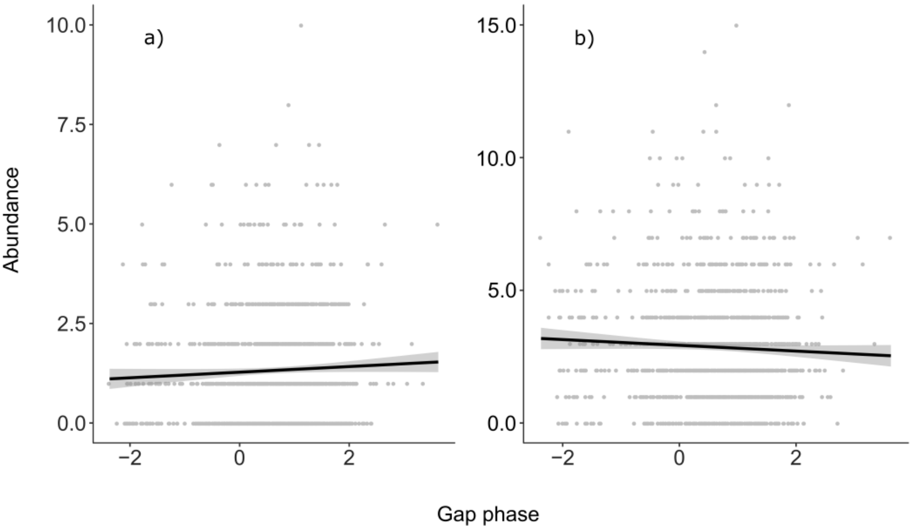

Figure 3. Linear response of abundance of a) frugivorous and b) insectivorous birds to gap phase. Lower values for the gap phase are typical for early successional stages where a high proportion of small stems persist, whereas high values of the gap phase are typical of mature stands. The shaded area represents standard error.

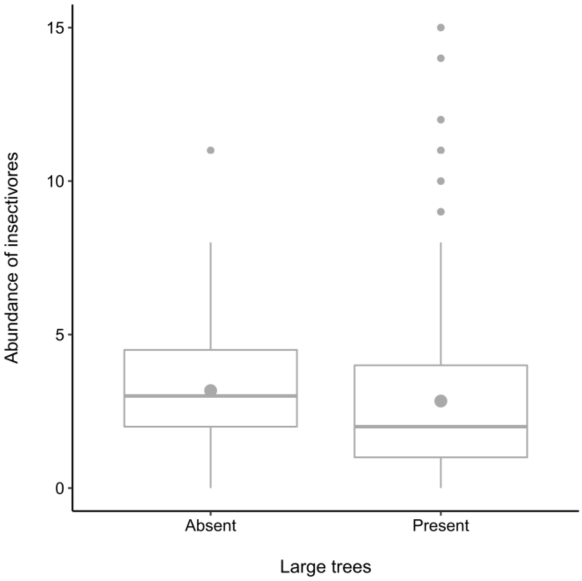

Figure 4. Abundance of insectivorous birds in quadrats where large trees (DBH > 30cm) are absent and present. Median, quartiles and non-outlier ranges together with outliers (diamonds) and mean abudance (circle) are displayed.

Analysis of co-occurrence showed that the vast majority of species pairs exhibited random distributions (1003 pairs, 92.4%), while only 82 (7.6%) species pairs had non-random associations. This was predominantly a positive association between species (71 pairs, 6.5%), whereas only 11 species pairs (1.0%) had negative associations (Fig. 5). The prevalence of positive associations is also supported by the variance ratio test: overall bird species associations in the quadrats were significantly positive ($v/N = 1.166$, $W = 1495$, $p < 0.01$). Positive pair-wise associations could be explained by similar microhabitat requirements in 15.5% ($N = 11$) of species pairs with positive associations, i.e. species shared a positive or negative response to topographic variables of the plot (Table S4). Divergent microhabitat requirements were responsible for 36.4% ($N = 4$) of negative associations between species pairs (Table S4). Positive and negative associations were recorded mostly between species belonging to different trophic guilds: 61.4% and 80.0%, respectively. Further, the proportion of positive and negative associations between species were very similar across trophic guilds (Table 3). Associations between the eight most abundant species were positive in two pairs of species (*C. megarhyncha* x *S. guttula* and *P. hypoleuca* x *P. kirhocephalus*) and negative in two pairs also (*Meliphaga spp. x P. kirhocephalus and Meliphaga spp. x T. galatea*). Both pairs with positive associations showed a significant preference for quadrats at lower elevations. While *Meliphaga* spp. and *P. kirhocephalus*, with their negative association, preferred sites with different altitudes (Table S3 and S4). Topography did not explain the negative association between *Meliphaga* spp. and. *T. galatea*. We did not observe any negative co-occurrence between congeneric species ($N = 17$). Congenerics had predominantly random associations (genera *Ducula*, *Philemon, Rhipidura and Symposiachrus*). A positive association was documented in the genus *Ptilinopus* (five species) with four species pairs exhibiting positive co-occurrence. *Gerygone chrysogaster* and *G. palpebrosa* were also positively associated.

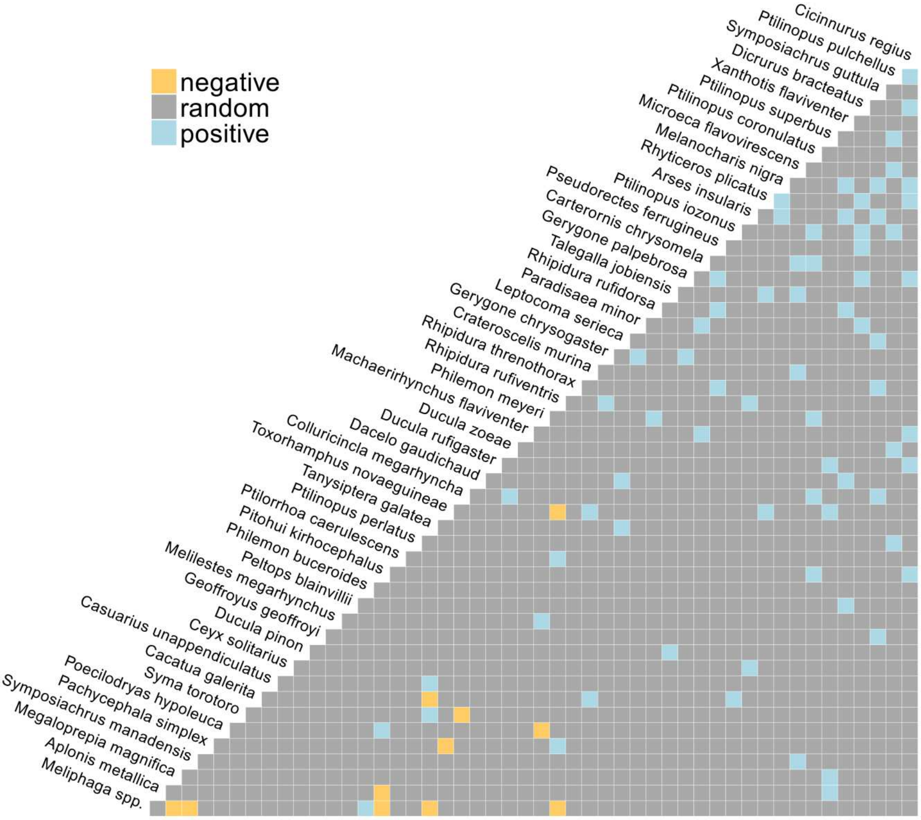

Figure 5. Visualisation of the species co-occurrence probabilistic model. Species pairs are classified as having random (grey colour), positive (blue) and negative (orange) associations.

Table 3. Mean proportion (% ± s.d.) of positive, negative and random associations between species within the avian community of the 50 ha plot. Values refer to associations within a given trophic guild, and only guilds represented by more than four species are presented (*N*). The proportion of associations did not significantly differ among guilds (GLM (gaussian); positive: df = 3, explained variation = 1.0%, P = 0.964; negative: df = 3, explained variation = 0.9%, P = 0.274; random: df = 3, explained variation = 1.0%, P = 0.767).

Guild	Positive	Negative	Random	*N*
FR	5.48 (±5.03)	0.27 (±0.82)	94.25 (±5.05)	18
FRIN	5.58 (±5.97)	0.75 (±1.62)	93.68 (±6.04)	10
IN	5.40 (±4.99)	0.65 (±1.46)	93.95 (±5.24)	30
INNE	6.59 (±4.04)	1.69 (±2.90)	91.72 (±2.80)	6

Discussion

Our results are consistent with patterns observed in other tropical forests, where a small proportion of species reach high abundance and density, while most remain relatively rare. From the following examples we can deduce that although the numbers of avian species differ among tropical regions, the majority of species are typically uncommon (i.e. species with an abundance below the community average) and their proportion is more or less constant among different tropical regions: Terborgh et al. (1990): Peru, number of species (*N*) = 245, proportion of uncommon species (unc) = 69.0% ; Thiollay (1994): French Guiana, *N* = 149, unc = 70.3%; Owiunji and Plumptre (1998): Uganda, *N* = 72, unc = 72.2%; Mulwa et al. (2012): Tanzania, *N* = 128, unc = 75.0%; Thiollay (1995): Sumatra, *N* = 185, unc = 65.9%; Bell (1982): New Guinea, *N* = 161, unc = 73.3%. Our study site, where 67.7% of species had an abundance below the community average, is not an exception. Pearson (1977) however, who carried out a pantropical comparison of avian communities, documented that the proportion of truly rare species (< 0.04 sightings/hour of observation) varied among tropical forest communities. Communities with the greatest proportion of rare species are found in South American (Peru = 81.8%, Ecuador = 79.5%, Bolivia = 76.8%), followed by African communities (Gabon = 72.7%), while in insular avian communities, including our study region, the proportion of rare species was much lower (Borneo = 59.9%, New Guinea = 49.7%). If we use the same criteria for rare species as Pearson (1977) did, their proportion (10.8%) was much lower at our study site. Although the different methodological approaches (transect survey vs. point count) likely contributed to this substantial difference, the proportion of truly rare species is presumably lower in New Guinea than in the neotropics or Africa.

The composition of feeding guilds appears to be similar throughout the lowlands of New Guinea. The order of trophic guilds was identical to Bell (1982) and Sam et al. (2017) (ordered by the highest species richness): 1. insectivores, 2. frugivores, 3. frugivoro-insectivores, 4. insectivoro-nectarivores. Also Pearson (1977) described insectivorous and frugivorous birds as the most abundant feeding-classes in East Sepik. These strategies are usually the two most common foraging tactics within tropical avian communities (Pearson 1977, Terborgh et al. 1990). However, in comparison with other tropical regions, the proportion of frugivorous birds in New Guinea is exceptionally high (Pearson 1977). This is probably caused by the absence of competition for fruits with primates (Fleming et al. 1987).

Abundance and diversity of recorded birds in our study plot differed among surveys. We excluded the possible influence of migratory species, because we recorded only two non-resident species (*Scythrops novaehollandiae* and *Eurystomus orientalis*) and both were observed at very low frequencies (Table S2). Montane species (several frugivorous birds), that may temporarily occur (Bell 1982), were too rare to influence fluctuations in abundance. Moreover, non-resident birds often do not vocalize, decreasing their detection probability (Blake 1992). We therefore assume that the observed variability among surveys reflects populations of resident birds. This would imply that detection patterns reflect variation in bird behaviour rather than seasonal variation in species composition (see also Antunes 2008). We recorded increased diversity and abundance during surveys that were carried out in drier periods of the year. Especially during the last survey, carried out during an extremely dry El Nino period, we recorded a profound upsurge in abundance and diversity of birds. This is probably connected with the timing of the breeding season. In tropical forests which experience seasonality in rainfall, birds tend to start breeding during the transition from the dry to the rainy season (Fogden 1972, Reif et al. 2006, Stouffer et al. 2013, Chiver et al. 2014, Langen and Berg 2016, pers. obs.) which is also connected with higher vocal activity (Topp and Mennill 2008, Chiver et al. 2015). The enlargement of gonads and increased vocal activity of males may already start at the height of the dry season (Wikelski et al. 2000). During El Nino, it is possible that birds anticipated the onset of breeding season and their high vocal activity during the exceptionally long dry period leads to their increased detection rate.

The significant effect of topography on avian community composition would not be surprising if our sampling covered a greater geographic and elevational range (Jankowski et al. 2013). However, our results document the small-scale influence of topography across distances of only tens to hundreds of metres and altitudinal differences within 100 m. Moreover, the topography influenced not only the total abundance but also relative representation of individual species, whereas the variation partitioning test (CCA) worked with the proportion of species across the plot's quadrats. Similarly, topography had the most pronounced effect on the distribution of birds on a relatively small scale in a 1500 ha forest plot in the Philippines (Lee and Marsden 2008), which was characterized by slightly more pronounced altitudinal differences (370 m). Based on our results we recognise that lower parts of the forest plot near the water courses showed higher bird abundance. However, the presence of ridges also contributed to overall diversity inside the plot, since some species showed a significant preference for higher elevations. Two species of Birds of Paradise exemplify this well. While *Cicinnurus regius* preferred lower parts of the plot, we recorded *Paradisaea minor* predominantly at the ridges (Appendix 2).

Our results showed that early stages of forest gaps are attractive for insectivorous species. They were more abundant in quadrats with a greater proportion of young stems. We believe that these quadrats contained an increased abundance of insects and thus also insectivorous birds, whereas gap colonizing plants are grazed by herbivorous insects at much higher rates than interior species (Coley 1983). Late gap phases, on the other hand, were increasingly exploited by frugivorous birds. This is in agreement with Tvardikova (2010), who documented a higher abundance of frugivores in primary vs. secondary forest. The latter is equivalent to vegetation in early gap phase. It is generally accepted that tree fall gaps contribute to the composition and richness of avian assemblages (e.g. Schemske and Brokaw 1981, Wunderle Jr et al. 1987). However, our results showed that this relationship applied only to two of the most common trophic guilds, but not for the abundance of the entire community.

Our results supported the earlier observations that avian assemblages on smaller spatial scales are associated more closely with floristic composition than the vegetation structure, i.e. within a single habitat type (Rotenberry 1985, Lee and Rotenberry 2005, Hasui et al. 2007, Jayapal et al. 2009, Pomara et al. 2012, Guerta and Cintra 2014). The vegetation structure becomes more important in defining avian species distribution and influencing the local species richness and abundance on larger spatial scales, where various forest types are spanned (Goetz et al. 2007, Kissling et al. 2008, Jankowski et al. 2013). However, we must underline that the floristic composition was to some extent determined by the terrain heterogeneity.

The topography, therefore, played the ultimate role in avian species distribution.

To some extent, positive associations between species pairs were caused by similar feeding habits like the common co-occurrence of mixed-species feeding flocks. The following species have been shown to take part in mixed feeding flocks (Bell 1983) and within our 50 ha plot they exhibited positive associations: *Cicinnurus regius*, *Dicrurus bracteatus*, *Melanocharis nigra*, *Pitohui kirhocephalus*, *Pseudorectes ferrugineus*, *Rhipidura threnothorax*, *Symposiachrus guttula*. Further positive associations between species are created when frugivorous birds aggregate at resource trees (Brown and Hopkins 2002). This is likely the case of frugivorous birds of genus *Ptilinopus*, where we observed a particularly high rate of positive associations. Shared environmental demands can lead to positive associations between species (Royan et al. 2016). We showed that a shared response to topography of the plot explained some of the positive associations between species (Table S4). Similarly, negative associations between four species pairs (*Cacatua galerita and Tanysiptera galatea, Meliphaga spp.* and *Megaloprepia magnifica*, *Meliphaga spp.* and *Symposiachrus manadensis*, *Meliphaga spp.* and *Pitohui kirhocephalus*) were likely caused by different altitudinal preferences (Table S4). The ecological causality between the remaining negatively associated species pairs is unclear, as these pairs do not coincide with our current understanding of direct interspecific competition for food or territories (Fig. 5). This applies also for the large proportion of positive associations. We would have to study species interactions by focusing on individual species pairs to be able to reveal whether there is a biological reason for such associations.

In conclusion, we give evidence that even at a small spatial scale the avian tropical species show patterns in spatial distribution that are driven by environmental factors. The most important factors at this scale are, rather surprisingly, related to topography. The topographic parameters are followed by floristic composition of the forest. Among the forest structural parameters, the growth successional stage played most important role in predicting abundance of frugivorous and insectivorous birds. Further, we document that most pair-wise species associations were random or positive, whilst negative associations, such as between competitors, were rare. Inter-specific competition therefore had a negligible effect on the patterns of species distribution we observed in the 50 ha forest plot in Papua New Guinea.

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Supporting information

Appendix 1

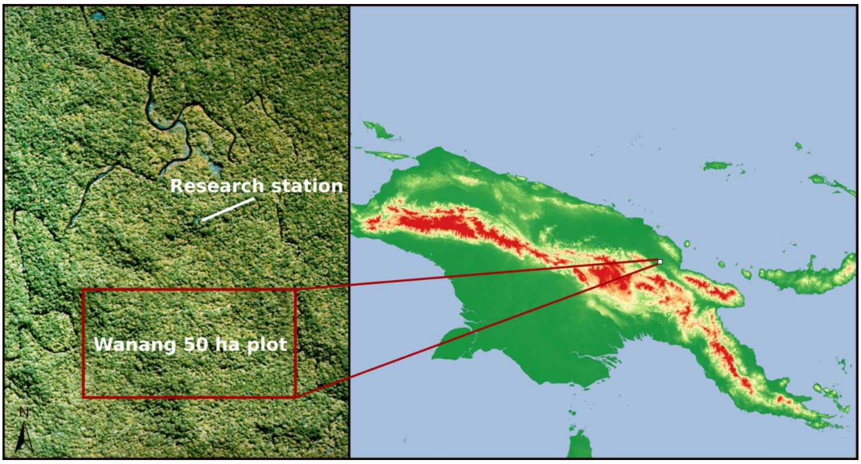


Figure S1 Wanang 50 ha forest plot and its geographic position within the New Guinea island.

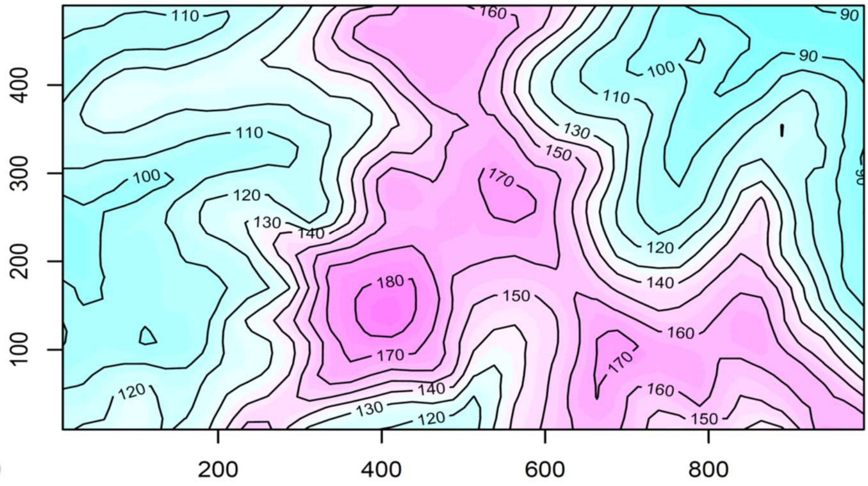


Figure S2 Topographic map of Wanang 50 ha plot. Contours and the color hues refer to elevation of the study plot.

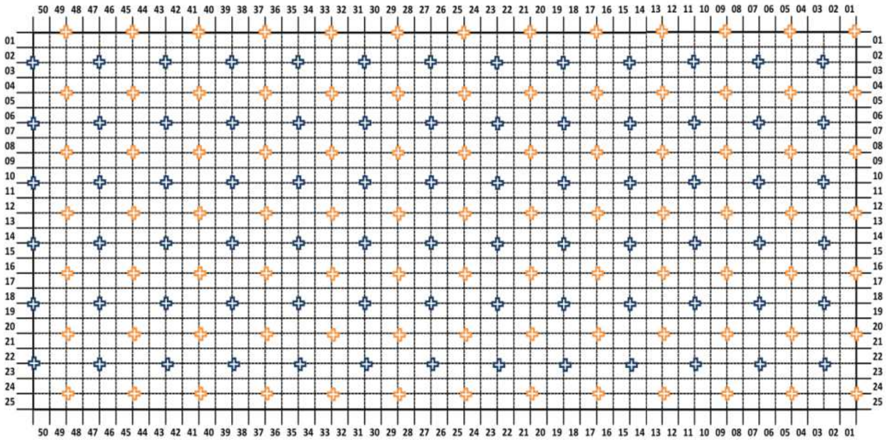
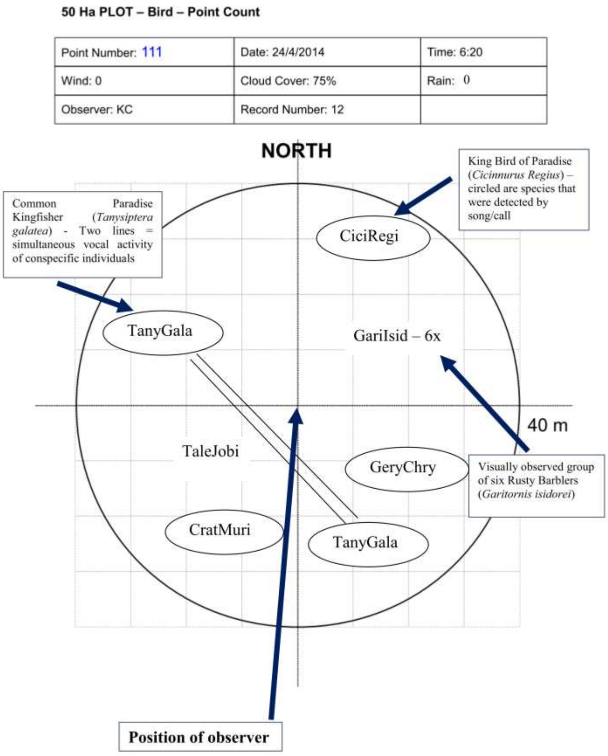


Figure S3 Distribution of 169 point count locations inside the Wanang 50 ha plot (blue and orange crosses). Axis labels indicate the plot quadrates (20 × 20 m).



