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DOCTORAL THESIS

**Functional relationships between birds and fruits
on an elevational gradient in Papua New Guinea**

Richard J. Hazell

Submitted for the degree of Doctor of Philosophy

University of Sussex

September 2019

DECLARATION

I hereby declare that this thesis has not been and will not be submitted in whole or in part to another university for the award of any other degree.

Richard J. Hazell

25th September 2019

This thesis is a product of my own work and I have led the conception, data collection, analysis and writing of all chapters. The text conforms to a “papers style” format, in which chapters 2 – 5 take the form of discrete articles written in a style appropriate for publication in peer-reviewed journals. Chapters 1 and 6 provide a general overview and discussion of the field and research undertaken.

Chapter 2 is submitted to Journal of Biogeography as “Spatial scaling of plant and bird diversity from 50 to 10,000 ha in a lowland tropical rainforest” (authors: Richard J. Hazell, Kryštof Chmel, Jan Riegert, Luda Paul, Brus Isua, Graham S. Kaina, Pavel Fibich, Kenneth Molem, Alan J. A. Stewart, Mika R. Peck, George D. Weiblen, Vojtech Novotny). Author contributions are as follows:

- RJH and KC conceived the study; RJH, KC, LP, GSK and KM conducted the fieldwork (with help from local field assistants); RJH and KC analysed the data with assistance from JR and PF; RJH led the writing with inputs from KC and comments from VN, MRP, AJAS, PF, JR and GW.

Chapter 3 is in preparation for submission to *Ecology and Evolution* as “Comparing facets of avian alpha- and beta-diversity along a tropical elevational gradient provides insights into community assembly processes” (authors: Richard J. Hazell, Ondřej Mottl, Joseph Tobias, Bonny Koane, Samson Yama, Luda Paul, Katerina Sam, Alan J. A. Stewart, Mika R. Peck). Author contributions are as follows:

- RJH conceived the study; RJH, BK, SY and LP conducted the fieldwork (with help from local field assistants); RJH and OM analysed the data; JT provided bird trait data; RJH led the writing with inputs from OM and comments from JT, KS, AJAS and MRP.

Chapter 4 is written in a style appropriate for submission to an ecological journal (authors: Richard J. Hazell, Graham S. Kaina, Katerina Sam, Daniel Souto, Alan J. A. Stewart, Mika R. Peck). Author contributions are as follows:

- RJH conceived the study; RJH and GSK conducted the fieldwork (helped by local field assistants); RJH analysed the data with help from DS and advice from KS; RJH led the writing with comments from AJAS and MRP.

Chapter 5 is submitted to *Oikos* as “Bird preferences for fruit size, but not colour, vary in accordance with fruit traits along a tropical elevational gradient” (authors: Richard J. Hazell, Katerina Sam, Rachakonda Sreekar, Samson Yama, Alan J. A. Stewart, Mika R. Peck). Author contributions are as follows:

- RJH and KS conceived the study; RJH and SY conducted the fieldwork (helped by local field assistants); RJH led the data analysis with assistance from RS; RJH wrote the manuscript with contributions from KS and RS and comments from AJAS and MRP.

University of Sussex

School of Life Sciences

Division of Evolution, Behaviour and Environment

DOCTORAL THESIS

Functional relationships between birds and fruits on an elevational gradient in Papua New Guinea

Richard J. Hazell

Abstract

Birds constitute a vital component of tropical rainforests, filling a wide range of functional roles spanning from predation to seed dispersal to pollination. Tropical mountains are typified by high bird diversity, and provide a unique opportunity to examine changing intertrophic functional relationships within relatively small distances. However, the relationships between birds and their food resources along tropical elevational gradients are poorly understood. This thesis investigates various components of bird alpha- and beta-diversity along an elevational gradient in Papua New Guinea. It then focuses on an important tropical feeding guild (frugivores) and relates observed bird diversity patterns to those of fruits found along the gradient, concentrating on the functional relationships between them. Within a single (lowland) elevational band, bird beta-diversity was found to be very low. With increasing elevation on a

tropical mountain, high bird beta-diversity and declining alpha-diversity did not seem to be driven by direct climatic effects. Functional and phylogenetic declines with increasing elevation may be driven in large part by a loss of large frugivores towards upland forest, corresponding to a decrease in large fruits at high elevations. Indeed, frugivorous birds at high elevations preferentially selected smaller fruits than those at lower elevations when given a choice, suggesting a close functional connection between frugivorous birds and the fruits they disperse. This research highlights the importance of functional diversity in maintaining intertrophic dynamics, and demonstrates the need to think beyond the species or even habitat level when considering measures to best protect biodiversity in a way that maintains these dynamics. By focusing on the relatively undisturbed forests of New Guinea, this research has demonstrated the importance of intertrophic functional connections which may have been lost in more degraded habitats.

*Dedicated to the memory of Christine Gray,
who always wanted to read what I'd written so far*

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If doing a PhD is a punishing endeavour, then attempting to self-fund a PhD perhaps requires a special level of masochism. The unorthodox route I have taken to reach this point has been pretty bumpy at times, and it's fair to say I have probably had to rely on the support and kindness of others even more than the average PhD student does. This means there are a lot of people to thank. I'll try not to go on too long!

Firstly I'd like to thank my supervisors Mika and Alan, who have been ever-supportive and full of wise words of advice ever since I stumbled onto Sussex campus in late 2013 with the vague idea of doing an MPhil in biology. I like to think that over the last few years you two have been not only supervisors but have also become good friends (ahhh). Thank you also for giving me the opportunity to work in the rainforests of Papua New Guinea, something I could only have dreamed of in my younger life. I am grateful to Deeptima and Jörn for enabling me to turn that original MPhil idea into a PhD, and to Jeremy for helping me through the intermission process last year. Gracias to Paola for the many cups of tea as we discussed our progress over the years. It was great to see you in Ecuador too! Thanks to Martin J for being a great office mate, for all our silly conversations about nothing in particular and for all the help with R... I hope my payments in chocolate Hobnobs were sufficient. Thanks to Jo for all the fascinating stories about PNG, to Joanne for watering my plants! I'm also grateful to Knud in Copenhagen for letting me measure some of your birds there.