50 Ha PLOT – Bird – Point Count

Point Number: 111	Date: 24/4/2014	Time: 6:20
Wind: 0	Cloud Cover: 75%	Rain: 0
Observer: KC	Record Number: 12	

King Bird of Paradise (*Cicinnurus Regius*) – circled are species that were detected by song/call

Common Paradise Kingfisher (*Tanysiptera galatea*) - Two lines = simultaneous vocal activity of conspecific individuals

Visually observed group of six Rusty Barblers (*Garitornis isidorei*)

Position of observer

Figure S4 Example of how birds were recorded on a field sheet during the point count survey.

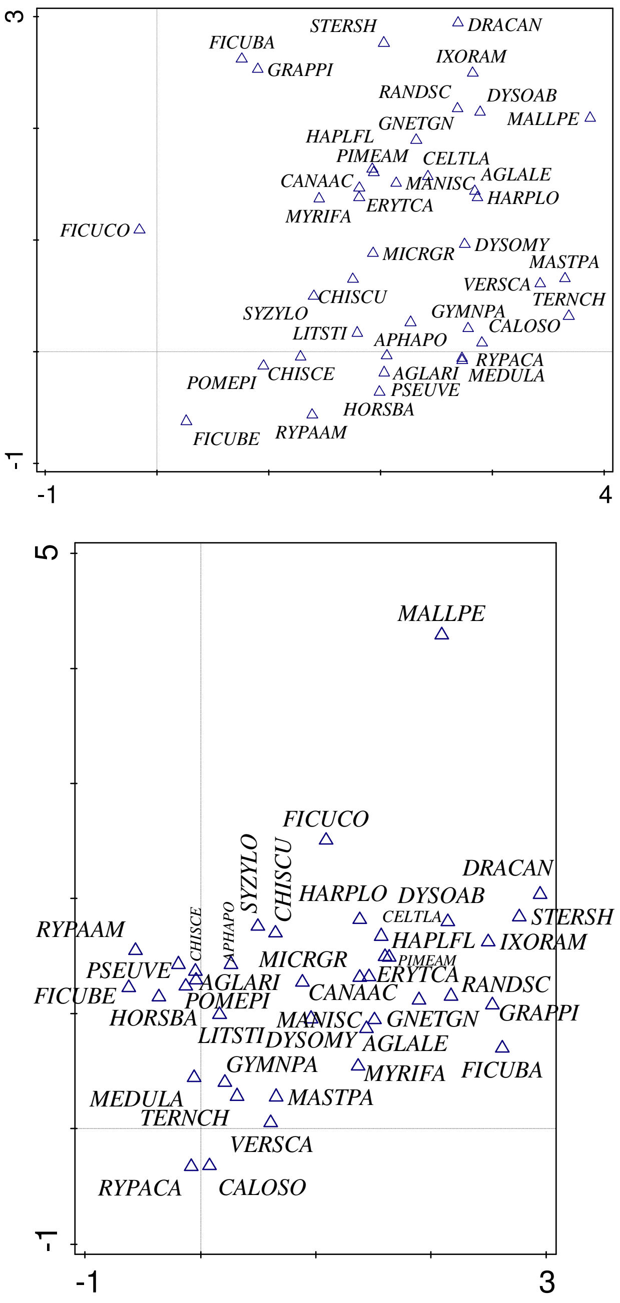


Figure S5 Top: Ordination diagram showing distribution of tree species (6-letter species code, Table S5) along 1st (horizontal) and 2nd (vertical) ordination axes. Down: distribution of tree species along 2nd (horizontal) and 3rd (vertical) ordination axes. In order to improve visual appearance of the graphs, only species with largest weight value (20-100%) were shown.

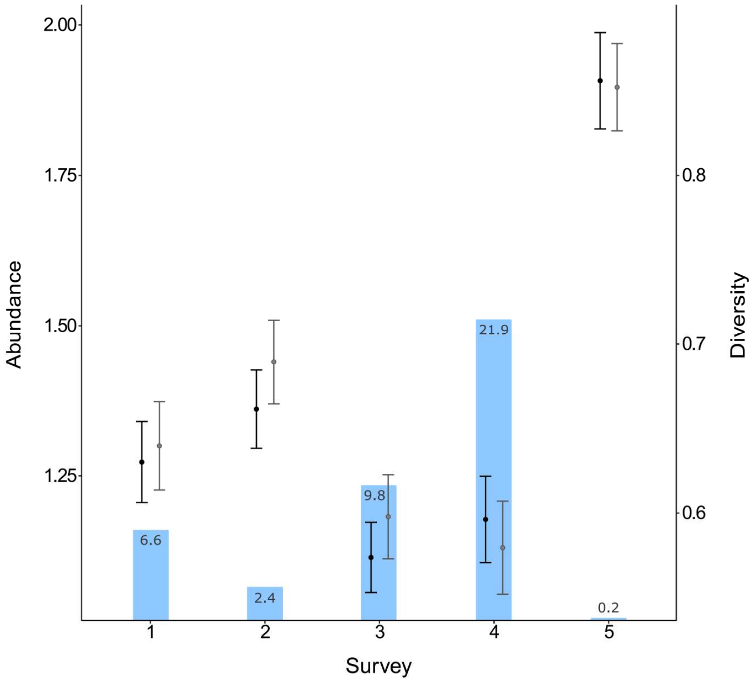


Figure S6 Error bar plot (mean ± 95% confidence interval) showing changes in abundance (black) and diversity (grey) over the course of five subsequent surveys. Blue bars with given labels denote to mean daily rainfall [mm] during the span of days when each survey was carried out.

Table S1 List of tree species with fruits attractive to frugivorous birds. In total 38 764 stems of listed species occurred in 50 ha plot. Prevalence (proportion of occupied quadrates) of each species inside the 50 ha plot is shown.

Scientific name	Family	Prevalence [%]
Aglaia lepiorrhachis	Meliaceae	75.4
Artocarpus lacucha	Moraceae	24.2
Canarium acutifolium	Burseraceae	80.2
Canarium indicum	Burseraceae	42.4
Canarium macadamii	Burseraceae	13.0
Celtis latifolia	Cannabaceae	96.3
Cryptocarya densiflora	Lauraceae	11.4
Cryptocarya depressa	Lauraceae	5.7
Cryptocarya massoy	Lauraceae	12.6
Dracontomelon dao	Anacardiaceae	25.1
Dracontomelon lenticulatum	Anacardiaceae	21.9
Dysoxylum gaudichaudianum	Meliaceae	4.3
Elaeocarpus sphaericus	Elaeocarpaceae	4.1
Ficus melinocarpa	Moraceae	9.0
Ficus subtrinervia	Moraceae	9.7
Ficus trachypison	Moraceae	11.8
Gastonia spectabilis	Araliaceae	4.2
Gnetum gnemon	Gnetaceae	97.0
Chisocheton ceramicus	Meliaceae	73.5
Chisocheton cumingianus	Meliaceae	68.6
Chisocheton trichocladus	Meliaceae	48.6
Chisocheton weinlandii	Meliaceae	48.0
Litsea collina	Lauraceae	44.2
Polyalthia glauca	Annonaceae	35.2
Pometia pinnata	Sapindaceae	79.8
Prainea papuana	Moraceae	9.8
Terminalia complanata	Combretaceae	33.9
Terminalia microcarpa	Combretaceae	8.3
Toona sureni	Meliaceae	5.2

Table S2 List of bird species that were recorded during point count surveys in Wanang 50 ha forest plot. Table contains affiliation to trophic guild (CA – carnivores, FR – frugivores, FRIN – frugivoro-insectivores, FRNE – frugivoro-nectarivores, IN – insectivores, INNE – insectivoro-nectarivores, OM – omnivorous birds with more than two types of food resources), prevalence – the percentage of occupied quadrates, and mean abundance per entire 50 ha plot over five consequent surveys. E – species endemic to New Guinea and adjacent islands, excluding Bismarck Archipelago. Species with mean abundance ≥1 included in the analyses.

Scientific name	Family	Trophic guild	Endemic species	Prevalence [%]	Mean abundance (±s.d.)
Accipiter hiogaster	Accipitridae	CA		0.6	1.6 (±1.8)
Ailuroedus buccoides	Ptilonorhynchidae	FRIN	E	2.1	5.2 (±1.3)
Alcedo azurea	Alcedinidae	IN		1.3	3.2 (±1.1)
Aplonis metallica	Sturnidae	FRIN		4.1	10.2 (±12.8)
Arses insularis	Monarchidae	IN	E	11.4	31.0 (±17.1)
Cacatua galerita	Cacatuidae	FR		5.7	14.8 (±7.3)
Cacomantis castaneiventris	Cuculidae	IN		1.4	3.6 (±4.0)
Cacomantis variolosus	Cuculidae	IN		2.2	5.4 (±2.2)
Carterornis chrysomela	Monarchidae	IN		22.1	65.8 (±16.6)
Casuarius unappendiculatus	casuariidae	FR	E	1.9	4.8 (±5.4)
Centropus menbeki	Cuculidae	IN	E	0.6	1.4 (±1.3)
Ceyx solitarius	Alcedinidae	IN	E	3.7	9.8 (±4.7)
Chalcophaps stephani	Columbidae	FR		1.0	2.6 (±1.1)
Cicinnurus regius	Paradisaeidae	FRIN	E	14.3	40.2 (±22.7)
Colluricincla megarhyncha	Pachycephalidae	IN		23.9	70.4 (±19.1)
Coracina boyeri	Campephagidae	FRIN	E	3.4	8.6 (±3.7)
Coracina melas	Campephagidae	IN	E	0.6	1.4 (±2.2)
Corvus tristis	Corvidae	FRIN	E	0.4	1.0 (±1.0)
Cracticus quoyi	Cracticidae	IN		2.1	5.2 (±2.6)
Crateroscelis murina	Acanthizidae	IN	E	7.4	19.8 (±9.3)
Dacelo gaudichaud	Alcedinidae	IN	E	5.9	16.2 (±6.2)
Dicaeum geelvinkianum	Dicaeidae	FR	E	3.0	7.6 (±7.9)
Dicrurus bracteatus	Dicruridae	IN		13.3	36.0 (±22.6)
Ducula pinon	Columbidae	FR	E	7.4	19.0 (±10.6)
Ducula rufigaster	Columbidae	FR	E	4.3	11.0 (±7.6)
Ducula zoeae	Columbidae	FR	E	5.2	13.4 (±7.4)
Eclectus roratus	Psittacidae	FRNE		1.6	4.0 (±4.8)
Eurystomus orientalis	Coraciidae	IN		0.6	1.6 (±1.8)

Scientific name	Family	Trophic guild	Endemic species	Prevalence [%]	Mean abundance (±s.d.)
Gallicolumba rufigula	Columbidae	FR	E	0.3	0.8 (±0.8)
Garritornis isidorei	Pomatostomidae	IN	E	2.4	6.0 (±3.5)
Geoffroyus geoffroyi	Psittacidae	FR		4.6	11.6 (±13.3)
Gerygone chloronota	Acanthizidae	IN		0.8	2.0 (±3.9)
Gerygone chrysogaster	Acanthizidae	IN	E	11.2	30.8 (±10.8)
Gerygone palpebrosa	Acanthizidae	IN		6.8	17.8 (±25.6)
Glycichaera fallax	Meliphagidae	INNE		0.7	1.8 (±4.0)
Goura victoria	Columbidae	FR	E	0.6	1.4 (±1.7)
Henicopernis longicauda	Accipitridae	CA	E	0.3	0.8 (±1.1)
Lalage atrovirens	Campephagidae	FRIN		14.8	40.6 (±15.1)
Leptocoma serieca	Nectariniidae	INNE		11.0	29.4 (±15.5)
Lonchura tristissima	Estrildidae	FRIN	E	0.3	0.8 (±1.3)
Lorius lory	Psittacidae	FRNE	E	3.2	8.2 (±3.3)
Macropygia amboinensis	Columbidae	FR		0.8	2.0 (±2.5)
Macropygia nigrirostris	Columbidae	FR	E	0.7	1.8 (±2.4)
Machaerirhynchus flaviventer	Monarchidae	IN		2.8	7.8 (±4.1)
Megaloprepia magnifica	Columbidae	FR		16.9	47.6 (±23.6)
Melanocharis nigra	Melanocharitidae	FRIN		6.6	17.2 (±12.6)
Melidora macrorrhina	Alcedinidae	IN	E	2.8	7.4 (±5.5)
Melilestes megarhynchus	Meliphagidae	INNE	E	4.6	11.8 (±9.1)
Meliphaga spp. *(M. analoga/aruensis)*	Meliphagidae	INNE	E	39.3	128.4 (±30.9)
Merops ornatus	Meropidae	IN		0.2	0.4 (±0.9)
Microcarbo melanoleucos	Phalacrocoracidae	CA		0.1	0.2 (±0.4)
Microdynamis parva	Cuculidae	FR	E	3.1	8.0 (±6.4)
Microeca flavovirescens	Petroicidae	IN	E	5.9	15.4 (±21.1)
Micropsitta pusio	Psittacidae	OM		3.0	7.4 (±3.6)
Mino dumontii	Sturnidae	FRIN	E	2.5	6.2 (±2.2)
Myiagra alecto	Monarchidae	IN		1.4	3.6 (±4.5)
Ninox theomacha	Strigidae	IN	E	0.1	0.2 (±0.4)
Pachycephala simplex	Pachycephalidae	IN		5.4	13.6 (±10.7)
Paradisaea minor	Paradisaeidae	FRIN	E	9.5	25.4 (±10.1)
Peltops blainvillii	Cracticidae	IN	E	4.4	11.4 (±5.8)
Philemon buceroides	Meliphagidae	OM		1.2	3.0 (±2.7)
Philemon meyeri	Meliphagidae	OM	E	10.2	26.6 (±15.8)
Pitohui kirhocephalus	Pachycephalidae	FRIN	E	35.1	117.8 (±39.1)
Pitta erythrogaster	Pittidae	IN		1.2	3.0 (±2.2)
Pitta sordida	Pittidae	IN		0.7	1.8 (±4.0)

Scientific name	Family	Trophic guild	Endemic species	Prevalence [%]	Mean abundance (±s.d.)
Podargus ocellatus	Podargidae	IN		0.2	0.6 (±0.9)
Poecilodryas hypoleuca	Petroicidae	IN	E	33.2	114.8 (±20.2)
Probosciger aterrimus	Cacatuidae	FR		1.3	3.2 (±3.0)
Pseudorectes ferrugineus	Pachycephalidae	FRIN	E	7.0	18.6 (±9.8)
Psittaculirostris edwardsii	Psittacidae	FRNE	E	0.7	1.8 (±1.3)
Ptilinopus coronulatus	Columbidae	FR	E	8.7	23.6 (±13.2)
Ptilinopus iozonus	Columbidae	FR	E	7.7	19.6 (±12.2)
Ptilinopus nainus	Columbidae	FR	E	0.6	1.6 (±2.6)
Ptilinopus perlatus	Columbidae	FR	E	1.7	4.2 (±5.5)
Ptilinopus pulchellus	Columbidae	FR	E	25.4	74.4 (±32.8)
Ptilinopus superbus	Columbidae	FR		9.4	26.2 (±15.4)
Ptilorrhoa caerulescens	Eupetidae	IN	E	5.6	14.8 (±5.0)
Reinwardtoena reinwardtii	Columbidae	FR		2.2	5.6 (±7.6)
Rhipidura leucothorax	Rhipiduridae	IN	E	0.4	1.2 (±1.6)
Rhipidura rufidorsa	Rhipiduridae	IN	E	6.2	16.6 (±8.9)
Rhipidura rufiventris	Rhipiduridae	IN		7.5	19.6 (±5.3)
Rhipidura threnothorax	Rhipiduridae	IN	E	6.9	18.2 (±4.5)
Rhyticeros plicatus	Bucerotidae	FR		9.7	25.2 (±17.8)
Scythrops novaehollandiae	Cuculidae	FRIN		0.2	0.6 (±0.9)
Syma torotoro	Alcedinidae	IN		4.1	10.4 (±7.1)
Symposiachrus guttula	Monarchidae	IN	E	8.2	21.8 (±19.0)
Symposiachrus manadensis	Monarchidae	IN	E	12.6	35.0 (±11.9)
Symposiachrus rubiensis	Monarchidae	IN	E	0.4	1.0 (±1.7)
Talegalla jobiensis	Megapodiidae	OM	E	9.7	25.8 (±18.4)
Tanysiptera galatea	Alcedinidae	IN		24.2	72.0 (±22.2)
Toxorhamphus novaeguineae	Melanocharitidae	INNE	E	25.6	74.6 (±47.0)
Trichoglossus haematodus	Psittacidae	FRNE		2.2	5.6 (±5.5)
Xanthotis flaviventer	Meliphagidae	INNE		9.3	25.2 (±20.0)

Table S3 Summarized results for the effects of the 50 ha plot topography (elevation, slope and convexity) on abundance of various species of birds (Generalized linear models with Poisson distribution and log link function). Species with a minimum of five observations (N = 85) are included. Significant results with P values ≤ 0.01 are in bold.