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CHAPTER 1

General introduction

“The forests of New Guinea are everywhere grand and luxuriant... and we cannot consider the collections yet made as affording more than very imperfect samples of the treasures they contain”

- Alfred Russel Wallace, 1879

1.1 Introduction

As human populations continue to expand, it is an unfortunate coincidence that the most biodiverse parts of the planet are also some of its most threatened. For example, tropical rainforests harbour the majority of the planet’s terrestrial diversity, but are under huge pressure from encroaching agriculture and resource exploitation: forest area across the tropics decreased by 7.8% from 1990 to 2010 (Kim et al. 2015). Knowing how most effectively to protect the remaining tropical forests relies on a better understanding of the networks of connections that make up these immensely complex ecosystems. One way of quantifying this complexity is by measuring functional traits of species that relate to the ways in which they interact with their environment. Indeed, an understanding of species’ functional roles and their importance in structuring intertrophic relationships may be more useful in terms of protecting habitats than simply knowing which species are present. With this in mind, large regions of undamaged forest whose functional relationships remain intact constitute a vital, and diminishing, study resource. The tropical island of New Guinea is one such region. This thesis explores functional diversity patterns of birds, the dominant vertebrate taxon in New Guinea, and their relationships with the forests they inhabit, in order to understand the processes driving bird diversity and their importance in maintaining ecosystem functions.

1.2 Species diversity on elevational gradients

While the latitudinal gradient in species richness is well recognised by naturalists and has been

studied extensively over many years (e.g. Fischer 1960, Stevens 1989, Gaston 2000, Kissling et al. 2012), elevational trends in species diversity are perhaps more complex and have received less attention. Nevertheless, different taxa are known to display contrasting patterns of diversity with elevation (McCain and Grytnes 2010, Guo et al. 2013). A number of meta-analyses have helped to reveal such patterns for a number of groups, which are briefly summarised here.

Rahbek (2005) found that most plant studies displayed mid-elevational peaks in species richness, challenging the earlier idea that plant richness generally decreases with elevation (Stevens 1992). Among insects, meta-analyses on elevational diversity patterns are generally lacking. Ants, however, are known to follow varying patterns in species richness, ranging from mid-elevational peaks to monotonic declines with elevation (Szewczyk and McCain 2016). In Neotropical regions a pattern of decreasing diversity and abundance with elevation, including a pronounced drop off above 1,500 m, was noted by Longino et al. (2014). Moth diversity was shown to follow similar patterns of low plateaus or low elevation peaks followed by decreasing diversity in sites across South East Asia (Beck and Kitching 2009). Vertebrate taxa, in a number of meta-analyses conducted by Christy McCain, also show a variety of different patterns (summarised in McCain and Grytnes 2010). Non-volant mammals showed a clear trend of mid-elevational peaks in species richness (McCain 2005), while bats showed a more mixed picture, displaying both mid-elevation peaks and decreasing richness patterns with elevation (McCain 2007a). Reptiles showed a range of patterns, although decreasing species richness with elevation was most commonly observed (McCain 2010). Finally, birds were found to display the most even spread of elevational diversity patterns of all taxa studied, with all of the aforementioned patterns (decreasing richness with elevation; low elevational plateau followed by a decrease, low elevation peak followed by a decrease and mid-elevational peak) represented almost equally (McCain 2009, McCain and Grytnes 2010).

A number of hypotheses have been proposed to attempt to explain the various species richness patterns displayed by different taxa across elevational gradients. Explanatory factors can be broadly categorised into direct abiotic factors such as temperature, water availability, soil quality and available land area, and indirect factors mediated through interaction with other organisms – these include habitat complexity, food availability and competition for resources (Hodkinson 2005, McCain and Grytnes 2010). Additionally, a mid-domain effect has commonly been proposed to explain mid-elevational peaks in species richness, whereby increasing overlap of species ranges in the middle of environmental (e.g. elevational) gradients leads to higher species richness at such mid-domain “meeting points” (Colwell and Lees 2000, Cardelus et al. 2005). In reality, diversity patterns with elevation are likely to reflect a complex interplay

between factors, whose relative importances differ depending on the taxon in question.

In the case of birds, McCain (2009) concluded that temperature and wetness of the different mountains studied were broadly responsible for the differences between elevational trends recorded. In wet tropical regions specifically, the general trend seems to be one of monotonically decreasing species richness with increasing elevation, as catalogued by several studies from across the tropics (Terborgh 1977, Jankowski et al. 2013, Dehling et al. 2014, Sam et al. 2019). In all cases, aspects of the biotic environment were found to be important factors contributing to the observed patterns, including tree species composition (Jankowski et al. 2013), habitat complexity (Jankowski et al. 2013, Sam et al. 2019) and food resources (Terborgh 1977, Sam et al. 2019). These studies highlight the importance of intertrophic interactions in shaping species richness patterns in complex tropical rainforest ecosystems.

1.3 Bird diversity: Patterns and processes

Local species richness (conventionally termed alpha-diversity) is, of course, only one aspect contributing to biodiversity as a whole. Another important component is beta-diversity (or turnover) which describes the change in species composition between communities (Whittaker 1960). Here, as with species richness, we see contrasting patterns depending on the taxon and environment under observation. The majority of studies investigating beta-diversity are focused either on broad regional-scale analyses (e.g. Qian et al. 2005, McKnight et al. 2007, Veech and Crist 2007, Zurita and Bellocq 2010, Tang et al. 2012) or on species' more local-scale responses to environmental gradients (e.g. Jankowski et al. 2009, Swenson et al. 2011). However, data are lacking on the beta-diversity of species communities at local to intermediate scales within relatively homogenous habitats. Here spatial factors such as dispersal limitation may be more important than environment in constraining species ranges (Myers et al. 2013). Lowland rainforest, for example, makes up a large percentage of total global forest cover but remains relatively understudied in terms of beta-diversity patterns. The evidence that we do have, for example from herbivorous insects in New Guinea (Novotny et al. 2007) and plants in Latin America (Condit et al. 2002), seems to suggest that low beta-diversity is the norm in the absence of environmental gradients such as rainfall (Condit et al. 2002, Ruokolainen and Tuomisto 2002) and seasonality (Davidar et al. 2007). As a highly mobile taxon less constrained by dispersal limitation than most, we should expect birds to be characterised by especially low beta-diversity in homogenous lowland forests. Chapter 2 explores this relationship in comparison with the much more sessile woody plants.