	Elevation				Slope				Convexity			
Species	Beta	s.e.	F	P	Beta	s.e.	F	P	Beta	s.e.	F	P
Accipiter biogaster	0.044	0.02	7.8	**0.005**	0.039	0.03	1.7	0.196	-0.021	0.12	0.03	0.862
Ailuroedus buccoides	-0.034	0.01	15.8	**<0.001**	-0.014	0.02	0.62	0.568	-0.134	0.06	4.3	0.038
Alcedo azurea	-0.01	0.01	0.98	0.679	-0.069	0.03	7.3	**0.007**	0.039	0.08	0.22	0.638
Aplonis metallica	-0.001	0.01	0.07	0.790	-0.005	0.01	0.14	0.710	0.02	0.05	0.19	0.67
Arses insularis	-0.004	0	1.7	0.185	-0.001	0.01	0.01	0.928	-0.019	0.03	0.5	0.524
Cacatua galerita	0.023	0	23.4	**<0.001**	-0.011	0.01	1.1	0.299	-0.018	0.04	0.21	0.641
Cacomantis castaneiventris	0.007	0.01	0.62	0.566	0.01	0.02	0.22	0.640	0.044	0.08	0.31	0.578
Cacomantis variolosus	-0.003	0.01	0.12	0.730	0.01	0.02	0.33	0.564	0.051	0.06	0.62	0.567
Carterornis chrysomela	0.001	0	0.23	0.635	-0.01	0.01	3.6	0.058	-0.041	0.02	4.8	0.028
Casuarius unappendiculatus	-0.015	0.01	3.5	0.062	-0.022	0.02	1.3	0.252	-0.017	0.07	0.06	0.805
Centropus menbeki	-0.006	0.01	0.15	0.702	0.045	0.03	1.9	0.164	-0.161	0.12	1.7	0.194
Ceyx solitarius	-0.028	0.01	20.8	**<0.001**	-0.018	0.01	1.9	0.172	-0.125	0.05	7	**0.008**
Cicinnurus regius	-0.026	0	77.4	**<0.001**	-0.012	0.01	3.6	0.058	-0.061	0.02	6.7	**0.009**
Colluricincla megarhyncha	-0.009	0	17.6	**<0.001**	-0.001	0	0.08	0.780	-0.087	0.02	24.1	**<0.001**
Coracina boyeri	0.004	0.01	0.37	0.546	0.044	0.01	11.5	**0.001**	0.124	0.05	5.8	0.016
Coracina melas	-0.02	0.02	1.6	0.204	-0.022	0.04	0.41	0.522	-0.362	0.1	10.3	**0.001**
Corvus tristis	-0.007	0.02	0.17	0.677	-0.022	0.04	0.29	0.591	0.082	0.15	0.31	0.582
Cracticus quoyi	-0.037	0.01	17.9	**<0.001**	-0.035	0.02	3.5	0.063	-0.079	0.06	1.5	0.227
Crateroscelis murina	0.005	0	1.5	0.229	-0.007	0.01	0.52	0.529	0.009	0.03	0.07	0.789

	Elevation				Slope				Convexity			
Species	Beta	s.e.	F	P	Beta	s.e.	F	P	Beta	s.e.	F	P
Dacelo gaudichaud	0.008	0	3.4	0.067	0.003	0.01	0.09	0.763	-0.036	0.04	0.94	0.671
Dicaeum geelvinkianum	-0.005	0.01	0.61	0.569	0.012	0.01	0.73	0.606	-0.101	0.05	3.5	0.062
Dicrurus bracteatus	-0.009	0	8.3	**0.004**	-0.004	0.01	0.37	0.545	-0.132	0.02	28.7	**<0.001**
Ducula pinon	0	0	0	0.960	-0.002	0.01	0.06	0.812	-0.011	0.03	0.09	0.758
Ducula rufigaster	0.007	0.01	1.8	0.183	-0.009	0.01	0.57	0.548	-0.01	0.05	0.04	0.831
Ducula zoeae	0.001	0	0.18	0.676	-0.011	0.01	0.89	0.655	-0.034	0.04	0.67	0.589
Eclectus roratus	0.006	0	0.41	0.522	-0.02	0.02	0.96	0.673	-0.049	0.07	0.42	0.514
Eurystomus orientalis	0.039	0.02	6.6	**0.010**	-0.094	0.04	6.2	0.013	0.262	0.11	5.2	0.023
Garritornis isidorei	-0.017	0.01	5.3	0.021	-0.011	0	2.4	0.122	0.005	0.06	0.01	0.937
Geoffroyus geoffroyi	-0.008	0.01	2.1	0.147	-0.016	0.01	1.8	0.186	-0.013	0.04	0.08	0.770
Gerygone chloronota	-0.007	0.01	0.34	0.560	0.03	0.03	1.2	0.281	-0.048	0.11	0.2	0.65
Gerygone chrysogaster	0.004	0	1.6	0.215	-0.03	0.01	15.8	**<0.001**	-0.057	0.03	4.5	0.033
Gerygone palpebrosa	0.012	0	8.4	**0.004**	-0.005	0.01	0.29	0.590	-0.022	0.04	0.39	0.528
Glycichaera fallax	0.012	0.01	0.86	0.644	-0.053	0.03	2.6	0.107	0.054	0.11	0.23	0.63
Goura victoria	-0.03	0.02	3.4	0.066	-0.052	0.04	2	0.160	-0.026	0.13	0.04	0.835
Chalcophaps stephani	-0.004	0.01	0.13	0.719	-0.015	0.03	0.36	0.551	-0.068	0.09	0.53	0.535
Lalage atrovirens	-0.002	0	0.01	0.937	0	0.01	0	0.982	0.016	0.02	0.47	0.503
Leptocoma serieca	0.007	0	4.8	0.029	0.01	0.01	2	0.160	0.027	0.03	0.02	0.868
Lorius lory	0.011	0.01	3	0.082	-0.002	0.01	0.02	0.883	0.08	0.05	2.4	0.125
Macropygia amboinensis	-0.01	0.01	0.62	0.569	-0.031	0.03	1.1	0.298	-0.117	0.1	1.3	0.262
Macropygia nigrirostris	0.006	0.01	0.19	0.668	0.068	0.03	5.9	0.015	0	0.11	0	0.999
Machaerirhynchus flaviventer	-0.046	0.01	37.5	**<0.001**	-0.002	0.01	0.01	0.911	-0.105	0.05	3.9	0.049
Megaloprepia magnifica	-0.01	0	15	**<0.001**	-0.002	0.01	0.12	0.730	-0.077	0.02	12.7	**<0.001**

	Elevation				Slope				Convexity			
Species	Beta	s.e.	F	P	Beta	s.e.	F	P	Beta	s.e.	F	P
Melanocharis nigra	-0.017	0	6.1	0.013	-0.009	0.01	0.88	0.651	-0.049	0.04	1.8	0.173
Melidora macrorrhina	-0.015	0.01	5.4	0.021	0.026	0.01	3.3	0.071	-0.104	0.05	3.6	0.056
Melilestes megarhynchus	-0.01	0.01	3.4	0.066	-0.039	0.01	9.6	**0.002**	-0.022	0.04	0.25	0.612
Meliphaga spp. *(M. analoga/aruensis)*	0.006	0	17.6	**<0.001**	0.003	0	0.69	0.593	0.001	0.01	0.01	0.927
Microdynamis parva	0.002	0.01	0.16	0.694	-0.005	0.01	0.1	0.751	0.045	0.05	0.73	0.604
Microeca flavovirescens	-0.002	0	0.23	0.627	0.007	0.01	0.51	0.526	-0.038	0.04	0.99	0.317
Micropsitta pusio	0.002	0.01	0.14	0.711	0.022	0.01	2.4	0.118	-0.029	0.05	0.28	0.593
Mino dumontii	0.005	0.01	0.56	0.544	0.008	0.02	0.26	0.608	0.059	0.06	0.97	0.672
Myiagra alecto	-0.018	0.01	3.5	0.061	-0.01	0.02	0.2	0.652	-0.088	0.08	1.2	0.264
Pachycephala simplex	-0.02	0.01	15.8	**<0.001**	-0.014	0.01	1.5	0.224	-0.064	0.04	2.4	0.117
Paradisaea minor	0.012	0	12.5	**<0.001**	-0.006	0.01	0.59	0.556	0.002	0.03	0.01	0.937
Peltops blainvillii	-0.015	0.01	8.1	**0.005**	-0.02	0.01	2.6	0.107	-0.029	0.04	0.42	0.516
Philemon buceroides	0.007	0.01	0.5	0.519	0.018	0.02	0.67	0.586	0.097	0.09	1.3	0.261
Philemon meyeri	-0.001	0	0.06	0.802	-0.003	0.01	0.19	0.661	-0.032	0.03	1.2	0.265
Pitohui kirhocephalus	-0.01	0	37	**<0.001**	-0.005	0	1.6	0.213	-0.057	0.01	16.8	**<0.001**
Pitta erythrogaster	-0.006	0.01	0.3	0.585	-0.005	0	0	0.990	-0.051	0.09	0.35	0.553
Pitta sordida	-0.008	0.01	0.35	0.552	0	0.02	3.1	0.078	-0.214	0.1	4	0.045
Poecilodryas hypoleuca	-0.015	0	81.5	**<0.001**	0.026	0.05	8	**0.005**	-0.08	0.01	32.9	**<0.001**
Probosciger aterrinus	-0.014	0.01	1.9	0.166	-0.026	0.02	0.01	0.905	-0.29	0.07	14	**<0.001**
Pseudorectes ferrugineus	0.004	0	1	0.308	-0.003	0.01	0.08	0.783	-0.01	0.03	0.09	0.764
Psittaculirostris edwardsii	0.002	0.01	0.03	0.863	-0.003	0.02	1.4	0.235	0.012	0.11	0.01	0.913
Ptilinopus coronulatus	-0.003	0	0.69	0.598	-0.004	0.01	8.2	**0.004**	-0.078	0.03	6.5	0.011

	Elevation				Slope				Convexity			
Species	Beta	s.e.	F	P	Beta	s.e.	F	P	Beta	s.e.	F	P
Ptilinopus iozonus	0.003	0	0.53	0.528	-0.025	0.01	0.09	0.758	0.019	0.03	0.32	0.573
Ptilinopus nainus	-0.018	0.01	1.5	0.224	0.002	0.01	0.25	0.616	-0.085	0.12	0.52	0.528
Ptilinopus perlatus	0.009	0.01	1	0.681	-0.016	0.03	1.4	0.231	-0.001	0.07	0	0.991
Ptilinopus pulchellus	-0.003	0	1.8	0.171	-0.024	0.02	11.9	**0.001**	-0.048	0.02	7.7	**0.005**
Ptilinopus superbus	-0.012	0	11.7	**0.001**	-0.016	0	4.5	0.033	-0.052	0.03	3.1	0.076
Ptilorhoa caerulescens	0	0	0.01	0.942	0.034	0.03	0.16	0.688	-0.047	0.04	1.5	0.223
Reinwardtoena reinwardtii	-0.015	0.01	3.9	0.048	-0.027	0.02	2.3	0.133	-0.08	0.06	1.6	0.202
Rhipidura leucothorax	-0.044	0.02	5.4	0.021	-0.025	0.04	0.43	0.513	-0.034	0.14	0.06	0.802
Rhipidura rufidorsa	-0.015	0	11.1	**0.001**	-0.02	0.01	3.9	0.049	-0.066	0.04	3.2	0.072
Rhipidura rufiventris	0.002	0	0.32	0.574	-0.021	0.01	5.1	0.025	-0.015	0.03	0.2	0.652
Rhipidura threnothorax	-0.016	0	14.8	**<0.001**	-0.022	0.01	5.1	0.024	-0.079	0.03	5.1	0.023
Rhyticeros plicatus	0.006	0	3.3	0.069	-0.008	0.01	1	0.312	0.002	0.03	0.01	0.935
Syma torotoro	-0.017	0.01	8.7	**0.003**	0.006	0.01	0.23	0.631	0.044	0.05	0.89	0.652
Symposiachrus guttula	-0.014	0	13.3	**<0.001**	-0.023	0.01	6.8	**0.009**	-0.021	0.03	0.41	0.517
Symposiachrus manadensis	-0.01	0	11.5	**0.001**	-0.016	0.01	5.2	0.023	-0.075	0.03	8.7	**0.003**
Symposiachrus rubiensis	-0.034	0.02	3	0.083	-0.017	0.04	0.18	0.672	-0.194	0.14	1.8	0.181
Talegalla jobiensis	0.003	0	0.01	0.94	-0.006	0.01	0.01	0.940	-0.09	0.03	9.4	**0.002**
Tanysiptera galatea	0.006	0	7.6	**0.006**	-0.014	0	7.9	**0.005**	-0.011	0.02	0.36	0.538
Toxorhamphus novaeguineae	-0.001	0	0.49	0.521	0.003	0	0.31	0.579	-0.034	0.02	3.8	0.050
Trichoglossus haematodus	0.005	0.01	0.42	0.518	-0.001	0.02	0	0.956	0.079	0.06	1.6	0.214
Xanthotis flaviventer	-0.015	0	17.6	**<0.001**	-0.017	0.01	4.4	0.037	-0.021	0.03	0.48	0.515

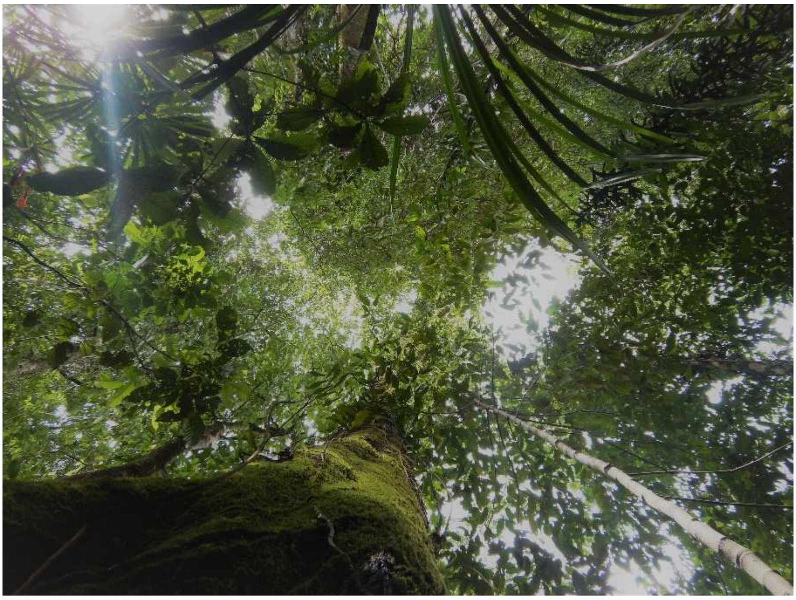
Table S4 List of avian species pairs that exhibited negative and positive associations based on analysis of co-occurrence. Some of the positive and negative associations between given species pairs can be explained by shared and divergent environmental demands, respectively. Here, we marked species pairs with shared or divergent response to the topography of 50 ha plot by comparing response of abundance to elevation, slope and terrain convexity within the given pair of species (only significant responses at P ≤ 0.01 were used, Table S3). Values in brackets (- or +) denote whether the species responded to the given element of topography negatively or positively (values for divergent responses are ordered in respect to the listed species).

			Response to topography		
Species pairs		Association	Elevation	Slope	Convexity
Aplonis metallica	*Pitohui kirhocephalus*	negative	-	-	-
Aplonis metallica	*Ptilinopus superbus*	positive	-	-	-
Arses insularis	*Ceyx solitarius*	positive	-	-	-
Arses insularis	*Melanocharis nigra*	positive	-	-	-
Arses insularis	*Symposiachrus guttula*	positive	-	-	-
Arses insularis	*Rhipidura rufiventris*	positive	-	-	-
Arses insularis	*Xanthotis flaviventer*	positive	-	-	-
Cacatua galerita	*Crateroscelis murina*	positive	-	-	-
Cacatua galerita	*Ptilinopus iozonus*	positive	-	-	-
Cacatua galerita	*Tanysiptera galatea*	negative	divergent (-/+)	-	-
Carterornis chrysomela	*Paradisaea minor*	positive	-	-	-
Carterornis chrysomela	*Ptilinopus coronulatus*	positive	-	-	-
Casuarius unappendiculatus	*Tanysiptera galatea*	positive	-	-	-
Cicinnurus regius	*Dicrurus bracteatus*	positive	shared (-)	-	shared (-)
Cicinnurus regius	*Ducula rufigaster*	positive	-	-	-
Cicinnurus regius	*Gerygone palpebrosa*	positive	-	-	-
Cicinnurus regius	*Rhyticeros plicatus*	positive	-	-	-
Cicinnurus regius	*Machaerirhynchus flaviventer*	positive	shared (-)	-	-
Cicinnurus regius	*Melanocharis nigra*	positive	-	-	-
Cicinnurus regius	*Pitohui kirhocephalus*	positive	shared (-)	-	shared (-)
Cicinnurus regius	*Ptilinopus pulchellus*	positive	-	-	shared (-)
Colluricincla megarhyncha	*Ducula zoeae*	positive	-	-	-
Colluricincla megarhyncha	*Symposiachrus guttula*	positive	shared (-)	-	-
Colluricincla megarhyncha	*Ptilinopus coronulatus*	positive	-	-	shared (-)
Colluricincla megarhyncha	*Syma torotoro*	negative	-	-	-
Crateroscelis murina	*Microeca flavovirescens*	positive	-	-	-
Crateroscelis murina	*Toxorhamphus novaeguineae*	positive	-	-	-
Dacelo gaudichaud	*Leptocoma serieca*	positive	-	-	-
Dacelo gaudichaud	*Xanthotis flaviventer*	positive	-	-	-
Dicrurus bracteatus	*Gerygone palpebrosa*	positive	-	-	-
Dicrurus bracteatus	*Rhyticeros plicatus*	positive	-	-	-
Dicrurus bracteatus	*Paradisaea minor*	positive	-	-	-
Dicrurus bracteatus	*Pseudorectes ferrugineus*	positive	-	-	-
Dicrurus bracteatus	*Ptilinopus iozonus*	positive	-	-	-
Ducula pinon	*Talegalla jobiensis*	positive	-	-	-
Ducula rufigaster	*Ptilinopus superbus*	positive	-	-	-
Ducula zoeae	*Ptilinopus pulchellus*	positive	-	-	-

Species pairs		Association	Elevation	Slope	Convexity
Geoffroyus geoffroyi	*Symposiachrus guttula*	positive	-	-	-
Gerygone chrysogaster	*Gerygone palpebrosa*	positive	-	-	-
Gerygone chrysogaster	*Paradisaea minor*	positive	-	-	-
Gerygone chrysogaster	*Rhipidura rufiventris*	positive	-	-	-
Gerygone palpebrosa	*Pseudorectes ferrugineus*	positive	-	-	-
Leptocoma serieca	*Symposiachrus guttula*	positive	-	-	-
Leptocoma serieca	*Tanysiptera galatea*	positive	-	-	-
Machaerirhynchus flaviventer	*Carterornis chrysomela*	positive	-	-	-
Megaloprepia magnifica	*Meliphaga spp. (M. analoga/ aruensis)*	negative	divergent (-/+)	-	-
Megaloprepia magnifica	*Ptilinopus superbus*	positive	shared (-)	-	-
Melanocharis nigra	*Symposiachrus guttula*	positive	-	-	-
Melanocharis nigra	*Xanthotis flaviventer*	positive	-	-	-
Melilestes megarhynchus	*Philemon meyeri*	positive	-	-	-
Meliphaga spp. (M. analoga/ aruensis)	*Symposiachrus manadensis*	negative	divergent (+/-)	-	-
Meliphaga spp. (M. analoga/ aruensis)	*Philemon buceroides*	positive	-	-	-
Meliphaga spp. (M. analoga/ aruensis)	*Pitohui kirhocephalus*	negative	divergent (+/-)	-	-
Meliphaga spp. (M. analoga/ aruensis)	*Rhipidura rufiventris*	negative	-	-	-
Meliphaga spp. (M. analoga/ aruensis)	*Tanysiptera galatea*	negative	-	-	-
Microeca flavovirescens	*Carterornis chrysomela*	positive	-	-	-
Microeca flavovirescens	*Symposiachrus manadensis*	positive	-	-	-
Microeca flavovirescens	*Ptilinopus pulchellus*	positive	-	-	-
Microeca flavovirescens	*Talegalla jobiensis*	positive	-	-	-
Pachycephala simplex	*Rhipidura rufiventris*	positive	-	-	-
Pachycephala simplex	*Toxorhamphus novaeguineae*	negative	-	-	-
Peltops blainvillii	*Xanthotis flaviventer*	positive	shared (-)	-	-
Philemon meyeri	*Poecilodryas hypoleuca*	negative	-	-	-
Philemon meyeri	*Ptilinopus coronulatus*	positive	-	-	-
Philemon meyeri	*Rhipidura rufidorsa*	positive	-	-	-
Pitohui kirhocephalus	*Poecilodryas hypoleuca*	positive	shared (-)	-	shared (-)
Pitohui kirhocephalus	*Ptilinopus coronulatus*	positive	-	-	-
Psedorectes ferrugineus	*Rhipidura rufidorsa*	positive	-	-	-
Psedorectes ferrugineus	*Rhipidura threnothorax*	positive	-	-	-
Ptilinopus coronulatus	*Ptilinopus iozonus*	positive	-	-	-
Ptilinopus iozonus	*Ptilinopus pulchellus*	positive	-	-	-
Ptilinopus perlatus	*Ptilinopus pulchellus*	positive	-	-	-
Ptilinopus pulchellus	*Ptilinopus superbus*	positive	-	-	-
Ptilinopus superbus	*Toxorhamphus novaeguineae*	positive	-	-	-
Ptilorrhoa caerulescens	*Rhipidura rufiventris*	positive	-	-	-
Rhipidura rufidorsa	*Xanthotis flaviventer*	positive	shared (-)	-	-
Rhipidura rufiventris	*Toxorhamphus novaeguineae*	negative	-	-	-
Rhyticeros plicatus	*Melanocharis nigra*	positive	-	-	-
Rhyticeros plicatus	*Talegalla jobiensis*	positive	-	-	-
Rhyticeros plicatus	*Toxorhamphus novaeguineae*	positive	-	-	-
Syma torotoro	*Tanysiptera galatea*	positive	-	-	-
Symposiachrus guttula	*Rhipidura threnothorax*	positive	shared (-)	-	-

Appendix 2

Available in the online version at:
https://issuu.com/birdsofwanang50haforestplot/docs/birds_of_wanang_50_ha_forest_plot



CHAPTER III

Vertical stratification of an avian community in New Guinean tropical rainforest.

Chmel K., Riegert J., Paul L. & Novotný V. (2016)

Population Ecology 58: 535-547

Abstract

Vertical stratification of avian communities has been studied in both temperate and tropical forests; however, the majority of studies used ground-based methods. In this study we used ground-to-canopy mist nets to collect detailed data on vertical bird distribution in primary rain forest in Wanang Conservation Area in Papua New Guinea (Madang Province). In total 850 birds from 86 species were caught. Bird abundance was highest in the canopy followed by the understory and lowest in the midstory. Overall bird diversity increased towards the canopy zone. Insectivorous birds represented the most abundant and species-rich trophic guild and their abundances decreased from the ground to canopy. The highest diversity of frugivorous and omnivorous birds was confined to higher vertical strata. Insectivorous birds did not show any pattern of diversity along the vertical gradient. Further, insectivores preferred strata with thick vegetation, while abundance and diversity of frugivores increased with decreasing foliage density. Our ground-to-canopy (0–27 m) mist netting, when compared to standard ground mist netting (0–3 m), greatly improved bird diversity assessment and revealed interesting patterns of avian community stratification along vertical forest strata.

Introduction

Tropical forests are characterised by vertical distribution of plant biomass that includes wood, leaves, fruits and flowers, leading to stratification of microhabitats and resources for avian communities (Allee 1926; Smith 1973; Parker and Brown 2000). In general, forests with higher vertical heterogeneity are expected to host more diverse avian communities (MacArthur and MacArthur 1961; Goetz et al. 2007; Huang et al. 2014). The main assumption of the hypothesis is that stratification of microhabitats allows the coexistence of bird species exploiting the same resources (and thus having similar morphology) due to reduced interference competition (Koen 1988; Styring and bin Hussin 2004; Bo¨hm and Kalko 2009; Kwok 2009). A structurally complex mature tropical forest with high vertical heterogeneity therefore represents a suitable environment to study habitat partitioning within an avian community as a mechanism for maintaining high species diversity (Cody 1974; Schoener 1974). Forest bird communities are known to be vertically stratified in terms of species composition (Turček 1951; Dickson and Noble 1978; Terborgh 1980; Koen 1988; Böhm and Kalko 2009) overall abundance (Pearson 1971; Bell 1982) and species diversity (Jayson and Mathew 2003). Therefore, preferences for certain strata can be one of the main factors leading to the separation of avian guilds (Holmes and Recher 1986). For example, the canopy of tropical primary forest is typically dominated by frugivorous birds (e.g., Shanahan and Compton 2001; Naka and Stouffer 2004).

Foliage density (i.e., habitat volume) is thought to be one of the main factors shaping the distribution of birds along the vertical forest gradient. In agreement, foliage density was positively correlated with bird diversity (MacArthur 1964; Jayson and Mathew 2003) and abundance (Pearson 1971; Bell 1982) in several tropical regions. Walther (2002a) found that species recorded in strata with dense vegetation had narrower vertical foraging niches than species from strata with lower vegetation density. Therefore, foliage density is likely linked to food resource availability, although we realize that a close relation to vegetation density may not apply to all of the particular food resources (Basset et al. 2003). For instance, insect abundance depends primarily on the biomass of young foliage, rather than on total plant biomass (Whitfeld et al. 2012). Nevertheless, correct assessment of available food density is extremely difficult to perform for the entire avian community (Hutto 1990). This applies especially to the New Guinean bird community due to poor description of diet composition for many species. Hereafter we therefore focused only on the effect of vegetation density on vertical distribution without sampling of food resources. Surveys on the stratification of avian communities in tropical forests are generally difficult to perform. Observations from the ground may be biased against canopy dwelling species, as they are often concealed by thick vegetation and may be detected at a lower rate (Blake and Loiselle 2001). Ground-based methods can be transferred to the canopy using canopy cranes (Walther 2002b, 2003) or walkways. However, it should be noted, that the latter method has, so far, only been used for studies on stratifi- cation of different taxa (Schulze et al. 2001) or for mist netting birds only at the same height as the walkways (Stokes et al. 1995). Moreover, although canopy cranes or canopy walkways provide access to higher forest strata, this is only over a limited area of the forest, usually up to 1 ha. Mist netting is another well-established method for bird community studies providing conditions for precise identification (including cryptic species), sampling of genetic material, collecting parasites and morphological data on captured birds. Although this method enables precise determination of the vertical position of caught birds it has rarely been used in higher forest strata and has not been used to assess the vertical stratification for the entire community along all strata (for examples see Humphrey et al. 1968; Meyers and Pardieck 1993; Derlindati and Caziani 2005; Vecchi and Alves 2015).

Here we developed a method of mist net sampling along the vertical forest gradient to explore the stratification of a bird community in lowland tropical rainforest in Papua New Guinea. Apart from ground-to-canopy mist netting optimization, we tested the following hypotheses: (1) forest bird abundances and diversity differ among different strata and change during the day; (2) main dietary groups show different patterns of abundances and diversity along the vertical gradient; and (3) foliage density is linked with the vertical distribution of the avian community.

Methods

Study site

Field work was carried out from June to November 2013 in the vicinity of the Swire Research Station located in the center of the Wanang Conservation Area, Madang Province, Papua New Guinea (5°6'49''S; 14°2'19''E, approximately 120 m a.s.l.). The conservation area covers 10,000 ha of primary forest and is surrounded by more than 100,000 ha of continuous primary and selectively logged forest. The annual rainfall is around 3,400 mm, with a mild dry season from July to September; mean monthly air temperature around 26° C (Anderson-Teixeira et al. 2015). The mean maximum height of trees at the study site was 31 m (excluding scattered emergent trees reaching over 40 m). The best description of local forest vegetation characteristics has been provided by a survey in adjacent Wanang 50 ha forest dynamic plot (located approximately 0.5 km from our study site), comprising of 288,000 stems with DBH>1 cm from 550 species and 211 tons per ha of live aboveground plant biomass (Anderson-Teixeira et al. 2015; Vincent et al. 2015). So far, 135 species of birds have been recorded in Wanang Conservation Area (K. Chmel, unpublished data). The vertical temperature profile of the forest was obtained from three data loggers installed at 1, 14 and 27 m above the ground in shaded locations avoiding direct sunlight. Temperature data were collected at 30 min intervals from 6th of August to 23rd of November 2013 at one of the mist netting sites.

Mist netting

The vertical distribution of the forest bird community was studied by installing mist nets from the ground to the canopy. The method of installation was similar to that of Humphrey et al. (1968). We selected a site in primary forest where we could stack a series of 3 m high and 18 m long mist nets one above the other, thus creating a large mist net stretching from the ground to the lower canopy. Smaller trees, branches and lianas (<10 cm in diameter) were cut in order to make room (approximately 1.5 m wide vertical space free of vegetation) for the mist nets. Thus, only the

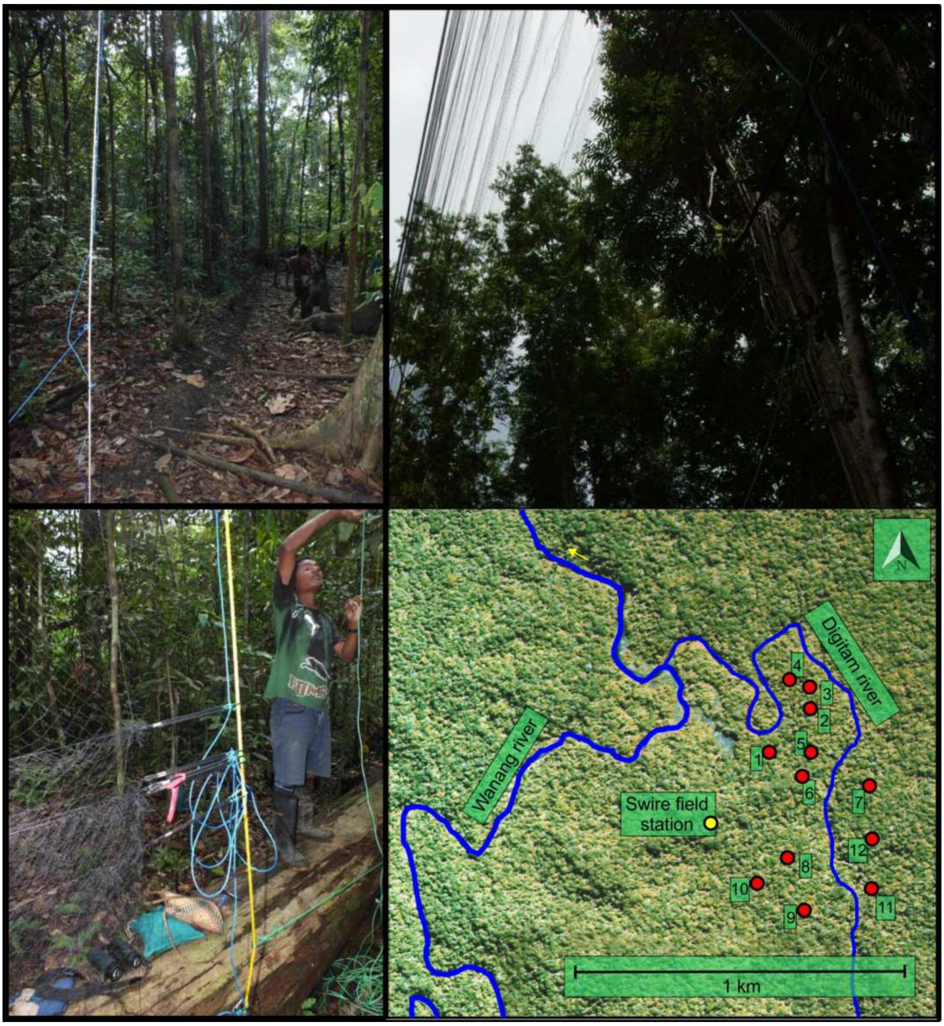


Figure 1. Mist netting site showing position and operation of ground-to-canopy mist nets. Bottom right map with positions of mist netting sites (1–12), Swire field station and small rivers (Wanang and Digitam rivers, approximately 3 m wide)

presence of larger trees (>10 cm in diameter) in the 18 × 1.5 m area limited mist net site selection. In three cases mist nets were installed along a fallen tree (between 5–15 years ago) that created just enough space for the panel of mist nets. We used a catapult to shoot guiding ropes for the mist nets over branches of large canopy trees, allowing us to open and close the entire stack of mist nets as needed (Figure 1). Mist netting was carried out at 12 primary forest sites (Figure 1) spaced 59–147 m apart (mean 103 m). We were able to stack nine mist nets, each of height 3 m, one above another, reaching a total height of 27 m above the ground at four sites. At the remaining eight sites, mist nets were installed up to 24 m above the ground (eight mist nets, each of height 3 m). We used mist nets with 19 mm mesh size, securing a good capture rate for small passerines to middle size birds. The largest species captured were Great Cuckoo-Dove (*Reinwardtoena reinwardtii*) and Eclectus Parrot (*Eclectus roratus*). Nevertheless, mist nets were not suitable for capturing large birds: e.g., Victoria Crowned Pigeon (*Goura victoria*), Papuan Hornbill (*Rhyticeros plicatus*), Sulphur-crested Cockatoo (*Cacatua galerita*), Palm Cockatoo (*Probosciger aterrimus*), Grey Crow (*Corvus tristis*) and birds of prey (Accipitriformes). In addition, large terrestrial species such as Northern Cassowary (*Casuarius unappendiculatus*) and Red-legged Brush Turkey (*Talegalla jobiensis*) were not present in our dataset.

Mist nets were opened at 6:00 and closed before 18:00 depending on weather conditions (mean 8.9, range 1–11.7 h). The mist nets were closed during strong windsor or rains to prevent captured birds from injury or hypothermia. We were able to carry out mist netting simultaneously at three out of 12 sites, this was usually done for two consecutive days. On average, mist netting was carried out for a total of 89 h (range 75–93 h) on 10 different days (9–11 days) at each site (Table 1) and the total exposure reached was 1,918,152 net-meter-hours.

Captured birds were extracted from mist nets and capture time, site number, and height above ground (at 3 m intervals) were recorded. Each bird was ringed with an individual color code or nail-varnish paint code (specific dots on the beak) for a few species where suitable size of color ring was not available. The birds were then measured and released.

Additional ground level mist netting, which served as a comparison with the ground-to-canopy technique, was conducted in 2015 (between 12 March and 10 April and between 28 November and 4 December) at 6 different sites in Wanang conservation area. All sites were located in primary forest. Mist netting was carried out for 3 days at each site resulting in a total of 18 mist netting days (138.5 h). Mist nets (mean length per site 174.2 m, range 120–252 m) were opened for a mean of 7.7 h per day (range 5.25–10 h) resulting in the total of 457,632 netmeter-hours of exposure. We used mist nets with identical dimensions to those used for ground-to-canopy mist netting (length 18 m, height 3 m, mesh-size 19 mm). These nets were installed only at ground level (reaching 3 m above ground).

Table 1. Mist netting sampling effort: At each site 8 or 9 mist nets (each 3 m high) were used to reach the corresponding total height, 24 or 27 m. Area covered by mist nets equals height reached × 18 m (length of individual mist nets). Numbers of birds and species caught are shown separately for ground-to-canopy and ground (0–3 m) mist nets.

Site	Mist nets exposure [hours]	Number (dates) of mist netting days	Reached height [m]	Total number of caught birds	Total number of caught species	Number of caught birds (0–3 m)	Number of caught species (0–3 m)
1	89.88	10 (7, 10, 30 and 31 July; 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	67	28	1	1
2	89.28	10 (7, 10, 30 and 31 July; 20 and 21 August; 25 and 26 October; 6 and 7 November)	24	62	26	2	2
3	88.02	9 (29 June; 1, 30 and 31 July; 20 and 21 August; 25 and 26 October; 7 November)	27	78	27	20	9
4	91.68	11 (7, 10 and 30 July; 1, 2, 20 and 21 August; 25 and 26 October; 6 and 7 November)	27	104	41	17	11
5	92.33	10 (29 June; 1 July; 1, 2, 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	101	41	11	7
6	92.30	11 (28 and 29 June; 1 July; 1, 2, 23 and 24 August; 23 and 24 October; 4 and 5 November)	24	62	28	14	10
7	82.07	9 (12 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	27	72	25	3	3
8	93.65	10 (9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1, 12 and 13 November)	27	124	44	15	9
9	93.38	10 (9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1, 12 and 13 November)	24	61	25	10	7
10	75.55	9 ((9, 10 and 30 August; 1 September; 18, 19 and 31 October; 1 and 12 November)	24	45	23	13	8
11	86.63	10 (12 and 13 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	24	145	42	9	7
12	90.87	10 (12 and 13 August; 3 and 4 September; 16, 17, 29 and 30 October; 12 and 13 November)	24	87	37	6	5

Vegetation survey

The heights of the tallest trees in the vicinity of each capture site were measured. Further, we estimated the foliage density profile according to Radtke and Bolstad (2001), who assessed the vegetation structure from its intercepts with multiple vertical laser beams. The final values of foliage density (leaf area index) between two heights (h1, h2) were computed using the following equation: $FD_{h1,h2} = \ln(\varphi(h_1) / \varphi(h_2))$, developed by (MacArthur and MacArthur 1961; MacArthur and Horn 1969), where u (h) is the number of intercepts with vegetation exceeding height h. We calculated foliage density for each 3 m vertical interval (0–3 m, 3–6 m, 6–9 m, 9–12 m, 12–15m, 15–18m, 18–21m, 21–24m, 24–27 m) at each of the 12 sites separately.

Vegetation measurements were taken with a Leica Disto D5 laser range finder (range: 0.05–200 m with measuring accuracy ± 1.5 mm). The range finder was fixed in a horizontal position to ensure vertical laser beams. Measurements of intercepts with vegetation were performed along four transects parallel to mist nets at each capture site, laid out at 1 and 2 m distances on each side of the mist net. The measurements were taken at approximately 25 cm intervals along the transects, resulting in approximately 70 measurements per transect and 280 measurements per one mist net site.

Statistical analyses

Spearman rank correlation was used for relationships between bird and environmental variables. Two-way ANOVA was used to test the differences in temperature between forest zones and time of day. The effect of capture site and repeated mist netting on abundance of caught birds was analyzed by Generalized linear model (GLM). An identical method was also used for the analyses of seasonal differences in abundances of trophic guilds along the vertical gradient, where two mist netting periods: 28 July – 4 September and 16 October – 13 November were compared. We also tested the interactions between height above ground and mist netting period. The influence of temperature (daily means per hour) on total abundance (pooled for twelve sites) was tested by linear regression models separately for three 9 m vertical bands (0–9 m, 9–18 m and 18–27 m above ground). The temperature measurements were carried out at one site only, therefore its effect was analyzed separately from the following model. Changes in abundance and diversity of captured birds with height above ground and foliage density and time of day were analyzed for the whole community and individual trophic guilds by Generalized linear mixed models (GLMM) with Gaussian distribution of dependent variables and using capture site as a random factor. We also tested interactions among explanatory variables as well as adding quadratic polynomial functions to the model to test if those significantly improved the process of finding the best fitting model. Models were fitted using R package Lme4 based on AIC values. Post-hoc pair-wise comparisons among different day times were made using Tukey contrasts (multicomp package in R). All the above mentioned tests and data visualization were performed in the programs: R 3.1.1 and STATISTIKA 12.

Canonical correspondence analysis (CCA) was performed for each trophic guild in order to assess the effect of height above ground and time of day (explanatory variables) on species abundances (response variables). Statistical significance was obtained by Monte Carlo permutation tests with 999 permutations, using software Canoco5 (ter Braak and Smilauer 2012). Singletons and doubletons (*n* = 29) were excluded from these analyses.

In all models, abundance of birds was represented by standardized net-meter-hour capture rate: (number of caught birds [*n*] / length of mist net [m] / mist nets exposure [hours]). Alternatively, we used a Shannon-Wienner diversity index (Shannon 1948) to analyze community and trophic guilds' diversity. The effect of individual sites was eliminated by setting site as a random factor in GLMM and as a covariate in CCA. In GLMM and CCA height above ground (in 3 m intervals) was used as a continuous explanatory variable. In contrast, time of day was divided into four three-hour intervals (between 6:00 and 18:00) and was considered as a categorical variable.

Species were divided into three main trophic guilds (frugivores, insectivores and omnivores; Supporting information Table S1) according to information on diet obtained from Tvardíková (2013) and del Hoyo et al. (2016). Among omnivores there were subgroups of birds feeding on a combination of fruit/nectar, fruit/insect or insect/nectar. However, in order to avoid misleading interpretation caused by small sample size, in statistical models these subgroups were pooled into omnivores only. Birds of prey with less than four recorded individuals (*Accipiter poliocephalus* – 3 inds., *Uroglaux dimorpha* – 1 ind.) were excluded from the analyses of trophic guilds. Small vertebrate prey that is part of the diet of several species (e.g., Alcedinidae) was classified as insect prey. The functional difference between large insect and small vertebrate prey was negligible for our purposes.

Results

The vertical foliage profile of forest surrounding the mist netting sites was characterized by very high foliage density in the lower strata (0–9 m) and at the vertical band between 24–27 m above the ground. Other vertical zones (between 9–24 m above ground) had much lower values of foliage density (Figure 2). However, we found a significant negative correlation between height above ground and foliage density at mist netting sites (Spearman rank correlation, $r_s = -0.55$, $n = 100$, $P < 0.001$), therefore foliage density was not used in individual models as an explanatory variable together with height above ground. Forest air temperature, measured at 1, 14 and 27 m above ground, differed vertically and temporally (Two-way ANOVA; height above ground: $F_2 = 480.8$, $P < 0.001$; day-time: $F_9 = 304.7$, $P < 0.001$). The highest temperatures were reached around 13:00 at 27 m above ground (Figure S1).

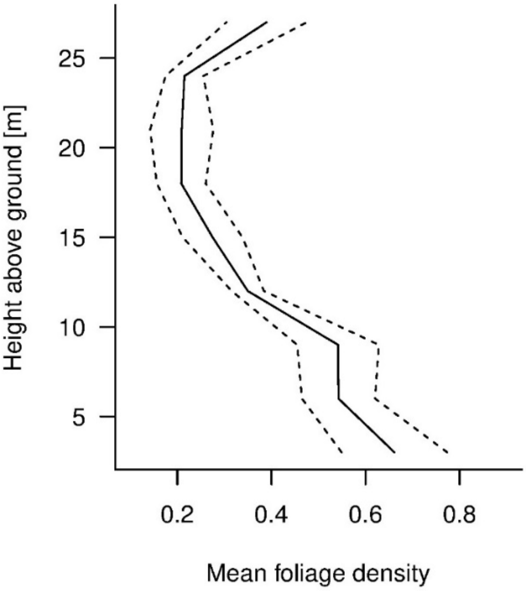


Figure 2. Vertical profile of mean foliage density from 12 capture sites (dashed lines represent standard error).

In total, 850 individual birds (from 84 species) were captured, some of them repeatedly, resulting in 1008 captures (Table S1) Abundance of birds (capture rate) differed significantly among the 12 sites but did not decrease or increase with repeated controls at the same study site (GLM; $n = 120$; site: $F = 6.62$, $P < 0.001$; repeated controls: $F = 0.29$, $P = 0.590$).

Apart from foliage density, both time of day and net height affected the capture rates (Table 2). The highest abundance of birds was recorded during the morning with a gradual decrease towards the evening (Figure 3). However, the abundance of birds did not differ significantly between the first two morning three-hour intervals (6:00-8:59 vs. 9:00-11:59, $P = 0.120$). Between the rest of the three-hour time intervals the difference in abundance was significant ($P < 0.001$). The highest capture rate was recorded in the top strata (21–27 m) and the lowest in the vertical band between 9 and 18 above ground. Capture rate near ground level (0–9 m) was slightly higher compared to midstory vertical bands (9–18 m, Figure 3). This explains why the best fitting model contained the quadratic polynomial function of height above ground (Table 2). Analysis of temperature and its effect on abundance of birds (compared for three 9 m vertical bands) showed a significant relationship only for the lowest strata (0–9 m), where abundance decreased with increasing temperatures (Figure S2).