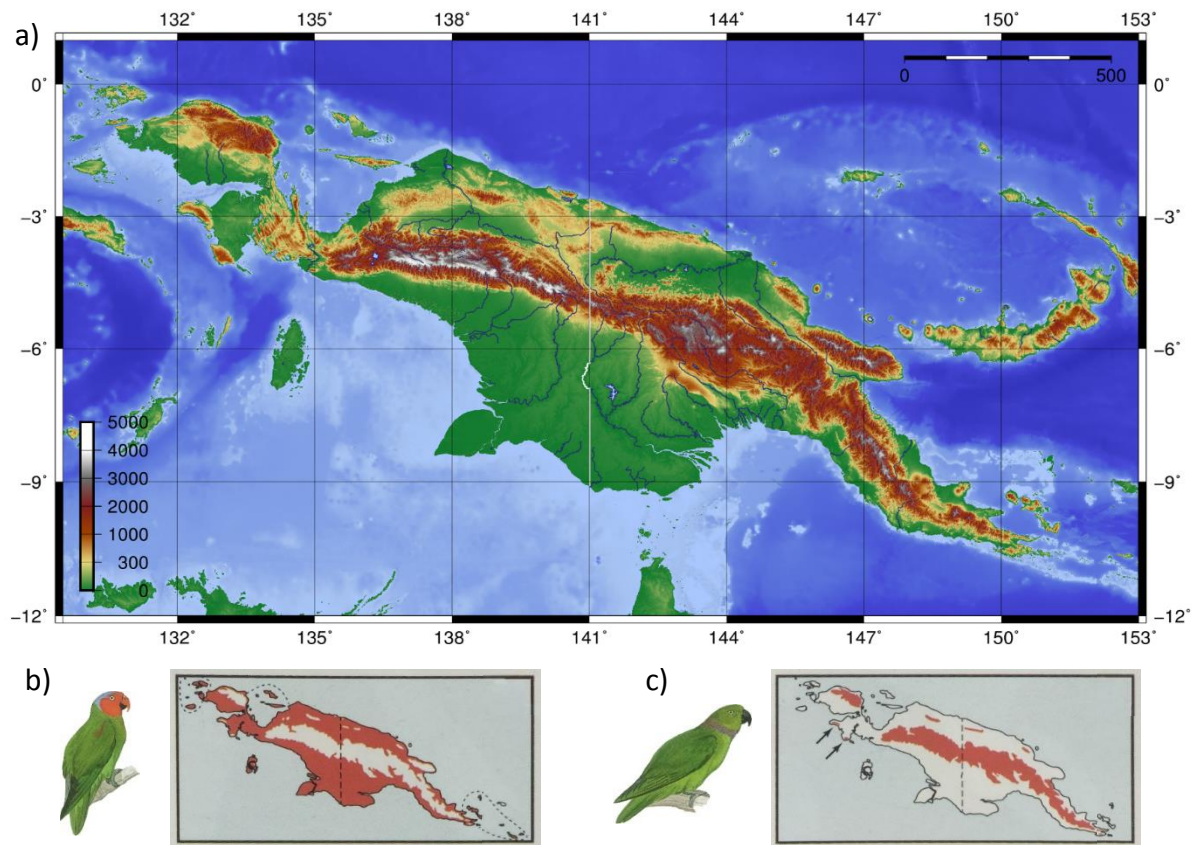


Figure 1.1. Topographical map of New Guinea and surrounding islands (a). Green colour represents lowlands below 300 m above sea level (asl) and brown represents highlands above 1,000 m asl. Horizontal scale bar in km. Range maps are provided for the red-cheeked parrot *Geoffroyus geoffroyi* (b) and blue-collared parrot *Geoffroyus simplex* (c), showing distinct elevationally defined distributions for both species. Such distribution patterns are common across many New Guinean bird taxa. Topographical map created using ETOPO1 Global Relief Model by Amante and Eakins (2009). Bird illustrations and range maps from Pratt and Beehler (2015). Bird illustrations by John C Anderton.

If beta-diversity patterns are driven primarily by environmental gradients, then tropical mountains form an ideal environment in which to study them. Here more than anywhere else on Earth climatic conditions change steadily and rapidly over relatively short distances (McCain 2009), meaning ecologists can avoid the logistical problems imposed by conducting fieldwork at regional or continental scales. New Guinea is characterised by high topographical diversity (Figure 1.1a), meaning it is ideally suited to the study of elevational effects on alpha- and beta-diversity patterns. The highest mountains of New Guinea's Central Range extend above the treeline located at approximately 3,700 m above sea level (asl), meaning a full range of possible forest types are represented. Birds in New Guinea, as in other parts of the world, are known to display strong beta-diversity patterns with changing elevation (Diamond 1973, Sam et al. 2019). Pratt and Beehler (2015) note that many bird taxa in New Guinea, in some cases up to family level, are restricted either to lowland or highland forest, with a transition zone around 1,500 m

asl (Figure 1.1b+c). However, while elevational trends in bird species communities are relatively well known in parts of New Guinea, the community assembly processes driving observed species alpha- and beta-diversity patterns are not.

Functional and phylogenetic approaches (see Box 1) may allow us to gain an understanding of the mechanisms responsible for observed patterns of alpha- and beta-diversity with changing elevation. Indeed, the importance of functional traits and phylogenetic relationships as means of

Box 1. Definitions

Functional Trait A morphological, behavioural or ecological feature of an organism that may be used to define its ecological role within a community.

Functional Diversity The diversity of functional traits present in a community, forming a measure of the range of ecological niches that are filled. As such, it reflects the ability of a community to maintain its ability to function effectively, for example in the face of external pressures.

Phylogenetic Diversity A measure of diversity that incorporates evolutionary relationships by accounting for phylogenetic distance between species. It reflects the taxonomic uniqueness present within a community, and its ability to produce evolutionarily unique solutions in response to change.

revealing various aspects of ecosystems overlooked by a focus on species have been emphasised in recent decades (Petchey and Gaston 2002, Isaac et al. 2007, Kraft et al. 2008, Swenson et al. 2012, Díaz et al. 2013, Newbold et al. 2014, Gagic et al. 2015, Voskamp et al. 2017, Cheesman et al. 2018). By contrasting taxonomic elevational diversity patterns with those of functional and phylogenetic diversity, we can start to understand whether, for example, species communities at a given elevation are constrained more by interspecific competition for resources or by abiotic environmental factors. The former (termed “niche differentiation”) should be represented as functional or phylogenetic over-dispersion, where interspecific competition for resources rather than the environment determines the limits of species’ coexistence, and species are consequently functionally and phylogenetically differentiated (Kraft et al. 2008). Conversely, functional or phylogenetic clustering may indicate “environmental filtering”, where abiotic filters restrict the range of traits that may be displayed in a community, and consequently coexisting species are more similar than expected by chance (Mouillot et al. 2007) (Figure 1.2). Environmental filtering should also manifest as higher than expected functional and phylogenetic turnover with increasing environmental divergence between sites (Siefert et al. 2013). Chapter 3 uses a functional and phylogenetic approach to examine the evidence for each of these processes occurring in birds along an elevational gradient.

While a focus on functional diversity may help us to understand community assembly processes in the broad sense, these processes alone may overlook some of the more specific mechanisms determining species occurrences at different sites. For example, abiotic environmental filtering

may be mediated through biotic factors such as habitat complexity and availability of food resources (Lebrija-Trejos et al. 2010, Best and Stachowicz 2014, Hanz et al. 2019). In a previous study along an elevational gradient in New Guinea, Sam et al. (2019) found insectivorous bird diversity to be driven primarily by food resources and habitat complexity. Frugivorous bird diversity, meanwhile, was shown to be related to fruit abundance on Mt Kilimanjaro (Ferber et al. 2014). When considering turnover between communities, a focus on individual traits (if they are related to ecosystem processes such as intertrophic interactions) has the potential to reveal information about the processes driving changes in community composition between sites. Chapters 4 and 5 use a trait-based approach to focus specifically on the relationships between frugivorous birds and fruits along an elevational gradient.

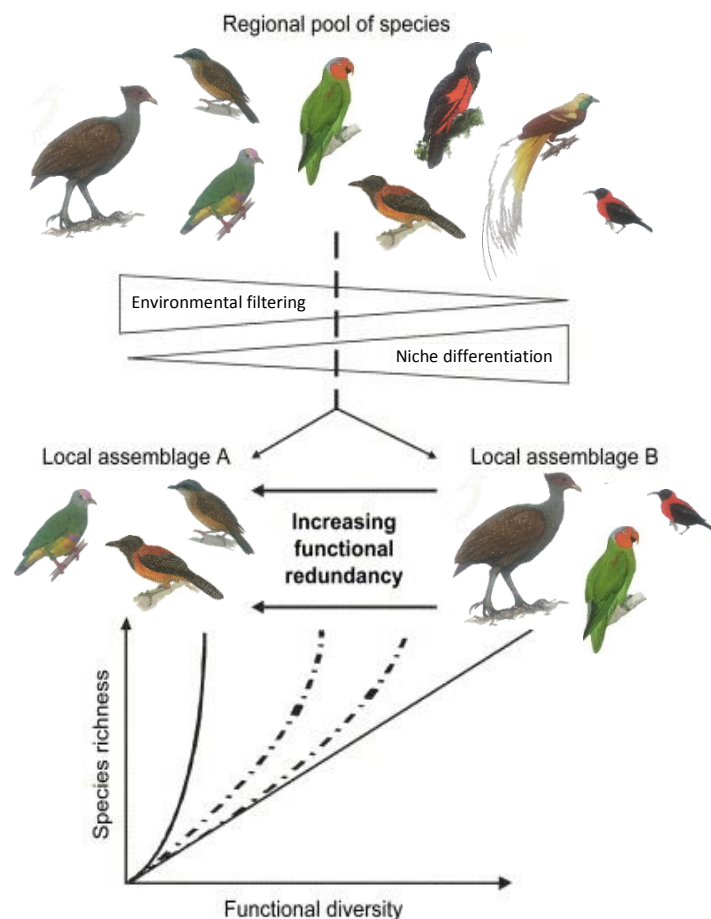


Figure 1.2. Framework detailing the relationship between functional diversity and community assembly processes. When environmental filtering is stronger than niche differentiation, functional redundancy is high in the resultant assemblage and functional diversity increases slowly relative to species richness. If niche differentiation is stronger than environmental filtering, functional diversity increases more rapidly relative to species richness as species display a wide range of functional traits. Dashed lines represent intermediate cases. Figure adapted from Mouillot et al. (2007). Bird illustrations by John C Anderton and Szabolcs Kóky from Pratt and Beehler (2015).

1.4 Frugivory and seed dispersal

The need for plants to disperse their seeds has intrigued biologists for many decades (Ridley 1930). While there is still debate on the evolutionary mechanisms behind seed dispersal, it likely confers a combination of benefits to plants including escape from density-dependent effects of natural enemies of the parent plant (Janzen 1970, Connell 1971), avoidance of resource competition from parents or siblings (Howe and Smallwood 1982) and the colonisation of sites with conditions favourable to seedling growth and survival (Wenny and Levey 1998, Wenny 2001). In turn seed dispersal is a key component in determining community assembly of plants (Chave et al. 2002, Levin et al. 2003). While plants have evolved numerous strategies to disperse their seeds, one of the most effective has proven to be through the evolution of fleshy fruits which are ingested by animals, allowing the dispersal of seeds via defecation or regurgitation. This mutualism dates at least as far back as the Carboniferous Period, from which there is evidence of cycad-like plants bearing fleshy fruits, presumably for dispersal by early reptiles (Howe 1986). Today seed dispersal by frugivores is widespread across the globe, although it is particularly prevalent in tropical regions (Snow 1981). Around 70 – 90% of tropical tree species are estimated to bear fleshy fruits that are primarily dispersed by vertebrate frugivores (Muller-Landau and Hardesty 2005).

Fruits have adapted to dispersal by a number of animal vectors including reptiles (Blake et al. 2012), fish (Galetti et al. 2008) and even insects (Hanzawa et al. 1988), but by far the majority of fleshy-fruited seed dispersal is by birds and mammals (Howe and Smallwood 1982). These two taxa clearly differ in the way they forage for and consume fruit. Notwithstanding the primates, terrestrial mammals are generally nocturnal or crepuscular foragers and use primarily olfactory cues when searching for food. Meanwhile the majority of birds possess acute colour vision and a poor sense of smell (Roper 1999), and feed during the day. Additionally, mammals have teeth and masticatory apparatus enabling them to chew fruits and consume them piecemeal, while birds do not (Lomáscolo et al. 2008). Other than pecking, a bird's only option when feeding on a fruit is to attempt to swallow it whole (Alcántara and Rey 2003). Birds (and bats) must also consider seed burden – the aerodynamic constraints imposed upon them by consuming seed “ballast” which is carried in the gut but does not provide any energy gain (Snow 1971).