Caught birds consisted mainly of insectivores (364 individuals, 449 including recaptures, 40 species) and omnivores (344 individuals, 411 including recaptures, 28 species) followed by frugivores (137 individuals, 144 including recaptures, 14 species). Abundance of frugivorous and insectivorous birds was related to foliage density (Table 2). Frugivorous birds showed a negative response to foliage density, while insectivorous birds were more abundant in strata with thicker vegetation (Figure 4). In all trophic guilds, the overall abundance of birds responded significantly to the time of day (Table 2, Figure 5a-c). Insectivores were most frequently caught between 6:00 and 8:59 contrary to omnivorous and frugivorous birds with highest frequency later in the morning between 9:00 and 11:59 (Figure 5a-c). Abundance of frugivores and omnivores increased significantly towards the canopy zone (Figure 5d,f) in contrast with insectivores that exhibited the highest density at the 0–3 m ground level (Table 2, Figure 5e).

Table 2. Results of the best GLMM models testing the influence of time of day (Time), foliage density (FD) and height above ground (Height) on the abundance (captures per net-meter-hour) and diversity (Shannon diversity index) of the avian forest community and three different trophic guilds (FR–frugivores, IN–insectivores, OM–omnivores). In all models, the capture site was used as a random factor. Quadratic polynomial functions are shown only when it improved the models. Significant models ($P < 0.05$) are typed in bold.

	N		Model	AIC	χ^2	*P* value
Abundance of birds	400		~1	-4001.8		
			~Time	-4094.7	98.92	**<0.001**
			~Time + FD	-4093.2	0.45	0.4983
			~Time + Height	-4109.9	17.15	**<0.001**
			~Time + Height + I(Height^2))	-4115.7	7.778	**0.005**
Abundance of trophic guilds	400	FR	~1	-4853.9		
			~VFD	-4850.1	14.07	**<0.001**
			~Height	-4897.4	45.50	**<0.001**
			~Height + Time	-4904.7	13.25	**0.004**
		IN	~1	-4385.7		
			~Time	-4481.5	89.82	**<0.001**
			~Time + FD	-4489.8	10.30	**0.001**
			~Time + Height	-4488.3	8.76	**0.003**
		OM	~1	-4502.6		
			~Time	-4530.7	34.10	**<0.001**
			~Time + FD	-4532.3	3.56	0.059
			~Time + Height	-4564.3	35.59	**<0.001**

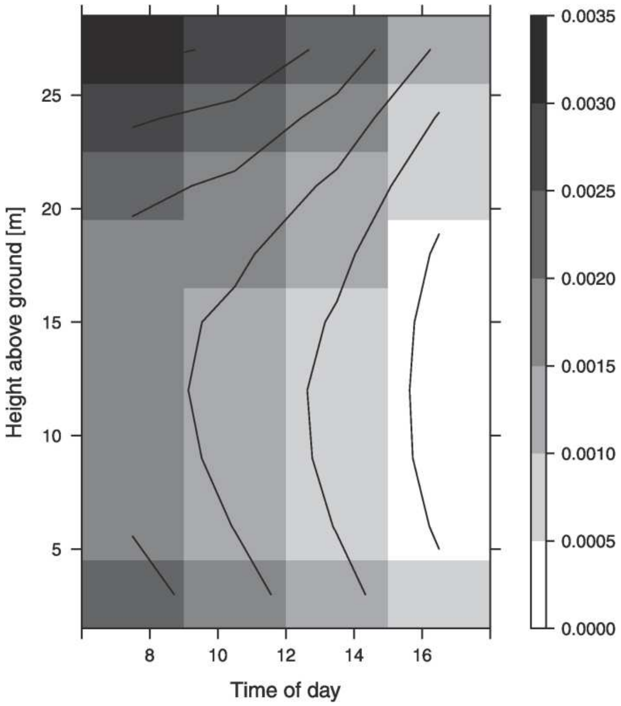


Figure 3. Abundance of birds (captures per net-meter-hour) in relation to height above ground (3-m intervals) and time of day (3-hour intervals). Post-hoc comparison showed that abundances differed significantly among all time intervals except between the first two, three hour intervals (6:00-8:59 x 9:00-11:59).

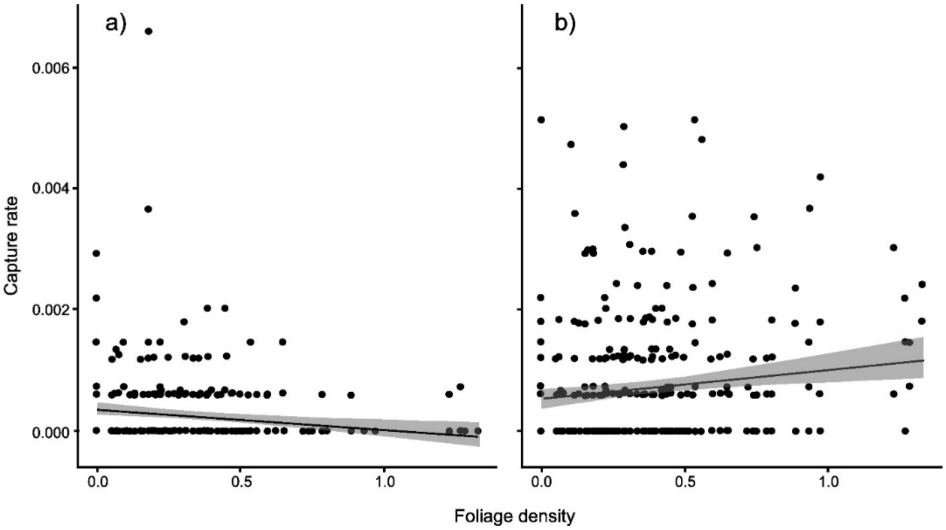


Figure 4. Linear relationship between abundance (captures per net-meter-hour) of trophic guilds (a: frugivores, b: insectivores) and foliage density (shaded area represents standard error).

Interaction of time and height above ground did not improve the models significantly. Finally, we found no seasonal differences in abundance (GLM, *P* at least 0.312) and vertical distribution (GLM, *P* at least 0.138) in any of the trophic guilds. Insectivores were most frequently caught between 6:00 and 8:59 contrary to omnivorous and frugivorous birds with highest frequency later in the morning between 9:00 and 11:59 (Figure 5a-c). Abundance of frugivores and omnivores increased significantly towards the canopy zone (Figure 5d,f) in contrast with insectivores that exhibited the highest density at the 0–3 m ground level (Table 2, Figure 5e). Interaction of time and height above ground did not improve the models significantly. Finally, we found no seasonal differences in abundance (GLM, *P* at least 0.312) and vertical distribution (GLM, *P* at least 0.138) in any of the trophic guilds.

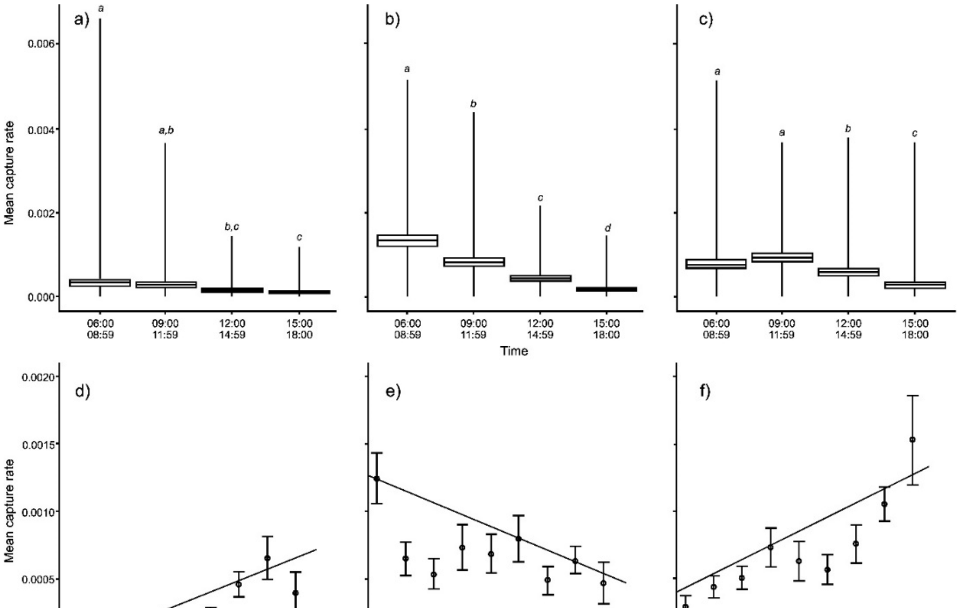


Figure 5. Abundance (mean captures per net-meter-hour ± SE, min., max.) of trophic guilds (frugivores: a,d, insectivores: b, e, omnivores: c, f) in response to time of day (top row) and height above ground (bottom row). Means with the same letter (positioned above outlines, top row) are not significantly different from each other (Tukey test, *P* > 0.05).

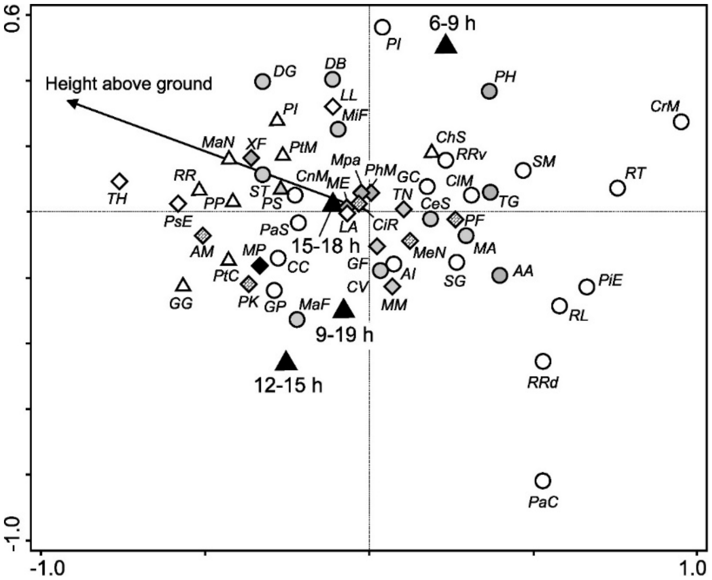


Figure 6. CCA diagram visualising the abundance of frugivorous (empty triangles), insectivorous (empty circles: gleaning species, filled circles: sallying species) and omnivorous (bricked diamonds: frugivoro-insectivores, grey diamonds: nectarivoro-insectivores, empty diamonds: nectarivoro-frugivores, black diamond: non-classified omnivore) species in relation to height above ground (height) and time of day (6–9 h, 9–12 h, 12–15 h, 15–18 h). The first two ordination axes explained 3.09 % of total variation. Values of explained variation (%), Pseudo-F statistics (*F*) and P level (*P*) for explanatory variables (height and time) obtained by Canonical Correspondence Analysis (covariate: capture site, Monte Carlo test with 999 permutations) of trophic guilds: frugivores (height: 7.5%, $F = 6.6$, $P = 002$; time: 3.3 %, $F = 2.8$, $P = 0.006$), insectivores (height: 2.5 %, $F = 4.9$, $P = 0{,}002$; time: 1.6 %, $F = 3.1$, $P = 0.002$), omnivores (height: 2.8 %, $F = 5.6$, $P = 0{,}002$; time: 1.3 %, $F = 2.6$, $P = 0.004$). Species codes: AA – *Alcedo azurea*, AI – *Arses insularis,* AM – *Aplonis metallica,* CC – *Carterornis chrysomela,* CeS – *Ceyx solitarius*, ChS – *Chalcophas stephani*, CiR – *Cicinnurus regius*, ClM – *Colluricincla megarhyncha*, CnM – *Coracina melas*, CrM - *Crateroscelis murina*, CV – *Cacomantis variolosus*, DB – *Dicrurus bracteatus*, DG – *Dacelo gaudichaud*, GC – *Gerygone chrysogaster*, GF – *Glycichaera fallax*, GG – *Geoffroyus geoffroyi*, GI – *Garritornis isidorei*, GP – *Gerygone palpebrosa*, LA - *Loriculus aurantiifrons,* LL – *Lorius Lory*, MA - *Myiagra alecto*, MaF - *Machaerirhynchus flaviventer*, MaN – *Macropygia nigrirostris*, ME – *Myzomela eques*, MeN – *Melanocharis nigra*, MiF – *Microeca flavovirescens*, MM – *Melilestes megarhynchus*, MP – *Micropsitta pusio*, Mpa – *Meliphaga analoga/M. aruensis.*, PaC – *Ptilinorrhoa caerulescens*, PaS – *Pachycephala simplex,* PF – *Pitohui ferrugineus*, PH – *Poecilodryas hypoleuca*, PhM – *Philemon meyeri*, PI – *Ptilinopus Iozonus*, PiE – *Pitta erythrogaster*, PK – *Pitohui kirhocephalus*, PP – *Ptilinopus pulcheus*, PsE – *Psittaculirostris edwardsii*, PtC – *Ptilinopus coronulatus*, PtM – *Ptilinopus magnificus*, PtS – *Ptilinopus superbus*, RL – *Rhipidura leucothorax*, RR – *Reinwardtoena reinwardtii,* RRd – *Rhipidura rufidorsa*, RRv – *Rhipidura rufiventris*, RT – *Rhipidura threnothorax*, SG – *Symposiachrus guttula*, SM – *Symposiachrus manadensis*, ST – *Syma torotoro*, TG – *Tanysiptera galatea,* TH – *Trichoglossus haematodus*, TN – *Toxorhamphus novaeguineae*, XF – *Xanthotis flaviventer*.

Abundance of individual species changed more with height above ground than with time of day in all trophic guilds. Frugivores showed the strongest response to height as well as time of day (Figure 6). The division of insectivorous species according to foraging strategies into gleaners and sallying birds (Figure 6) showed that the group of insectivores found exclusively in the understory is formed only by gleaners (*Rhipidura threnothorax* and *R. rufidorsa*, *Pitta erythrogaster* and *Ptilorhoa caerulescens*). In contrast, sallying species such as Rufous-bellied Kookaburra (*Dacelo gaudichaud*) or Yellow-billed Kingfisher (*Syma torotoro*) preferred higher strata and showed the strongest positive response to height above ground. Frugivorous species were most abundant in the canopy zone, except for the specialised ground-feeding Stephan's Dove (*Chalcophaps stephani*). Two subgroups of omnivorous birds (foraging on insects/nectar and fruits/insects) included species preferring higher strata as well as species more abundant in lower strata. Birds that feed on nectar and fruits on the other hand preferred mostly higher strata (Figure 6).

The diversity of the avian forest community expressed by the Shannon index increased with height above ground, but did not change with foliage density (Table 2, Figure 7a). When we divided the species according to their trophic requirements, we found that the diversity of frugivorous and omnivorous birds changed with foliage density (Table 2). Frugivorous species expressed higher diversity in strata with low vegetation density (Figure 7b). Insectivores were, in contrast, more diverse in strata with thicker vegetation (Figure 7c). Finally, diversity of omnivores was not related to foliage density (Table 2). Diversity of frugivores and omnivores increased with height above the ground. Frugivores especially exhibited extremely low diversity in lower forest zones. In contrast, diversity of insectivorous birds did not change significantly with height above ground (Table 2, Figure7d-f).

Traditional mist netting, limited only to ground level, leads to reduced species richness in the sample. Recorded species richness was significantly lower when ground nets (0–3 m) were compared to the complete set of ground-to-canopy mist nets 0 to 27 m at the same mist netting sites (numbers of species per site; 0–3m: median = 7, range: 1–11; 0–27m: median = 28, range: 23–44; Mann-Whitney U Test, $z_{2,24} = 4.128$, $P < 0.001$). In total, the lowest net captured 100 individuals of 30 species, while the full set of ground-to-canopy nets captured 850 individuals of 84 species.

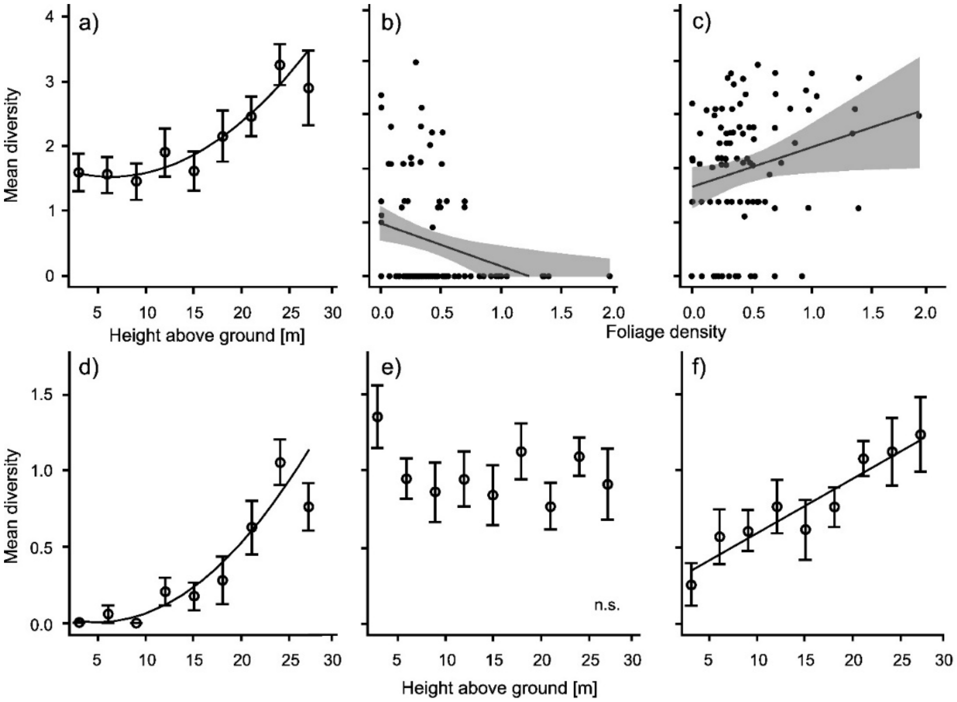


Figure 7. Diversity (Mean Shannon-Wienner diversity index ± SE) of avian community (a) and trophic guilds (frugivores: d, insectivores: e, omnivores: f) and its profile across vertical forest strata (height above ground). Linear relationship of diversity (Shannon-Wienner diversity index) and foliage profile of frugivorous (b) and insectivorous (c) birds (shaded area represents standard error).

Even with increased sampling effort, the species richness recorded with ground nets remains far lower. This was shown by the ground mist netting (0–3 m) survey that was carried out in 2015 in the same conservation area. In total 427 individuals (485 including recaptures) were captured, but only 46 species were recorded. Moreover, rarefaction curves comparing both sampling techniques showed that ground level mist netting became saturated at a faster rate (Figure 8). Therefore, even if the sample size of ground-to-canopy mist netting was reduced to the same value as ground mist netting (485 captures), elevated mist nets would capture approximately 24 species more than ground mist nets. The most underscored group of birds caught by ground mist nets were frugivores with only three captured species: *Chalcophaps stephani*, *Gallicolumba rufigula* and *Ptilonopus coronulatus*; the first two species are ground foraging birds. In contrast, the proportion (both abundance and species richness) of insectivorous birds caught by ground mist nets was much higher compared with ground-to-canopy mist nets (Figure 8). Insectivorous birds that were caught only in ground-to-canopy mist nets were canopy dwelling cuckoos (Cuculidae, 7 species), other birds preferring higher strata (*Carterornis chrysomela*, *Dicrurus bracteatus*, *Gerygone palpebrosa*, *Microeca flavovirescens*, *Peltops blainvillii*) and aerial species such as Papuan Spinetail (*Mearnsia novaeguineae*). The proportion of omnivorous birds was similar in both ground-to-canopy and ground mist nets. Omnivorous birds that were not captured by ground mist nets were mainly parrots (*Cyclopsitta diopthalma*, *Charmosyna placentis*, *Eclectus roratus*, *Lorius lory*, *Psittaculirostris edwardsii*, *Trichoglossus haematodus*) and other birds that are not often encountered in the understory: *Glycichaera fallax*, *Lalage atrovirens*, *Leptocomus serieca*, *Mino dumontii, Paradisaea minor.*

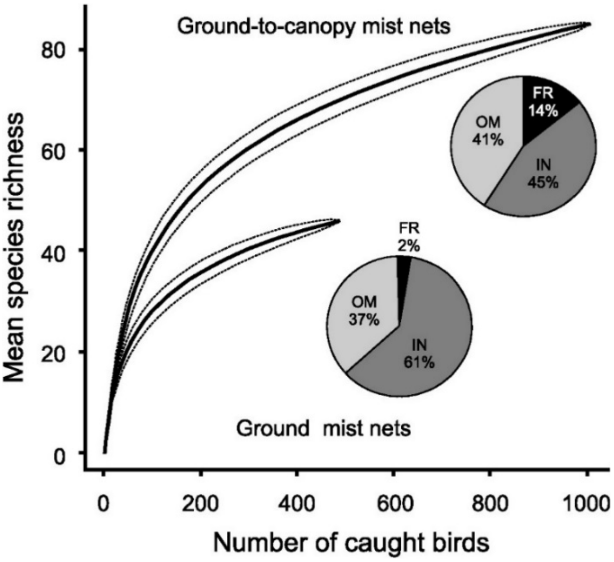


Figure 8. Rarefaction curves (± SE: dashed lines) showing species accumulation for ground based (lower curve) and ground-to-canopy (top curve) mist netting. In total, we made 485 captures of 46 species and 1008 captures of 84 species in ground mist nets and ground-to-canopy mist nets, respectively. The following numbers of birds (including recaptures) and species of different trophic guilds were caught by both mist netting techniques: FR - frugivores (ground: 12 birds, 3 species; ground-to-canopy: 144 birds, 14 species), IN - insectivores: (ground: 296 birds, 28 species; ground-to-canopy: 449 birds, 40 species), OM - omnivores: (ground: 177 birds, 15 species; ground-to-canopy: 411 birds, 28 species).