It is logical to conclude that traits of the fruits consumed by mammals and birds should reflect the differing sensory abilities and physiological capabilities of each taxon. For example, we might expect mammals to preferentially feed on large fruits that provide maximum nutritional rewards for a given searching effort, and strong-smelling fruits that are easily located by olfaction. As

most mammals lack acute colour vision (Jacobs 1993), colour constraints are unlikely to be important for mammal-dispersed fruits. Therefore colours that impose fewer physical constraints on plants and are less attractive to seed predators are likely to be selected for (Schaefer and Schmidt 2004, Valenta et al. 2015, Valenta et al. 2018). Meanwhile, birds are likely to choose brightly coloured fruits that are easily visible against a background of foliage (Schaefer and Schmidt 2004). The limitations posed by gape size and limited ability to handle fruits should also affect the size of fruits selected by birds, imposing a maximum diameter for fruits selected by birds (Wheelwright 1985). According to the dispersal syndrome hypothesis (Van der Pijl 1969, Janson 1983, Gautier-Hion et al. 1985), fruit traits have evolved according to dispersal by different frugivore guilds. Thus we should expect to observe correlated evolution of combinations of relevant fruit traits in separate clades. However, some doubt exists on this adaptive hypothesis (Fischer and Chapman 1993). An alternative non-adaptive hypothesis suggests frugivore preferences match pre-existing combinations of fruit traits by a process called “ecological fitting” (Lomáscolo et al. 2008). Chapter 4 examines the evidence for adaptation of fruits to dispersal by birds and mammals.

While between-guild comparisons are perhaps the most obvious way to explore the relationship between fruit and frugivore traits, differing morphological constraints and preferences within a single frugivore guild may also be important. One notable example that has already been mentioned is that of gape limitation in frugivorous birds. Wheelwright (1985) noted that the gape size of birds should have predictable effects on the sizes of fruits selected by them, as had previously been observed in certain predation interactions (Zaret 1980). He found that the mean and maximum size of fruits consumed by birds correlated with their gape size, while minimum fruit size did not – large-gaped birds still fed on small fruits (Figure 1.3). Such a trend has important implications for the evolutionary pressures on fruit size. It suggests that plants maximise their probability of dispersal by producing small fruits which are available to a wider range of avian dispersers than larger fruits. However, germination and seedling survival rates may be higher for large seeds (Foster 1986, Alcántara and Rey 2003), which of course require correspondingly large fruits. This means fruit size could face an evolutionary trade-off between seed dispersal likelihood and survivability (Wotton and Kelly 2011).

If gape limitation is an important factor in determining which birds are able to feed on which fruits, then we might expect to see a correspondence between patterns of fruit size and frugivore gape size in a spatial context (Brodie 2017). Since Diamond's (1973) observations on the sizes of fruits preferred by different-sized New Guinean fruit doves, a number of studies have explored the concept of “trait matching” – that is, the covariation in functional trait

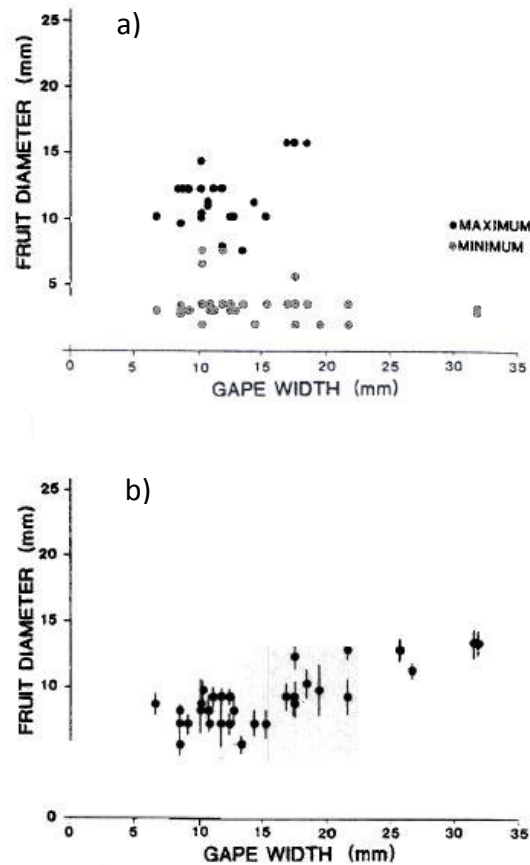


Figure 1.3. The relationship between gape width and sizes of fruits consumed by birds in the lower montane forests of Monteverde, Costa Rica. a) Maximal and minimal diameters of fruits included in the diets of 32 bird species are represented by black and grey circles respectively. b) Mean diameters of fruits consumed by birds are represented +/- 1 standard deviation (represented by vertical lines). Figure adapted from Wheelwright (1985).

diversities across trophic levels (Dehling et al. 2014). While this concept has indeed been explored in relation to fruits and frugivores across environmental gradients (Burns 2013, Dehling et al. 2014, Bender et al. 2018), such an approach cannot tease apart the evolutionary mechanisms that might have led to the observed complementarity of traits. For example, we should expect to see preferences for particular fruit traits based on the bird community found at each site: if a site is characterised by having large fruits and large-gaped birds, are large fruits preferentially chosen here? An experimental approach may be necessary to resolve this question. As previously discussed, tropical elevational gradients are often characterised by high beta-diversity, which provides the potential for rapid changes in trait values with changing elevation. Chapter 5 explores whether elevational trends in fruit size and gape size are closely related by testing fruit trait preferences of bird communities at different elevations. New Guinea, which is characterised by a prominent avian frugivore guild (Pratt and Beehler 2015),

makes an ideal study location to answer this question.

1.5 New Guinea and its avifauna

The tropical island of New Guinea is located in the south-western Pacific Ocean to the north of Australia and east of the Malay Archipelago. With an area of approximately 786,000 km² it is the world's second largest island (after Greenland) and is also its highest, reaching almost 5,000 m above sea level at its highest point. Politically divided between the Indonesian states of Papua and West Papua to the west and the nation of Papua New Guinea to the east, geographically its major division is roughly perpendicular to this. A rugged central mountain range extends 1,900 km west to east across the length of the island, bisecting lowland alluvial plains, broad river basins and smaller isolated mountain ranges to the north and south (Figure 1.1a). The island owes its topographical diversity in part to its complex geological history: originally part of the supercontinent of Gondwanaland and occupying the northern part of the Australian tectonic plate, New Guinea took its current mountainous form relatively recently during the Cenozoic Era with the convergence of the Australian and Pacific plates (Dow 1977, Baldwin et al. 2012). Its geological youth is today indicated by the presence of steep v-shaped valleys, cliffs, waterfalls and frequent landslides (Pieters 1982).

New Guinea's geological connection with Australia has had a strong influence on the fauna of the island. While the two landmasses are today separated by the shallow Arafura Sea and Torres Strait, they were connected as recently as 8,000 years ago before land bridges were submerged by rising sea levels after the last Pleistocene glaciation (Hudjashov et al. 2007). As a result of their shared history and frequent faunal exchange during glacial periods, New Guinea and Australia share a relatively large proportion of their vertebrate taxa, at least at broad taxonomic levels. In contrast, deep ocean channels to the west have maintained a permanent separation between Australia-New Guinea (termed "Sahul") and South East Asian landmasses (termed "Sunda") even during glacial maximum periods of low sea levels (Figure 1.4). As was noted by the 19th Century naturalist Alfred Russel Wallace (1860), this separation has led to relatively distinct faunas occurring in the two regions. For example, most placental mammal orders such as primates, carnivores and artiodactyls are absent from New Guinea, while monotremes and marsupial orders such as Diprotodontia (kangaroos and wallabies) are absent in Asia. A similar pattern can be observed in birds: lacking common Asian families such as pheasants, woodpeckers, trogons and bulbuls, New Guinea instead houses birds-of-paradise, bowerbirds and honeyeaters (Pratt and Beehler 2015).

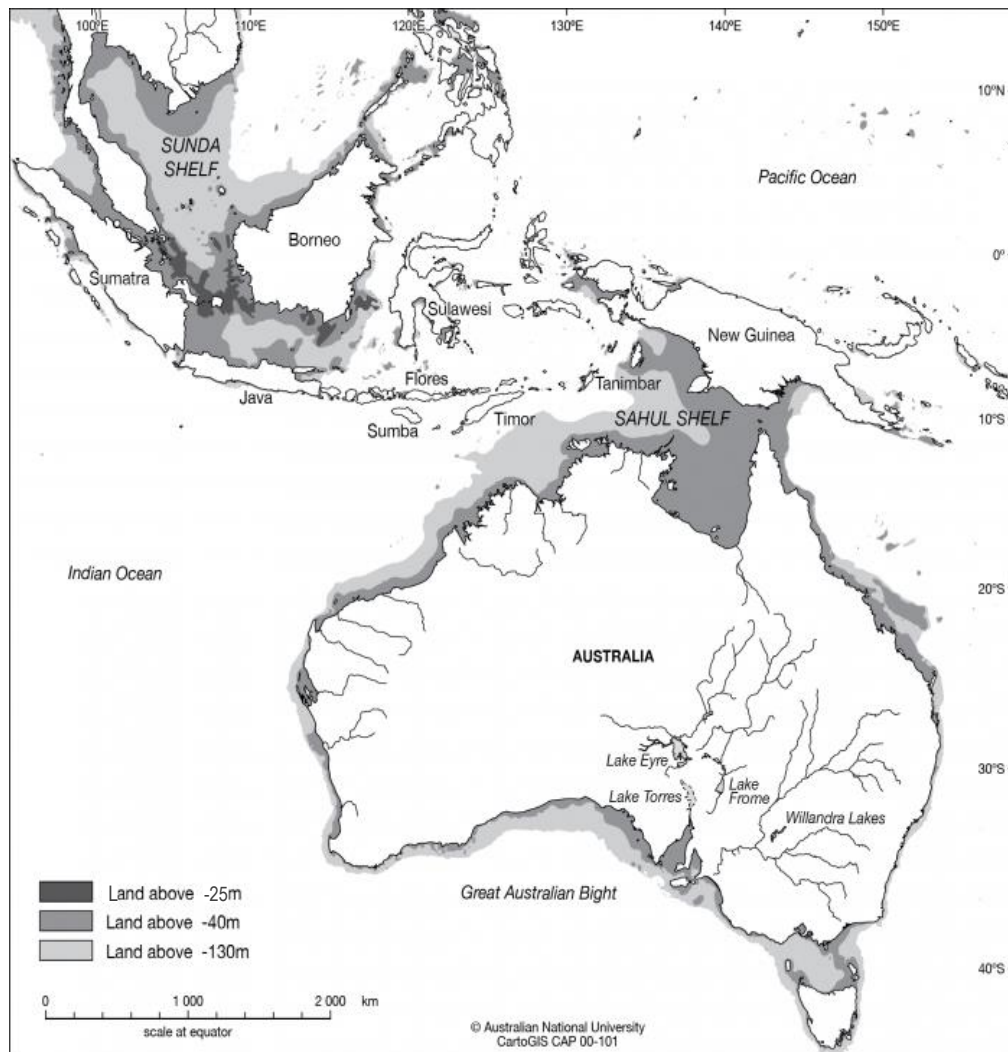


Figure 1.4. South East Asia, the Malay Archipelago, New Guinea and Australia, highlighting areas where the ocean floor is less than 25 m (dark grey), 40 m (mid grey) and 130 m below the surface (light grey). Sea levels during the last glacial maximum are estimated to be 120 – 135 m lower than today’s levels (Clark and Mix 2002), forming the landmasses of Sunda and Sahul. The region in between, sometimes termed “Wallacea”, is characterised by deeper waters that have provided barriers to dispersal even during glacial periods. Map adapted from CartoGIS Services, The Australian National University (2019).

A lack of large and diurnal mammals in New Guinea means that birds perhaps take on a relatively more important ecological role here than in many other parts of the tropics. For example, ecological niches such as diurnal frugivory are almost exclusively filled by birds in New Guinea (Fischer and Chapman 1993), whereas in most parts of the tropics primates and in some cases ungulates would also typically occupy these roles. New Guinea’s notable diversity of ground-feeding birds, including several species each of cassowaries, megapodes and ground pigeons, also indicates the radiation of birds into typically mammalian niches (Pratt and Beehler 2015). All told, this makes New Guinea a unique and highly appropriate place in which to study birds

and their ecological roles. This uniqueness is emphasised by a high level of endemism, despite the close biogeographical links with Australia. Of a total of 769 species and 110 families recorded in New Guinea, over 350 species and seven families – the satinbirds (Cnemophilidae), berrypeckers and longbills (Melanocharitidae), painted berrypeckers (Paramythiidae), berryhunters (Rhagologidae), ploughbills (Eulacestomatidae), ifrits (Ifritidae) and melampittas (Melampittidae) – are endemic (Beehler and Pratt 2016). Perhaps New Guinea's most famous residents, the aforementioned birds-of-paradise (Paradisaeidae) are mostly confined here as well, with 36 of 41 species endemic to New Guinea and its surrounding islands.