Discussion

The mean foliage density profile from our capture sites resembled profiles from other tropical forests characterized by two peaks of foliage density, one peak in the understory and the second peak in the canopy strata (Pearson 1971; Schemske and Brokaw 1981; Bell 1982; Meir et al. 2000; Walther 2002b). Both Pearson (1971) and Bell (1982) suggested a positive correlation between foliage density and abundance of birds, but they did not support their assumptions with statistical tests. Further, they both admitted certain deviance from the claimed relationship in some strata. Walther (2002a) reported that birds recorded in lower strata were surrounded by thicker vegetation compared with birds in higher strata. This is in agreement with our study where insectivorous birds with highest abundances in the understory showed positive preference for thicker vegetation, whereas frugivorous birds avoided (both in terms of abundance and diversity) the understory with high vegetation density. However, we did not find a relationship between overall abundance or diversity of the avian community and foliage density. This suggests that foliage density of different forest strata explains the vertical distribution of birds at a finer scale rather than at community level.

Our results showed that birds were most abundant and had highest diversity in the topmost sampled strata. This is in agreement with the general assumption that tropical forest canopy is the center of diversity, although only Pearson (1971) has empirically confirmed this for Neotropical birds. In contrary to our results, Bell (1982) reported from Papua New Guinea that birds were most abundant in the understory. Nevertheless, in agreement with our results, both Pearson (1971) and Bell (1982) reported lowest abundance of birds in the midstory. However, Jayson and Mathew (2003) reported a different pattern of vertical distribution of birds from Indian tropical evergreen forest, where abundance of birds decreased from ground to canopy. Previous studies were based on ground surveys, which may under-estimate bird abundance in the canopy. Moreover, Pearson (1971) and Bell (1982) included only foraging birds while our mist netting allowed capture of nearly all birds, independent of whether feeding or just moving through the forest.

The increased diversity and abundance of birds towards the canopy may be explained by high fruit and flower availability in the canopy, which is indirectly supported by the increased diversity of frugivorous and omnivorous birds in higher strata. This result is consistent with studies on vertical distribution of trophic guilds from other tropical sites (Terborgh 1980; Greenberg 1981; Bell 1982; Frith 1984; Koen 1988). However, the diversity of frugivores in the understory might be slightly underestimated in our dataset, because mist nets are not designed to capture large frugivorous birds foraging on the ground (e.g., *Goura victoria*, *Casuarius unappendiculatus*). Insectivorous birds did not exhibit any pattern of vertical distribution of species diversity, although their abundance was slightly higher in the understory. Higher abundance of insectivores in the understory compared with the canopy was also reported from the neotropics (Greenberg 1981) and Africa (Koen 1988). One could expect that the vertical distribution of insectivorous birds may be linked with the abundance and diversity of insects in different strata. Several studies reported higher diversity or abundance of different groups of insects in the canopy (e.g., Sutton et al. 1983; Schulze et al. 2001; Charles and Basset 2005). Other studies have shown that insects in the understory can be as abundant as in the canopy (Basset et al. 2001; Schulze et al. 2001; Stork and Grimbacher 2006). Our results document an increased abundance of insectivores in the understory, which may indicate that insects in the lowland primary forests of New Guinea are most abundant there. Insect availability may also be higher in the understory due to thicker vegetation and the presence of the forest floor, which provides a microhabitat missing in other strata.

We observed highest abundances of birds during the morning hours with gradual decrease towards the evening. This is in agreement with other studies from tropical forests (Bell 1982; Blake 1992). In contrast, vertical shifts downwards during the midday hot period observed in nectarivorous birds (Bell 1982) or a decrease in bird abundance in the topmost stratum (Pearson 1971) were not confirmed by our results at either community or trophic level. Temporal activity (capture rate) of birds differed among birds with different foraging strategies. Insectivores, in contrast to frugivores and omnivores were caught mainly during the early morning period (6:00–8:59). Thus if mist netting was carried out only during early morning periods, the relative proportion of insectivores would increase. A possible cause for the earlier onset of activity (movements through the forest) in insectivores can be explained by their fast metabolic rate, which is related to their small body size (Nagy 2005). The mean body mass of insectivorous birds caught during our survey was considerably lower compared to frugivorous and omnivorous birds (mean ± SD: insectivores 30.7 ± 20.1 g, frugivores 115.8 ± 50.5 g, omnivores 40.6 ± 43.7 g). Small insectivores probably start to forage earlier in order to regain energy lost during the long tropical night.

Our results show the efficiency of ground-to-canopy mist netting. Although the installation of mist nets in the canopy was time consuming and mist netting did not acquire behavioral data (e.g., foraging, singing, displaying, resting), this method allowed us to obtain detailed data on the vertical distribution of bird guilds and obtained a fuller picture of bird diversity. Moreover, a considerable number of bird species would not have been recorded by a ground-based census, due to their secretive life-style or preference for higher canopy strata. Finally, we showed that elevated mist nests can be used to survey the stratification of avian forest communities and to the best of our knowledge this is the first study using this method.

Acknowledgments

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Supporting information

Appendix 1

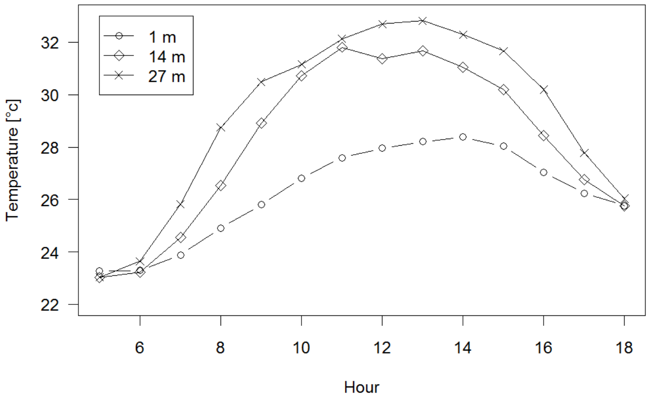

Figure S1 Mean temporal and vertical (1, 14 and 27 m above ground) temperature profile at our primary forest study site.

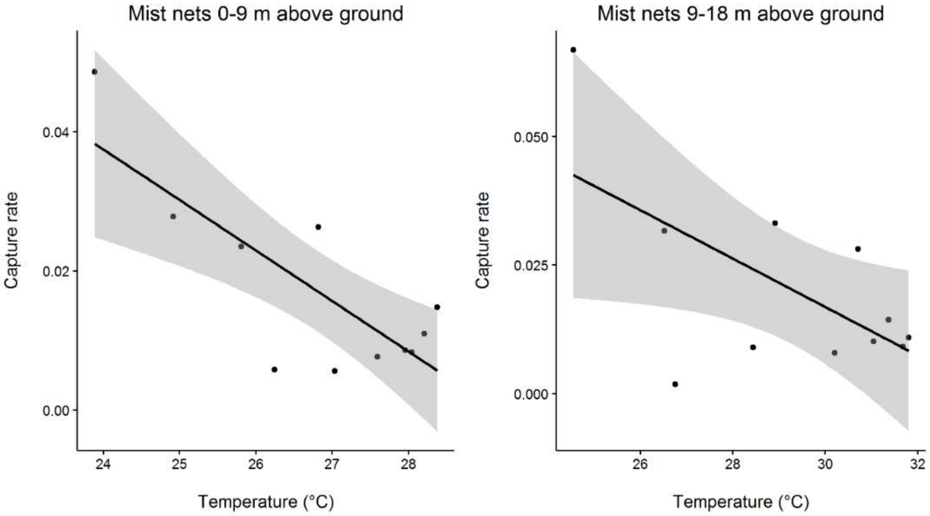

Figure S2 Linear regression of bird abundance (captured birds/net-meter-hour) and mean temperature at two vertical bands between 0-9 m (β = -0.007, t_{11} = -3.95, *P* = 0.003) and 9-18 m above ground (β = -0.005, t_{11} = -2.34, *P* = 0.044). Both variables refer to one hour intervals (7:00–17:00). Shaded area represents standard error. Changes in daily temperature had no effect on abundance of birds in the third top most vertical band (18-27 m above ground: β = -0.002, t_{11} = -1.23, *P* = 0.251).

Table S1: Number of individuals captured in total and at different heights above ground. Value in brackets indicate to number of repeatedly captured individuals. E–species endemic to New Guinea. Trophic guilds: CA–carnivores, FR–frugivores, IN–insectivores, FRIN–frugivoro-insectivores, INNE–insectivoro-nectarivores, FRNE–frugivoro-nectarivores, OM–omnivores.

				Height above ground [m]									
Species	Family	Endemic	Trophic guild	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	Total
Accipiter poliocephalus	Accipitridae	E	CA	2	-	-	-	-	-	1	-	-	3
Ailuroedus buccoides	Ptilonorhynchidae	E	FRIN	-	-	-	-	-	1	-	-	-	1
Alcedo azurea	Alcedinidae		IN	-	3 (2)	1	-	-	1	-	-	-	5 (2)
Alcedo pusilla	Alcedinidae		IN	-	-	-	-	-	-	1	-	-	1
Aplonis metallica	Sturnidae		FRIN	-	-	-	2	3	-	6	12	6	29
Arses insularis	Monarchidae	E	IN	4	5	3	11 (4)	4	3	7 (2)	1 (1)	1	39 (7)
Cacomantis castaneiventris	Cuculidae		IN	-	-	-	-	1	-	-	-	-	1
Cacomantis flabelliformis	Cuculidae		IN	-	-	-	-	-	-	-	2 (1)	-	2 (1)
Cacomantis variolosus	Cuculidae		IN	-	-	1	1	2 (2)	-	-	-	-	4 (2)
Ceyx solitarius	Alcedinidae	E	IN	5 (2)	6 (1)	2	5 (2)	1	3	1	4 (1)	1 (1)	28 (10)
Chalcophaps stephani	Columbidae		FR	1	4	9	4 (1)	2 (1)	2	3	2	-	27 (2)
Charmosyna placentis	Psittacidae		FRNE	-	-	-	-	-	-	1	1	-	2
Chrysococcys lucidus	Cuculidae		IN	-	-	-	-	-	1	-	-	-	1
Chrysococcyx meyerii	Cuculidae	E	IN	-	-	-	-	-	1	-	-	-	1

Species	Family	Endemic	Trophic guild	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	Total
Chrysococcyx minutillus	Cuculidae		IN	-	-	-	-	-	1	-	-	-	1
Dacelo gaudichaud	Alcedinidae	E	IN	-	-	-	1	-	-	2	3	2(1)	8 (1)
Dicaeum geelvinkianum	Dicaeidae	E	FR	-	-	-	-	1	-	-	-	-	1
Dicrurus bracteatus	Dicruridae		IN	-	-	-	-	-	2	-	1	-	3
Eclectus roratus	Psittacidae		FRNE	-	-	-	-	-	-	-	1	-	1
Gallicolumba rufigula	Columbidae	E	FR	-	1	-	-	-	-	-	-	-	1
Geoffroyus geoffroyi	Psittacidae		FR	-	-	-	-	-	-	-	4	-	4
Gerygone chrysogaster	Acanthizidae	E	IN	5	-	3	-	4	3	2	1	-	18
Gerygone palpebrosa	Acanthizidae		IN	1	-	-	-	-	1	2	1	2	7
Glycichaera fallax	Meliphagidae		INNE	-	1	1	4 (1)	1	2	-	2	-	11 (1)
Halcyon nigrocyanea	Alcedinidae	E	IN	1	-	-	-	-	-	-	-	-	1
Henicophaps albifrons	Columbidae	E	FR	1	-	-	-	-	-	-	-	-	1
Lalage atrovirens	Campephagidae		FRIN	-	-	-	-	-	-	-	-	2	2
Leptocoma serieca	Nectariniidae		INNE	-	-	-	-	1	-	1	-	-	2
Lonchura tristissima	Estrildidae	E	FRIN	1	1	-	-	-	-	-	-	-	2
Loriculus aurantiifrons	Psittacidae	E	FRNE	-	1	-	-	-	-	-	-	2	3
Lorius lory	Psittacidae	E	FRNE	-	-	-	1	1	-	2	2	-	6
Machaerirhynchus flaviventer	Monarchidae		IN	-	-	-	1	2	2	-	2 (1)	-	7 (1)

Species	Family	Endemic	Trophic guild	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	Total
Macropygia amboinensis	Columbidae		FR	-	-	-	-	-	-	1	-	1	2
Macropygia nigrirostris	Columbidae	E	FR	-	-	-	-	2	1	4	9	-	16
Mearnsia novaeguineae	Apodidae	E	IN	-	-	-	-	-	-	-	1	-	1
Melanocharis nigra	Melanocharitidae	E	FRIN	2	9 (1)	15 (6)	11 (5)	7 (4)	8 (2)	3 (1)	4 (1)	-	59 (20)
Melidora macrorrhina	Alcedinidae	E	IN	-	-	-	-	1	-	-	-	-	1
Melilestes megarhynchus	Meliphagidae	E	INNE	1	2 (1)	2	3	2	2 (1)	1	-	1	14 (2)
Meliphaga analoga/M. aruensis	Meliphagidae	E	INNE	5 (1)	4 (1)	5 (1)	8 (2)	5 (1)	7 (1)	8	10 (3)	1	53 (10)
Microdynamis parva	Cuculidae	E	FR	-	-	-	1	1	-	-	-	-	2
Microeca flavovirescens	Petroicidae	E	IN	-	-	2 (1)	1 (1)	-	2	2	2	1	10 (2)
Micropsitta pusio	Psittacidae		OM	-	-	3 (1)	6 (1)	12 (2)	4	2 (1)	13 (1)	8 (1)	48 (7)
Mino dumontii	Sturnidae	E	FRIN	-	-	-	-	-	-	-	1	-	1
Monarcha guttula	Monarchidae	E	IN	8 (1)	14 (7)	8 (1)	6 (3)	8 (3)	4	2 (1)	2	1	53 (16)
Monarcha chrysomela	Monarchidae	E	IN	-	-	1	1	2	1	3	4	1 (1)	13 (1)
Monarcha manadensis	Monarchidae	E	IN	5 (2)	4	2	-	-	5	1 (1)	-	-	17 (3)
Monarcha rubiensis	Monarchidae	E	IN	-	-	1	-	-	-	-	-	-	1
Myiagra alecto	Monarchidae		IN	3 (1)	1	-	-	2	-	-	1 (1)	-	7 (2)
Myzomela equea	Meliphagidae	E	INNE	-	1	-	-	-	-	-	2	-	3
Oedistoma pygmaeum	Melanocharitidae	E	INNE	-	-	-	-	1	-	-	-	-	1

Species	Family	Endemic	Trophic guild	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	Total
Pachycephala simplex	Pachycephalidae		IN	1 (1)	-	2	5 (1)	4 (1)	6 (2)	8 (2)	9	2	37 (7)
Paradisaea minor	Paradisaeidae	E	FRIN	-	-	-	-	-	-	-	1	-	1
Peltops blainvillii	Cracticidae	E	IN	-	-	-	-	-	1	-	-	-	1
Philemon meyeri	Meliphagidae	E	FRIN	-	2	-	-	1	-	3	1	-	7
Pitohui ferrugineus	Pachycephalidae	E	FRIN	-	-	3	1	-	-	-	-	-	4
Pitohui kirhocephalus	Pachycephalidae	E	FRIN	1	1	2	-	1	3	2	6	5 (1)	21 (1)
Pitta erythrogaster	Pittidae		IN	4 (1)	-	-	-	-	-	-	-	-	4 (1)
Pitta sordida	Pittidae		IN	1	-	-	-	-	-	-	-	-	1
Poecilodryas hypoleuca	Petroicidae	E	IN	6	4	-	5 (3)	2 (1)	2	-	2	-	21 (4)
Pomatostomus isidorei	Pomatostomidae	E	IN	-	-	-	1	5	6	1	3	-	16
Psittaculirostris edwardsii	Psittacidae	E	FRNE	-	-	-	-	-	1	3	7 (1)	5	16 (1)
Ptilinopus coronulatus	Columbidae	E	FR	-	-	1 (1)	2	-	-	1	7	2 (2)	13 (3)
Ptilinopus iozonus	Columbidae	E	FR	-	-	-	-	1	1	3	3	1	9
Ptilinopus magnificus	Columbidae		FR	-	-	-	2	2	5 (1)	9	9 (1)	-	27 (2)
Ptilinopus perlatus	Columbidae	E	FR	-	-	-	-	-	1	-	-	-	1
Ptilinopus pulcheus	Columbidae	E	FR	-	-	-	1	-	4	7	7 (1)	4	23 (1)
Ptilinopus superbus	Columbidae		FR	-	-	-	1	2	2	5	4	1	15
Ptilorhoa caerulescens	Eupetidae	E	IN	4	-	-	-	-	-	-	-	-	4

Species	Family	Endemic	Trophic guild	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	24-27	Total
Reinwardtoena reinwardtii	Columbidae		FR	-	-	-	-	-	-	-	2	1	3
Rhipidura leucothorax	Rhipiduridae	E	IN	2	1	-	-	-	-	-	-	-	3
Rhipidura rufidorsa	Rhipiduridae	E	IN	6 (2)	-	3 (1)	-	-	-	-	-	-	9 (3)
Rhipidura rufiventris	Rhipiduridae		IN	-	3 (2)	-	3 (1)	4 (1)	2	-	-	-	12 (4)
Rhipidura threnothorax	Rhipiduridae	E	IN	10 (1)	-	-	-	-	-	-	-	-	10 (1)
Syma torotoro	Alcedinidae		IN	-	-	1	-	-	-	-	3	1	5
Tanysiptera galatea	Alcedinidae		IN	19 (6)	5	4 (1)	4 (2)	3 (1)	5	1	4 (1)	-	45 (11)
Toxorhamphus novaeguineae	Melanocharitidae	E	INNE	9 (1)	7 (4)	3 (1)	12 (4)	5	6 (2)	11 (2)	5 (2)	2 (1)	60 (17)
Trichoglossus haematodus	Psittacidae		FRNE	-	-	-	-	-	-	-	-	4	4
Uroglaux dimorpha	Strigidae	E	CA	1	-	-	-	-	-	-	-	-	1
Xanthotis flaviventer	Meliphagidae		INNE	-	-	1	-	-	1	4	3	4	13

CHAPTER IV

Predation on artificial and natural nests in the lowland rainforest of Papua New Guinea

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Bird Study – accepted for publication

Abstract

Capsule: Report on nest predation rates in continuous and fragmented forest in underexplored tropical region.

Aims: To estimate natural nest predation rate in continuous primary forest, compare it with predation rates in forest fragments; assess the reliability of survival rates determined by the use of artificial nests with clay eggs; and identify the main nest predators.

Methods: We observed survival of natural nests during incubation period at continuous primary forest site. Some nests were monitored with infra-red cameras. We also used artificial nests deployed with clay eggs.

Results: We revealed a considerably high predation rate in natural nests (50% nests depredated). Clutch daily survival rates differed among nest types. Major predators of natural nests were snakes. Artificial nests daily survival rate (0.977) did not statistically differ from natural cup nests (0.969). Survival rate of artificial nests were similar in forest fragments and continuous forest. Forest fragments had, however, a higher proportion of avian predators than continuous forest.

Conclusion: Although, we observed similar survival rates in artificial and natural nests, the composition of nest predators was different between natural and artificial nests. Artificial nests were not suitable for estimating the real predation caused by reptiles. Nevertheless, we assume that participation of avian nest predators can be estimated correctly with the use of artificial nests.

Introduction

Nest predation is a major cause of avian nest failure (Ricklefs 1969, Martin 1993). It applies to tropical birds all the more, because they are considered to suffer from higher nest predation rates than birds breeding in temperate regions (Ricklefs 1969, Martin 1996, Remeš et al. 2012). Therefore, it can be expected that tropical habitats have a more diversified and abundant predator community causing a higher proportion of nest failure (Skutch 1966). Further, nest predation has been considered to be one of the drivers in the evolution of latitudinal differences of life history traits, e.g. smaller clutch size and many nesting attempts per year in tropical vs. temperate passerines (Cody 1966, Ricklefs 1980, Slagsvold 1982, Skutch 1985, Martin 1996, Martin and Clobert 1996). However, this paradigm has been questioned several times, since variation within regions can overshadow latitudinal differences (Snow and Snow 1963, Oniki 1970, Martin et al. 2007, Brawn et al. 2011). Within regions a substantial variation in nest predation was documented among different habitats (Martin 1993, Thompson and Burhans 2003, Martin et al. 2006) or with the degree of human impact on the environment (Martin and Clobert 1996, Spanhove et al. 2009). Predation rate can also differ interspecifically and seasonally (Robinson et al. 2000, Brawn et al. 2011).