The unique and often spectacular nature of New Guinea's bird fauna has long attracted naturalists to the island. Since the days of Wallace, a number of prominent figures, such as Ernst Mayr in the 1930s-50s and Jared Diamond from the 1970s-present have made important contributions to ecology and evolutionary biology based in part on their expeditions to New Guinea. However, compared to most other parts of the tropics it remains relatively understudied. This is probably due mainly to the difficulties involved in working there, with steep terrain and a lack of infrastructure such as roads making access difficult and preventing the establishment of major field centres for international research.

The majority of bird species in New Guinea are forest specialists, inhabiting the broad swathe of rainforest and cloud forest that covers much of the island. Although it has come under increasing pressure in recent years from commercial logging, agriculture and extractive industries (Laurance et al. 2011, Bryan and Shearman 2015, Acosta and Curt 2019), New Guinean forests have so far escaped the large-scale destruction and degradation seen on similarly sized tropical islands such as Borneo, Sumatra and Madagascar. Consequently over 80% of its original forest remains intact, covering around 571,000 km² or 72.7% of the total land area of the island (Abood et al. 2015, Bryan and Shearman 2015). This represents the third largest area of contiguous tropical forest in the world, after the Amazon and Congo basins. As a result of its relatively stable history, very few birds in New Guinea are considered threatened: the IUCN lists only 3 species as endangered and another 21 as vulnerable (<http://www.iucnredlist.org>), while no species are known to have gone extinct historically (Pratt and Beehler 2015). However, a lack of protected areas coupled with high rates of illegal logging and poor governance in both Indonesia and Papua New Guinea makes the future less secure for New Guinea's avifauna (Laurance et al. 2011).

1.6 Aims of this thesis

In this thesis, I attempt to understand the processes responsible for driving avian alpha- and

beta-diversity patterns within a lowland rainforest site and along a continuously forested elevational gradient, while especially focusing on frugivorous birds and their functional relationships with fruit traits. To achieve this goal I use data collected during three separate field expeditions to Papua New Guinea from 2014 – 2017. The findings represent an original contribution to knowledge on various aspects of bird and plant diversity, as detailed below.

In **Chapter 2**, I investigate woody plant and bird alpha- and beta-diversity across a 10,000 hectare area of lowland rainforest – the Wanang Conservation Area (WCA). The site is located in the Madang Province of Papua New Guinea, in the Ramu river basin to the north of the island's Central Range (Figure 2.1). The chapter focuses specifically on the topic of spatial scaling of diversity estimates for woody plants and birds. It asks to what extent a 50 hectare Forest Dynamics Plot located within the conservation area is able to provide a representation of the broader scale diversity across a relatively climatically homogenous region of rainforest, focusing on differences in the patterns observed between the two groups.

Chapters 3 – 5 explore aspects of avian alpha- and beta-diversity along an elevational gradient located on the eastern slopes of Mt Wilhelm, at the northern edge of the Central Range (Figure 3.1). The gradient is located close to the WCA and spans vertically from a similar elevation (200 m asl) up to the treeline at 3700 m asl (Mt Wilhelm itself is Papua New Guinea's highest mountain reaching a total height of 4,509 m). Study sites are separated by 500 m in elevation, giving a total of eight sites, the lower six of which (200 – 2,700 m) are used in this study. The highest two sites were omitted for logistical reasons. **Chapter 3** focuses on bird diversity patterns with changing elevation along the gradient. It uses both functional trait and phylogenetic approaches in comparison with species patterns, in order to understand the processes responsible for structuring bird communities at different elevations.

Chapters 4 and 5 then focus on a specific feeding guild (frugivores) and its functional relationship with its food source (fruits). **Chapter 4** quantifies a number of fruit traits related to frugivory from fruiting plants surveyed along the gradient – size, proportion of seeds to pulp, colour and presentation – and assesses elevational changes in these traits. It then investigates the evidence for “fruit syndromes” – correlated evolution of fruit traits that indicate adaptation to different frugivore guilds. **Chapter 5** focuses specifically on avian frugivory, using an experimental approach with artificial fruits. It assesses avian attack rates on artificial fruits of different sizes and colours across three elevations, in an attempt to answer the question: do birds select fruits in accordance with real fruit traits (size, colour) and bird traits (gape size) across the gradient? The answer to this question may reveal whether birds are able to act as a selection pressure on fruit traits across elevations.

Finally, **Chapter 6** summarises the findings of each of the previous four chapters, before discussing the findings within a broader ecological context and suggesting avenues for further research. The implications of these findings are subsequently explored in the context of New Guinea and the conservation of its rainforests.

CHAPTER 2

Spatial scaling of plant and bird diversity from 50 to 10,000 ha in a lowland tropical rainforest

Abstract

While there exist numerous studies of diversity patterns both within local communities and on a regional scale, the intermediate scale of tens to thousands of km² is often neglected. Here we demonstrate whether woody plant and bird diversity measured within a 50 ha area provides an accurate representation of the surrounding 10,000 ha of forest in a lowland rainforest. Woody plants ≥ 5 cm DBH (diameter at breast height) and bird communities were surveyed at two spatial scales: inside a 50 ha ForestGEO plot and in the surrounding 10,000 ha Wanang Conservation Area in northern Papua New Guinea. Plant surveys used 20 x 20 m plots and bird surveys used point counts. For each taxon, species richness was compared across the spatial scales using rarefaction. Beta-diversity was calculated across the pooled datasets using Chao-Jaccard and Bray-Curtis dissimilarity indices. Woody plant species richness was lower within 50 ha than 10,000 ha, even when surveyed with identical sampling effort. In contrast, bird communities exhibited identical diversity and species accumulation patterns. The similarity in species composition (Chao-Jaccard) remained constant while the similarity in dominance structure (Bray-Curtis) decreased with increased distance between samples across the range from < 1 to 13.8 km for both plant and bird communities. The similarity decay was more rapid in plants, but in both cases was slow. In summary, we reveal low to zero beta diversity on the spatial scale from 1 to 14 km in a lowland tropical forest, particularly for birds but also for woody plants. A 50 ha plot provided a highly accurate representation of broader-scale diversity and community composition within 10,000 ha for birds, and a relatively good representation for woody plants. This suggests potential for wider generalization of data from ForestGEO plots that are almost always locally unreplicated, at least for those in lowland tropical forest.