Natural forests are globally becoming degraded and fragmented at an increasing rate (Wright 2005). Forest fragments of substantial size can host a relatively large proportion of the original avian diversity from intact forests (Laurance et al. 2002, Sam et al. 2014). The concern in relation to nest predation is associated with the extinction of the local avian population from forest fragments through decreased nest success (Willis 1974, Andren and Angelstam 1988). This is often caused by the disappearance of top predators from forest fragments, which can lead to an upsurge of previously downwards controlled nest predators (Terborgh et al. 2001, Sodhi et al. 2004). Decreased nest survival in forest fragments has been proved several times (Robinson 1995: U.S.A, Burke and Nol 2000: Ontario, Newmark and Stanley 2011: Tanzania). Nonetheless, various contradictory examples of reduced nest predation rates in tropical forest fragments were also witnessed (Maina and Jackson 2003, Spanhove et al. 2009, Visco and Sherry 2015). This may often be connected with increased human activities (e.g., hunting, increased population of dogs) substituting the effect of top predators, which in turn leads to a lower abundance of nest predators reducing the predation rate. This inconsistency suggests that the nest predation rate in forest fragments depends mainly on local conditions such as the composition of nest predators. Therefore, local knowledge on nest predation is extremely valuable for conservation planning as it can predict the effect on avian populations in small-to-large scale conservation areas that usually, sooner or later, become isolated.

Natural nests in the tropics are hard to find in sufficient numbers, hence most estimates of nest survival in tropical environments are based on artificial nests (e.g. Söderström 1999, Noske et al. 2008, Djomo et al. 2015). However, these estimates have been criticised (Faaborg 2004, Moore and Robinson 2004), mainly because depredation rates of natural and artificial nests may differ (Wilson et al. 1998, Buler and Hamilton 2000, Weidinger 2001, Mezquida and Marone 2003, Robinson et al. 2005a) and/or different predators prey on natural and artificial nests (Willebrand and Marcstròm 1988, Thompson and Burhans 2004). Thus, there is an urgent need to validate predation estimates and predator identity based on artificial nests by parallel studies on real nests (Moore and Robinson 2004).

We studied nest predation in the understory of lowland primary rainforest in Papua New Guinea, in a region with a high proportion of largely intact forest, where patterns in nest predation are still largely unexplored. Our main objectives were to: (1) estimate the survival rate of natural nests in continuous primary forest and its variation among seasons and years, with vertical position of nests and among different types of nests; (2) compare nest predation rates between natural and artificial nests; (3) assess whether survival rates of artificial nests differ between continuous and fragmented primary forest; and (4) identify the main nest predators using artificial clay eggs and a camera surveillance system for natural nests.

Materials and methods

Field data collection was carried out in lowland primary forest in Madang Province, Papua New Guinea in June - November 2013, January - June 2015 and December 2015 - April 2016. Two study sites were located within >10,000 ha of continuous lowland primary forest in the Wanang Conservation Area (1: 5°13.5’ S, 145°04.9’ E; 2: 5° 14.1' S, 145° 11.1’ E; 120 m asl). Three more sites were located in different fragments of primary forest surrounded by relatively densely settled and farmed landscape (Baiteta: 5°01.73’S, 145°46.01’E, 100 m asl, 1200 ha; Baitabag: 5°07.99’S, 145°45.47’E, 100 m asl, 600 ha; Ohu: 5°16.2’S, 145°41.1’E, 170 m asl, 300 ha). For more details on the study sites see Sam *et al.* (2014).

Artificial nests were constructed from halved tennis balls (Major et al. 1996, Noske et al. 2008). Each half tennis ball representing an open nest cup was painted dark brown (using water-based latex paint) and plant material (mainly moss) was glued on the outside of the cup. Nest cups were prepared at least one week prior to the start of the experiment in order that the paint and glue got aired and dried thoroughly. Moss was used as covering plant material according to our personal experience with natural nests from our study site. The artificial nests resembled mostly those of Monarch flycatchers (family Monarchidae), common understory birds. After Haskell (1999), we used two clay eggs placed in each artificial nest. Eggs were made from white modelling clay (Koh-I-Noor Hardmuth brand, Czech Republic). This type of modelling clay remained stable during high daytime temperatures and has been used for predation experiments before (Tvardikova and Novotny 2012). The scent of clay eggs can attract small mammals (Maier and Degraaf 2001). In order to avoid this bias, we rubber-coated the clay eggs (using PlastiDip) as described by (Purger et al. 2012). The eggs were ca. 2.5 x 1.5 cm in size and were moulded and coated seven days prior to the experiments, to allow eggs to dry completely.

Each artificial nest with two clay eggs was attached to a tree 1.0 - 1.5 m above the ground using a wire (see example of nest placement in Supporting information, Figure S1) and exposed for 14 days. Artificial nests were spaced a minimum distance of 40 m apart. We carried out regular nest checks every three or four days. During the nest visits, the surveyor wore wellington boots and rubber gloves in order to avoid leaving scent marks on the ground or the nest. Depredated nests (with visible predator imprints on clay eggs) were removed from the experiment, eggs were photographed and stored in plastic containers. In total, 122 nests were placed in continuous primary forest (92 placed at one site in the centre of the conservation area: 30 nests installed on 18 August 2013, 30 on 11 November 2013 and 32 installed between 31 January and 30 March 2015; other 30 nests were placed nearer the margin of the conservation area on 21 November 2013). Another 90 nests were placed in three primary forest fragments (30 nests placed in each fragment during the end of September 2013).

Natural nests (*N* = 161) were located either during targeted nest search or discovered accidentally by paraecologists and field assistants working on different research projects in our study area. Data on natural nests were collected within the continuous forest of Wanang Conservation Area during the entire period of our field work (2013, 2015 and 2016). Nests were photographed, their height above the ground measured and they were visited in 3 - 4 day intervals. Species were determined during nest visits (Table 1), when birds were flushed or sat tightly while we approached the nest. However, due to the very cautious behaviour of some species and the lack of published information on nest appearance of many local species, we were occasionally unable to identify the species of birds occupying monitored nests (*N* = 4 nests). Additionally, we used a digital infrared camera system to monitor predation events at 23 natural and 18 artificial nests. Nests in incubation period were monitored, but when hatchlings appeared we continued with video recording. We assembled the camera surveillance system from a waterproof car rear view infrared camera, connected to a digital video recorder and powered by a 12V car battery. Camera (black colour, width: 30mm, length: 42mm, 8 IR led lights (illumination = 0 Lux), angle of view = 120°) was installed in close distance from the nest (50-100cm). Digital video recorder, connected to the camera with 5m long cable, was placed into a plastic container on top of the car battery that was positioned on the ground. Recorder and battery were roofed with small (50cm × 50cm) camouflaged fabric. The recorder was set in continuous recording mode (resolution: 676 × 540, 30 frames per sec.).

We used the program Mark (White and Burnham 1999) to estimate the nest daily survival rate (DSR) and to examine the effects of explanatory variables on DSR (Dinsmore et al. 2002, Rotella et al. 2004). Natural nest visits were coded into Mark by specifying: 1) day when nest was found; 2) last day when nest contained eggs and 3) day when nest was found empty (for depredated nests) or the last day when nest contained eggs (for successful nests). Artificial nests were coded into Mark in three similar steps: 1) day of placement; 2) last day when clay eggs did not carry predator imprints and 3) day when predator imprints were found (depredated nests) or day of the last control (successful nests). Statistical significance of explanatory variables (year, time of year, nest type, nest height, forest type: continuous vs. fragmented, study site) was assessed by Likelihood ratio test. Hereafter, we refer to DSR of natural nests only within the incubation period. Natural nests that were abandoned, likely due to our activities ($N = 4$), were excluded from the analyses. Summaries of nest exposure period for different nest categories and species were counted by summing the number of observation days, while the period between last two nest checks (active vs. failed or active vs. hatched nest) was halved.

Additional data on abundances of potential avian predators were collected in June 2010, October 2010, January 2011 and June 2013 at exactly the same sites as our artificial nest experiment was conducted (Sam et al. 2014). Birds were surveyed by point count method. At each site, point counts were conducted at 16 points regularly spaced along a 2250-m transect (successive points were 150±5m apart to avoid double-counting). All points were at least 150 m from forest edge and all birds seen or heard within 50 m of the point were recorded. We started censuses 15 min before 6 AM and we counted birds for 15 min at each point so all 16 points were surveyed before 11 AM. Each transect was surveyed twelve times, resulting in 48 h of observation along each transect (Sam et al. 2014). We compared mean number of recorded individuals of 14 bird species for continuous (two sites) and fragmented forest (three sites). This analysis was computed by Wilcoxon matched pairs test in software Statistica 12 (pair represents mean abundance of given species in continuous and fragmented forest). We applied weights according to species potential for nest predation (medium = 0.5, high = 1, see Table S1).

Table 1. Number of nests (*N)* of given bird species found during the survey. Nests are classified, according to their shape, into a three types: open cup, platform, and enclosed nest with a side entrance. The nest occupants were identified to species in 148 cases (26 identified species), to genus in nine cases, and to family in one case, while four nests remained unidentified completely. Number of depredated nests (D), daily survival rate (DSR), exposure period (E) and length of incubation period (I) are summarized for individual species. The measured survival parameters refer exclusively to nests in incubation period.

Nest type	Species	*N*	D	E (days)	I (days	DSR
Cup	White-eared Catbird *Ailuroedus buccoides*	3	1	29.5	22	0.966
	Ochre-collared Monarch *Arses insularis*	5	3	56	14	0.946
	Little Shrikethrush *Colluricincla megarhyncha*	10	6	105	19	0.943
	Black Berrypecker *Melanocharis nigra*	1	0	6	14	1.000
	Long-billed Honeyeater *Melilestes megarhynchos*	1	0	17	17	1.000
	Shining Flycatcher *Myiagra alecto*	4	0	43	14	1.000
	Black-sided Robin *Poecilodryas hypoleuca*	7	2	83	14	0.976
	Rusty Pitohui *Pseudorectes ferrugineus*	3	0	60	20	1.000
	Sooty Thicket Fantail *Rhipidura leucothorax*	1	0	14	14	1.000
	Northern Fantail *Rhipidura rufiventris*	1	1	18	14	0.944
	Spot-winged Monarch *Symposiachrus guttula*	14	3	165	14	0.982
	Hooded Monarch *Symposiachrus manadensis*	6	3	51	14	0.941
	Monarch *Symposiachrus sp.*	3	2	18.5	14	0.892
	unidentified	3	1	26	14	0.962

Nest type	Species	*N*	D	E (days)	I (days	DSR
Enclosed	Papuan Babbler *Garritornis isidorei*	1	1	2	21	0.500
	Yellow-bellied Gerygone *Gerygone chrysogaster*	3	2	19.5	14	0.897
	Black Sunbird *Leptocoma aspasia*	1	0	14	14	1.000
	Philippine Pitta *Pitta erythrogaster*	5	2	78.5	14	0.975
	unidentified	1	1	1	14	0.000
Platform	Stephan's Emerald Dove *Chalcophaps stephani*	2	2	4.5	18	0.556
	Pigeons Columbidae	1	1	5.5	18	0.818
	Cinnamon Ground Dove *Gallicolumba rufigula*	7	5	79	18	0.937
	Cuckoo-Dove *Macropygia sp.*	1	1	1	17	0.000
	Wompoo Fruit Dove *Ptilinopus magnifica*	28	17	373	21	0.954
	Coroneted Fruit Dove *Ptilinopus coronulatus*	21	13	222.5	18	0.942
	Orange-bellied Fruit Dove *Ptilinopus iozonus*	6	2	83.5	18	0.976
	Beautiful Fruit Dove *Ptilinopus pulchellus*	10	7	88.5	18	0.921
	Fruit Dove *Ptilinopus sp.*	5	3	42.5	18	0.929
	Superb Fruit Dove *Ptilinopus superbus*	6	3	63.5	14	0.953
	Great Cuckoo-Dove *Reinwardtoena reinwardtii*	1	1	6	22	0.833

Results

In total we monitored 161 natural nests. Nests were constructed by 32 different species of birds (Table 1) at heights ranging from 0.0 to 9.5 m (median = 3 m) above ground. We recorded three types of nests based on the shape: platform, cup and enclosed nests (Table 1, Figure S2). All recorded natural nest failures during incubation period were caused by predation (evidenced by the disappearance of a clutch from the nest). Natural nest's DSR did not significantly differ among years (Table 2-3, 2013 (mean DSR±SE): 0.946±0.020, 2015: 0.951±0.013, 2016: 0.955±0.006), with time of year, nor with the height above ground (Table 2-3). However, DSR differed among the three recorded nest types (Tables 2-3). DSR (0.943±0.007) was lowest in simple platform type nests, built exclusively by species of the Columbidae family. Slightly higher DSR (0.949±0.020) was recorded for enclosed nests and the cup nests (typical for most of the studied passerines species) were characterized by highest DSR (0.969±0.007, Table 2).

Table 2. Number of sampled nests (N), Number of depredated nests (D), number of observation days and daily survival rate (DSR ± SE) of natural and artificial nests. Values are listed separately for different types of natural nests (cup, platform and enclosed nests) and artificial nests placed in continuous and fragmented primary forest. Natural nest survival was observed during incubation period only.

		N	D	Observation days	DSR (±S.E.)
Natural nests in continuous forest	cup	62	22	692.0	0.969 (± 0.007)
	platform	88	55	969.5	0.943 (± 0.007)
	enclosed	11	6	115.0	0.949 (± 0.020)
	all natural nests	161	83	1776.5	0.954 (± 0.005)
Artificial nests	continuous forest	122	26	1213.5	0.979 (± 0.004)
	forest fragments	90	21	790.0	0.975 (± 0.005)
	all artificial nests	212	47	2003.5	0.977 (± 0.003)

Table 3. Effect of explanatory variables (year, time of year, nest height above ground, species-specific length of incubation period and nest type) on natural nest survival during incubation period (Likelihood ratio test).

	df	Beta	SE	X^2	*P*
Year	2	-	-	1.580	0.454
Time of year	1	-0.015	0.007	1.199	0.274
Time of year^2	1	0.001	0.001	5.279	0.071
Nest height	1	-0.067	0.054	1.445	0.229
Nest type	2	-	-	7.685	0.021

We found no significant difference in the DSR of artificial nests between continuous and fragmented forests (Likelihood ratio test, $\chi^2 = 0.266$, df = 1, $P = 0.606$) nor among five different study sites (two in continuous forest and one in each of the three different forest fragments, Likelihood ratio test, $\chi^2 = 1.601$, df = 4, $P = 0.809$). Artificial nests exhibited a significantly higher DSR than all natural nests (Likelihood ratio test, $\chi^2 = 16.467$, df = 1, $P < 0.001$), but their DSR did not differ from that of the natural cup-shaped nests they most resembled (Likelihood ratio test, $\chi^2 = 0.970$, df = 1, $P = 0.325$, Table 2).

According to marks left by predators on clay eggs (impressions of jaws/beaks), artificial nests were depredated mostly by birds (68.1%, *N* (number of depredated nests) = 32), followed by mammals (17.0%, *N* = 8) and reptiles (10.6%, *N* = 5). In two cases (4.3%), we were unable to identify the type of predator. Clay eggs were also attacked by insects (e.g. ants or grasshoppers, 40.1% of all artificial nests, *N* = 85), but these cases were not considered as predation events. Birds caused predation of artificial nests at increased rate in forest fragments (85.0%, *N* = 17) than in continuous forest (55.6%, *N* = 15). The lower nest predation rate by birds in continuous forest was counterbalanced by increased predation from mammals and reptiles (Figure 1), thus the overall artificial nest survival rate did not differ between forest fragments and continuous forest. However, based on our point count surveys, we did not observe increased abundance of potential avian nest predators in forest fragments in comparison to continuous forest (Wilcoxon matched pairs test, $N = 14$, $T = 35.5$, $P = 0.484$).

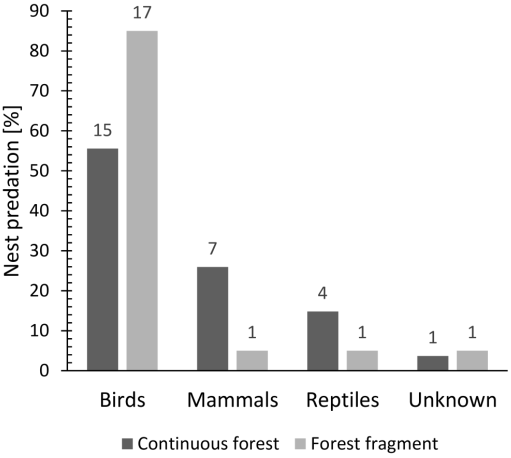

Figure 1. Participation (%) of different groups of predators on artificial nest predation in continuous forest and forest fragments. Numbers of recorded predation events are displayed above each bar.

Eight of the 23 natural nests and one of the 18 artificial nests that were monitored using infrared-cameras provided a record of nest predation events. Two out of the eight predations were recorded during nestling period. Four of the natural nests were depredated by snakes, three by birds and one by a mammalian predator. A single species of snake (Brown Tree Snake *Boiga irregularis)* is likely to have depredated all four nests (Little Shrikethrush *Colluricincla megarhyncha* - eggs, Philippine Pitta *Erythropitta erythrogaster* - chicks, Wompoo Fruit Dove *Ptilinopus magnifica* – egg and Beautiful Fruit Dove *Ptilinopus pulchellus* - chick). The obtained video material was not, in this case, suitable for species determination with absolute certainty, but the physical characteristics of the recorded snakes indicate this species. Two of the bird nest predators were birds of prey (Long-tailed Honey Buzzard *Henicopernis longicauda*, and an unidentified species) that depredated platform nests (Wompoo Fruit Dove and Cuckoo Dove *Macropygia sp.*, respectively) and the third was Black Butcherbird *Melloria quoyi* recorded while depredating the cup-shaped nest of Hooded Monarch *Symposiachrus manadensis.* The only mammalian predator was identified as *Antechinus sp.* – a carnivorous marsupial from the order Dasyuromorphia. This small arboreal marsupial depredated a platform type nest belonging to Coroneted Fruit Dove *Ptilinopus coronulatus.* The only video recorded predator at an artificial nest was a female King Bird-of-Paradise *Cicinnurus regius* that pecked the clay egg twice and left the nest.

We have composed a list of putative nest predators that are likely to be present at our study site (Table S1). Hereafter, we refer to nest predators that represent a medium to high risk for breeding birds. The most numerous potential predators, with 15 species, are birds (Figure 2). Concerning mammals, we expect that six species from the families Dasyuridae and Muridae engage in nest predation. Further, seven species of snakes rank among the potential nest predators. Of the other reptiles we expect that only agamas (genus: *Hypsilurus*) and two species of monitor lizards (*Varanus jobiensis* and *V. prasinus*) are likely to cause nest predation. The invasive cane toad (*Rhinella marina*) is the only potential amphibian nest predator.

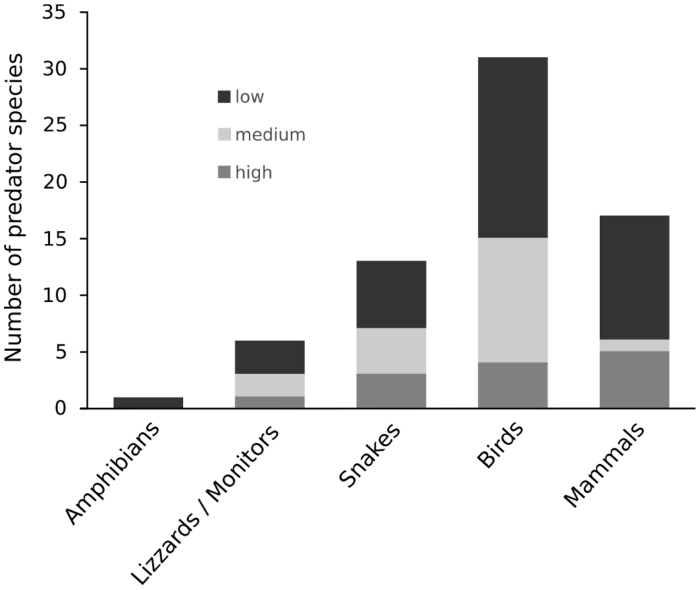

Figure 2. Number of species (genera where species are unknown) of different groups of potential predators that may participate in nest predation at our study site. Potential predators are separated into three categories according to the degree of probability that they are likely to cause and participate in nest predation (dark grey: low potential; light grey: medium potential; grey: high potential). Figure data source is located in Table S1.

Discussion

Time of year and specific year did not affect the natural nest DSR suggesting that abundances of predators were stable without pronounced between-year or seasonal fluctuations. Although the height of natural nests has been both positively (cavity nesting birds: Mahon and Martin 2006, platform nests: Newmark and Stanley 2011) and negatively (cup nests: Newmark and Stanley 2011) associated with nest survival, we did not evidence such a relationship within the forest understory where the height of nests varied between 0.0 - 9.5 m. Thus, it seems that height above ground did not affect the nest availability for predators at our study site. The fact that all predators recorded on video were capable to fly or climb trees only confirm this. Survival of natural nests varied among nest types. Typically, a higher survival rate has been reported for cavity compared to open-nesting birds (Martin and Li 1992, Robinson et al. 2000, Brawn et al. 2011). Our results showed that survival rate can also vary between different types of open nests. We found that simple platform nests suffered higher predation than cup-shaped nests. This is probably due to increased visibility of clutches, and is similar to what Newmark and Stanley (2011) reported from tropical Africa. As we mentioned earlier, this type of nest was built exclusively by phylogenetically distinct group (Columbidae), therefore the other possible explanation for lower survival may be found in shared incubation behaviour that led to increased predation rate compared to passerine species. Contrary to our results, Newmark and Stanley (2011) found that enclosed nests were the safest. However, we should note that the number of enclosed nests, we sampled, was rather low (*N* = 11).

New Guinea is part of Australasia, where we can, similarly to temperate vs. tropical America (Robinson et al. 2000), observe a latitudinal gradient in nest survival. Remeš et al. (2012) reported that birds from northern tropical Australia have lower nest survival rates (DSR ~ 0.965) than birds from lower temperate latitudes (DSR ~ 0.970). The latitudinal gradient may be extended further to New Guinea, because the DSR we observed was even lower. Further, this shows that the general presumption of poor nesting survival in tropical areas (Cody 1966, Ricklefs and Bloom 1977, Martin 1996, Robinson et al. 2000) applies likely also to New Guinean forest.

Our experimental nests were designed to mimic natural cup-shaped nests. In agreement, we found that their DSR was similar to that of natural cup-shaped nests. Nevertheless, we suspect that composition of predators may be different between artificial and natural nests, even though values of DSRs were similar. Half of the video-recorded predation events of natural nests were caused by snakes. This proportion is far higher than we found in artificial nests. Although based on low number of video-recordings (eight cases of natural nest predation), we assume that the proportion of predation caused by snakes may be under-rated in artificial nests. Similarly, Thompson and Burhans (2004) reported snakes as major predators of natural nests, while artificial nests were predated mostly by birds and mammals. We assume that our artificial clay eggs were unattractive to olfactory-orientated snakes and therefore, they were mostly predated by visually-orientated birds. Therefore, artificial nests of design we used can provide useful tool for detecting nest predation patterns (spatial or temporal differences) mainly in respect to avian predators.

DSRs did not differ between artificial nests placed in continuous and fragmented forest. This suggests that the avian inhabitants did not suffer from increased nest predation in fragmented forest. However, the composition of nest predators in forest fragments is likely to be different from that in continuous forest, since the proportion of predation events caused by birds was much higher in forest fragments. We could assume that abundance of birds that participated in nest predation was higher in forest fragments compared to continuous forest, where mesopredators (nest predators) are often released (Crooks and Soule 1999, Beier et al. 2002, Maina and Jackson 2003) after extinction of top predators. However, we did not document increased abundances of avian nest predators in forest fragments. Theoretically, the higher participation of birds in nest predation may have been caused by a compensatory nest predation. Birds in fragmented forests lost certain food resource that was formerly presented in continuous forest and instead they switched to nest predation. Our artificial experiment also documented low nest predation by mammalian and reptilian predators in forest fragments. We assume this is results of increased human activities and persecution of snakes and mammals in fragmented forests that are in the vicinity to human settlements.

It appears, based on our results obtained by natural nest surveillance, that New Guinea is another tropical region where snakes cause a high proportion of avian nest mortality. In Central America snakes were reported to be responsible for 80% and 89% of predation events: Robinson et al. 2005b, and Visco and Sherry 2015, respectively. The two regions may differ in temporal patterns of nest predation as all predations in Central America were recorded during the day (Robinson et al. 2005b, Libsch et al. 2008), while we recorded all four predation events caused by snakes at night. The predator we recorded was most likely Brown Tree Snake, a strictly nocturnal species of snake. This species is infamous for devastating the majority of the native bird population on Guam island, where it was accidentally introduced (Savidge 1987). It is probable that Brown Tree Snake represents a significant nest predator also in New Guinea, its native environment. Similarly, in Costa Rican lowland rainforest single species of snake (Puffing Snake *Pseustes poecilonotus)* caused 80% of all nest losses (Visco and Sherry 2015). Participation of other reptiles (e.g. monitor lizards, skinks; Table S1) in nest predation remains unclear, owing to the fact that we were unable to distinguish snakes from other reptiles based on jaw impressions in clay eggs and our cameras only recorded snakes.

Although the invasive cane toad was very abundant at our study site and this species was documented to predate ground nests in Australia (Boland 2004), we did not confirm its participation in nest predation. Mainly due to its ground habits we expect the cane toad does not represent asignificant threat to understory breeding birds, whereas the majority of them build nests in trees or shrubs above the ground.

The mammalian fauna of New Guinea includes only a few highly specialized nest predators (four carnivorous species at our study site: Table S1). Based on the results from the video surveillance system and artificial nests, we expect that mammals cause fewer nest predations than birds and snakes. Further, birds are probably responsible for a higher proportion of nest predation in New Guinea compared to Central America, where no bird predators were reported (Robinson et al. 2005b) or predation by birds was recorded only in one of 46 cases (Visco and Sherry 2015). However, four out of five nest predation events in Barro Colorado Island (Panama) were caused by birds (Tarwater 2008), which may be due to the artificial isolation of this island, altering the composition of nest predators.

In conclusion, our results indicate that the predation rate on natural nest was considerably high and it differed significantly among nest types. The DSR of artificial nests did not differ between continuous forest and forest fragments, but more birds predated the nests in forest fragments than in continuous forest. The DSR measured by artificial cup-shaped nests corresponded to the DSR of natural nests of similar type. However, more research, specifically video monitoring of natural nests, is needed to clarify the actual composition of nest predators and verify the results obtained by our experiments with artificial nests.

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Supporting information

Figure S1 Typical placement of artificial nests containing clay eggs.

Cup nests

Spot-winged Monarch (*Symposiachrus guttula*)

Little Shrikethrush (*Colluricincla megarhyncha*)

Enclosed nests

pendant nest: Papuan Babbler (*Garritornis isidorei*)

ground dome nest: Red-bellied Pitta (*Erythropitta erythrogaster*)

Platform nests

Coroneted Fruit-Dove (*Ptilinopus coronulatus*)

Wompoo Fruit-Dove (*Megaloprepia magnifica*)

Figure S2 Three different nest types (cup, enclosed and platform) observed in the study area.

TABLE S1 The list of putative nest predators. Only taxa that were recorded or are likely to be present in the lowlands of Madang province, where our study sites were located, are included in the list. The level of risk that predators represented to understory bird nests (inclination to nest predation) was estimated by combining information on diet, spatial habits (A-arboreal, SA-semi-arboreal, G-ground dwelling and the abundance of predators. The literature source is given when a report of nest predation was found. Potential predators were selected using resources/checklists on Papuan fauna: amphibians and reptiles: PBS – A Bishop Museum project (http://pbs.bishopmuseum.org/papuanherps/taxa.html, 2.6.2016) and O'Shea *et al.* 1996, birds: del Hoyo et al. 2016 and mammals: Flannery 1995.

Species	**Family**	**Spatial habits**	**Diet**	**Inclination to nest predation**	**Nest predation records**	**Literature resource of nest predation records**
Rhinella marina	Bufonidae	G	Insectivorous/carnivorous	Low	Y	Boland 2004, Beckmann & Shine 2012
Hypsilurus spp.	Agamidae	A	Insectivorous/carnivorous	Medium	N	
Eugongylus spp.	Scincidae	SA	Insectivorous	Low	N	
Lamprolepis smaragdina	Scincidae	A	Insectivorous	Low	N	
Tiliqua gigas	Scincidae	G	Insectivorous/carnivorous	Low	N	
Varanus jobiensis	Varanidae	A	Carnivorous	Medium	Y[a]	Soanes *et al.* 2015
Varanus prasinus	Varanidae	A	Insectivorous/carnivorous	High	Y[a]	Soanes *et al.* 2015
Candoia carinata	Boidae	A	Carnivorous	High	Y[a]	Berkunsky *et al.* 2011
Morelia viridis	Pythonidae	A	Carnivorous	Medium	Y[a]	Soanes *et al.* 2015
Morelia amethistina	Pythonidae	A	Carnivorous	Medium	Y[a]	Soanes *et al.* 2015
Leiopython albertisii	Pythonidae	SA	Carnivorous	Low	Y[a]	Soanes *et al.* 2015
Apodora papuana	Pythonidae	A	Carnivorous	Medium	Y[a]	Soanes *et al.* 2015
Tropidonophis spp.	Colubridae	A	Carnivorous	High	Y[a]	Bashir *et al.* 2012
Dendrelaphis spp.	Colubridae	A	Carnivorous	Medium	Y	Noske *et al.* 2008
Stregonotus spp.	Colubridae	G	Carnivorous	Low	Y	Brown *et al.* 2002
Boiga irregularis	Colubridae	A	Carnivorous	High	Y	Conry 1988
Toxicolamus spp.	Elapidae	G	Insectivorous/carnivorous	Low	N	
Rhinocephalus spp.	Elapidae	G	Insectivorous/carnivorous	Low	N	
Acanthophis spp.	Elapidae	G	Carnivorous	Low	N	
Micropechis ikaheka	Elapidae	G	Carnivorous	Low	N	

Species	Family	Spatial habits	Diet	Inclination to nest predation	Nest predation records	Literature resource of nest predation records
Casuarius unappendiculatus	Casuariidae	G	Mostly frugivorous	Low	N	
Megapodius decollatus	Megapodidae	G	Omnivorous	Low	N	
Talegalla jobiensis	Megapodidae	G	Omnivorous	Low	N	
Scythrops novaehollandiae	Cuculidae	A	Frugivorous/insectivorous	Low	N	
*Centropus menbeki**	Cuculidae	A	Insectivorous/carnivorous	High	N	
Rallina tricolor	Rallidae	G	Invertebrates	Low	N	
Tyto tenebricosa	Tytonidae	A	Carnivorous	Low	N	
Ninox rufa	Strigidae	A	Carnivorous	Low	Y[a]	Brown *et al.* 2002
Ninox connivens	Strigidae	A	Carnivorous	Low	Y[a]	Brown *et al.* 2002
Uroglaux dimoprha	Strigidae	A	Carnivorous	Low	N	
*Henicopernis longicauda**	Accipitridae	A	Carnivorous	High	Y[b]	
Aviceda subcristata	Accipitridae	A	Insectivorous/carnivorous	Medium	Y	del Hoyo *et al.* 2016
Harpyopsis novaeguineae	Accipitridae	A	Carnivorous	Low	N	
Aquila gurneyi	Accipitridae	A	Carnivorous	Low	N	
Hieraaetus weiskei	Accipitridae	A	Carnivorous	Low	N	
*Accipiter hiogaster**	Accipitridae	A	Carnivorous	Medium	N	
*Accipiter poliocephalus**	Accipitridae	A	Insectivorous/carnivorous	Medium	N	
Megatriorchis doriae	Accipitridae	A	Insectivorous/carnivorous	Medium	N	
Haliastur sphenurus	Accipitridae	A	Insectivorous/carnivorous	Low	Y	del Hoyo *et al.* 2016
Haliastur indus	Accipitridae	A	Insectivorous/carnivorous	Low	N	
*Dacelo gaudichaud**	Alcedinidae	A	Insectivorous/carnivorous	Medium	Y[a]	del Hoyo *et al.* 2016
*Pitohui dichrous**	Oriolidae	A	Frugivorous/insectivorous	Medium	N	
*Pitohui kirhocephalus**	Oriolidae	A	Frugivorous/insectivorous	Medium	N	
*Pseudorectes ferrugineus**	Pachycephalidae	A	Frugivorous/insectivorous	Medium	N	
*Philemon buceroides**	Meliphagidae	A	Omnivorous	Medium	Y	del Hoyo *et al.* 2016
Dicrurus bracteatus	Dicruridae	A	Insectivorous/carnivorous	Low	N	
*Cracticus quoyi**	Cracticidae	A	Insectivorous/carnivorous	High	Y[b]	
*Cracticus cassicus**	Cracticidae	A	Insectivorous/carnivorous	High	Y	del Hoyo *et al.* 2016
*Ailuroedus buccoides**	Ptilonorhynchidae	A	Omnivorous	Medium	Y[a]	del Hoyo *et al.* 2016

Species	**Family**	**Spatial habits**	**Diet**	**Inclination to nest predation**	**Nest predation records**	**Literature resource of nest predation records**
*Cicinnurus regius**	Paradisaeidae	A	Frugivorous/insectivorous	Medium	Y[b]	
Corvus tristis	Corvidae	A	Omnivorous	Low	Y[a]	del Hoyo *et al.* 2016
*Mino dumontii**	Sturnidae	A	Omnivorous	Medium	Y	del Hoyo *et al.* 2016
Antechinus melanurus	Dasyuridae	A	Carnivorous	High	Y[b]	Flannery 1995
Dasyurus albopunctatus	Dasyuridae	A	Carnivorous	High	Y	Flannery 1995
Murexia longicaudata	Dasyuridae	A	Carnivorous	High	Y	Flannery 1995
Myoictis melas	Dasyuridae	A	Carnivorous	High	Y	Flannery 1995
Echymipera kalubu	Peroryctidae	G	Omnivorous	Low	N	
Peroryctes raffrayana	Peroryctidae	G	Insectivorous	Low	N	
Phalanger gymnotis	Phalangeridae	A	Frugivorous/folivorous	Low	N	
Phalanger orientalis	Phalangeridae	A	Frugivorous/folivorous	Low	N	
Spilocuscus maculatus	Phalangeridae	A	Frugivorous/folivorous	Low	N	
Distoechurus pennatus	Acrobatidae	A	Omnivorous	Low	N	
Dactylopsila trivirgata	Petauridae	A	Insectivorous	Low	N	
Anisomys imitator	Muridae	A	Mostly herbivorous	Low	N	
Melomys platyops	Muridae	G	Mostly frugivorous	Low	N	
Melomys rufescens	Muridae	A	Mostly frugivorous	Low	N	
Pogonomys loriae	Muridae	A	Mostly frugivorous	Low	N	
Uromys caudimaculatus	Muridae	SA?	Omnivorous	High	Y	Flannery 1995
Rattus praetor	Muridae	SA?	Omnivorous	Medium	N	

a: records of nest predation for other members of the same family/genus

b: predation event recorded during our fieldwork

* avian species that were used for comparison of avian nest predators abundances between continuous and fragmented forest

CHAPTER V

Summary of results

« Summary of results »

Chapter II and III summarise spatial patterns of lowland rainforest bird community on small spatial scale, intentionally excluding regional differences that are caused by dispersal limitations and differences in species pools. Distribution of bird community in 50 ha plot in Papua New Guinea was determined primarily by topography. It shows that even relatively small altitudinal variability (around 100 m differences) together with heterogeneous terrain can shape the distribution of bird species and their overall abundance. I expected that distribution of tree species will influence spatial patterns of bird community as it can directly determine microhabitat productivity. My results indicate that this may apply to bird-plant spatial relationships although the importance of tree species composition appears to be less important than topography, because variability in topography is partly reflected in distribution of forest tree species. Structural parameters like density or number of trees per unit appear to be weak predictors of bird abundance and species composition. The important structural predictor was a growth successional stage (defined by the density ratio of old to young trees). Insectivorous birds were more abundant at early successional sites created by tree falls, while frugivorous birds tend to be more numerous in forest interior with prevalence of large trees. Further, we documented that most pair-wise species associations were random or positive, while negative associations between competitors were rare. Thus, we believe that at our scale of observations the inter-specific competition had a negligible effect on the patterns of species distribution in the 50 ha forest plot in Papua New Guinea.

My thesis further documents patterns in spatial distribution of birds along vertical forest strata. I surveyed vertical stratification of rainforest bird community with the use of ground to canopy mist nets. My results showed that rainforest birds are stratified in terms of species composition and overall abundance and diversity. Birds tend to be most abundant in the canopy and understory. The forest midstory had typically lowest abundance of birds. Diversity of rainforest species was greatest in the canopy. Vertical distribution of birds differed according to their trophic requirements. Abundance of insectivorous birds, the most species-rich trophic guild, was highest in the understory. Nevertheless, their species diversity was distributed equally along the vertical strata. Conversely, abundance of frugivorous and omnivorous birds was primarily confined to the canopy. Similarly, their diversity increased towards the canopy. In relation to foliage profile insectivorous birds preferred strata with thick vegetation whereas diversity and abundance of frugivorous birds increased negatively with vegetation density. My results document that ground to canopy mist-netting proofed to be a useful tool for the assessment of bird community vertical distribution. Moreover, a considerable number of bird species would not have been recorded by a ground-based census, due to their secretive life-style or preference for higher canopy strata.

Chapter IV represents a first complex study on nest predation conducted in New Guinea. Here I analysed the impact of nest predation on incubating birds in lowland continuous and fragmented rainforest. Nest predation was measured both experimentally on artificial nests and naturally observing real bird nests. 50% of natural nests in continuous forest were depredated, which represents considerably high nest predation rate typical for tropical regions. Daily survival rate differed among observed nest types (cup, platform and enclosed nests). Preliminary results of nest predator identity suggest that major predators of natural nests in New Guinea forest are snakes. Artificial nests exhibited a similar survival rate as the natural cup nests, which they were substituting. Fragmentation did not affect survival rate of artificial nests, underlining that nest predation does not contribute to increased extinction rate of birds inhabiting rainforest fragments in New Guinea.

My thesis contributed to understanding of several ecological aspects of rainforest bird community in remote and underexplored region. Moreover, the methodical approaches namely the use of botany datasets from forest dynamic plot and ground to canopy mist-netting are relatively innovative and may become a source of inspiration for further researches exploring spatial distribution of bird communities.

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PUBLICATIONS

Szefer P., Carmona C. P., **Chmel K.**, Konečná M., Libra M., Molem K., Novotný V., Segar S. T., Švamberková E., Topliceanu T. S. and Lepš J. 2017: Determinants of litter decomposition rates in a tropical forest: functional traits, phylogeny and ecological succession. *Oikos*. doi:10.1111/oik.03670

Chmel K., Riegert J., Paul L. and Novotný, V. 2016: Vertical stratification of an avian community in New Guinean tropical rainforest. *Population Ecology*, *58*(4): 535-547.

Chmel K. 2015: Statut ochrany ústřičníků celého světa. *Vanellus* 10: 138-140. – In Czech

Chmel K. 2014a: Hnízdní atlas bahňáků arktického Ruska (knižní recenze). *Vanellus* 9: 94-95. - In Czech

Chmel K. 2014b: Pozorování jespáka klínoocasého (Calidris acuminata) na tropické tahové zastávce – Papui Nové Guinei. *Vanellus* 9: 101-104. - In Czech

Chmel K. 2013: Za bahňáky Jižní Aljašky. *Vanellus* 8: 74-80. – In Czech

Chmel K. 2012: Složení potravy vodouše kropenatého (Tringa ochropus) a bekasiny otavní (Gallinago gallinago). *Vanellus* 7: 38-40. -In Czech

Chmel K. 2011a: Monitoring ptáků na jezeře Rusanda v Srbsku. *Vanellus* 6: 55–58. In Czech

Chmel K. 2011b: Koliha tenkozobá (Numenius tenuirostris) v roce 2010. *Vanellus* 6: 59. - In Czech

Chmel, K., Mulau Riegert, J., Paul, L., Mulau, M., Sam, K. and Novotný, V. Predation on artificial and natural nests in the lowland rainforest of Papua New Guinea. Bird Study – *Accepted for publication (18.10.2017).*

INTERNATIONAL CONFERENCES AND ORAL PRESENTATIONS

2014 Sociaty for Conservation Biology – Asia, Melaka, Malaysia

"Vertical stratification of avian forest community in Papua New Guinea"

- oral talk

TEACHING

2013 – 2016 (3x) University of South Bohemia

- teaching ornithology at the one week field course for first year students

2015 (November-December) FAO of the United Nations, New Guinea Binatang Research Center

- tutor on intensive ornithology training on lowland avifauna, Papua New Guinea

OTHER SKILLS AND ACHIEVEMENTS

2014 Australian Bird and Bat Banding Scheme

- became a holder of class A banding licence

2011 University of South Bohemia

- tropical ecology course, Papua New Guinea
- participation on the basis of selection procedure

2008 National Museum Praha, Czech Republic

- became a holder of bird ringing licence

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