Key Words: Beta-diversity, community composition, dissimilarity, forest dynamics plot, lowland rainforest, rarefaction, spatial scale, species richness

2.1 Introduction

Diversity patterns are scale-dependent (Willis and Whittaker 2002, Rahbek 2005, Jackson and Fahrig 2015), and various processes seem to determine diversity at different spatial scales (Rahbek and Graves 2001, Rahbek 2005, Reif et al. 2008). For example, Lennon et al. (2001) found that patterns of British bird species richness when measured at a scale of 10 km were statistically unrelated to those measured at a scale of 90 km. Inconsistency in methodologies make the study of diversity across spatial scales and taxa difficult (Whittaker et al. 2001, Barton et al. 2013) meaning the responses of different taxa to environmental heterogeneity have been little explored (Whittaker et al. 2001, Soininen et al. 2007, Barton et al. 2013). For instance, although the nature of the data obtained by surveys of plant and bird communities using vegetation plots and bird point counts respectively is essentially identical, comprising the list of all individuals from a defined area often between 0.05 and 1 ha, the two taxa are rarely studied simultaneously (but see Schulze et al. 2004).

Forest dynamics plots provide an effective means of assessing long term changes in biodiversity patterns of vegetation mapped in a great detail but on a relatively small spatial scale of 15 – 50 ha (Condit 1995). The Forest Global Earth Observatory (ForestGEO) now comprises a global network of such plots (Anderson-Teixeira et al. 2015). The comprehensive inventories of all woody plants ≥ 1 cm diameter at breast height (DBH) in these plots quantify plant species diversity in a standardised manner for forests across the tropics (Ashton 1995, Condit 1998). The detailed spatially explicit information on plants in forest dynamics plots presents an opportunity for complementary surveys of animal communities, including birds, which has not been used so far. Interestingly, most of the ForestGEO plots lack complementary estimates of plant diversity for the surrounding wider areas of 10 – 100 km², relying thus on extrapolation of species diversity patterns across wider spatial scales (Kochummen and LaFrankie 1990, Lee et al. 2002, Kenfack et al. 2007). Systematic quantitative surveys of biodiversity within tens to hundreds of km² of relatively homogeneous habitats, such as lowland rainforests, are rare, compared to local community data on the one hand and data on regional floras and faunas on the other (e.g. Novotny et al. 2006, Basset et al. 2012).

This study aims to fill two gaps in rainforest biodiversity studies by (i) providing detailed spatially-explicit data on community composition of birds within a 50 ha ForestGEO plot, thus matching similarly detailed information on plants, and (ii) examining the plant and bird data from the 50ha plot in the context of the surrounding 10,000 ha of lowland rainforest, focusing on the alpha and beta diversity patterns. Evidence for the level of beta-diversity in lowland tropical forest systems in particular is varied and often conflicting (Condit et al. 2002, Novotny et al. 2007, Kraft et al.

2011), with little consensus over whether such patterns are driven primarily by environmental factors, spatial factors such as dispersal limitation or by local stochastic processes (Veech and Crist 2007, Kraft et al. 2011, De Cáceres et al. 2012, Myers et al. 2013, Yang et al. 2015). By including data from both plants and birds and thus incorporating a broad trophic range, this study aims to provide a more complete picture of spatial diversity patterns than those produced by studies focusing on plants alone. Such studies currently comprise the vast majority of data from forest dynamics plots (e.g. Hubbell and Foster 1983, Condit et al. 1996, Plotkin et al. 2001, Lee et al. 2002, Volkov et al. 2005, 2009, Kenfack et al. 2007, Metz 2012, Chen et al. 2016). As such, this study is additionally the first to our knowledge to specifically assess the suitability of forest dynamics plots as a monitoring tool for assessing bird diversity.

2.2 Methods

2.2.1 Study site

The Wanang Conservation Area (WCA) comprises 10,770 ha of primary lowland rainforest in the Middle Ramu region of Madang Province, northern Papua New Guinea. The forest is classified as tropical, wet mixed evergreen (Paijmans 1976). The climate, with an average temperature of 25.8°C and annual precipitation of 4,000 mm (Vincent et al. 2015), has a mild dry season from July to September. Although a lowland site, the topography is variable and comprises steep ridges separated by a network of streams and rivers. The sample sites range in elevation between 80 and 250 m above sea level (asl), encompassing the full topographical range of the WCA. The 50 ha forest dynamics plot (FDP), part of the global ForestGEO network (Anderson-Teixeira et al. 2015), is located centrally within the WCA (Figure 2.1), and comprises a 1,000 x 500 m rectangle divided into 1,250 individual 20 x 20 m plots. Its location was selected in part to encompass as fully as possible the topographical range of the WCA, with elevation ranging from 90 to 180 m asl.

2.2.2 Vegetation surveys

Plants in the FDP were surveyed using a standard methodology for ForestGEO plots (see Anderson-Teixeira et al. 2015). That is, all free-standing trees with DBH \geq 1cm were tagged, mapped, measured and identified to species level. Only woody plants \geq 5 cm DBH were included in the present analysis. The WCA was surveyed by a regular grid comprising 43 sites 1.5 km apart, fitted to the conservation area using ArcGIS 10.02 (Figure 2.1). Each sample location included a single 20 x 20 m plot, mirroring the sample design of the FDP. All plant stems with DBH \geq 5 cm

were measured and identified within each plot. Data collection took place from 4 October to 17 December 2014 in the WCA and from 2010 to 2012 in the FDP. In addition to species composition, in each plot we collected data on canopy height, canopy closure, total tree basal area, number of stems and plot elevation. Canopy closure was calculated in Matlab version 2015a (Mathworks 2015) by measuring the mean percentage cover of foliage in four canopy photos from each 20 x 20 m plot, using code developed by Korhonen & Heikkinen (2009) (Appendix Figure A2.1). In the field, sample points were located using GPS (Garmin GPSmap 62s).

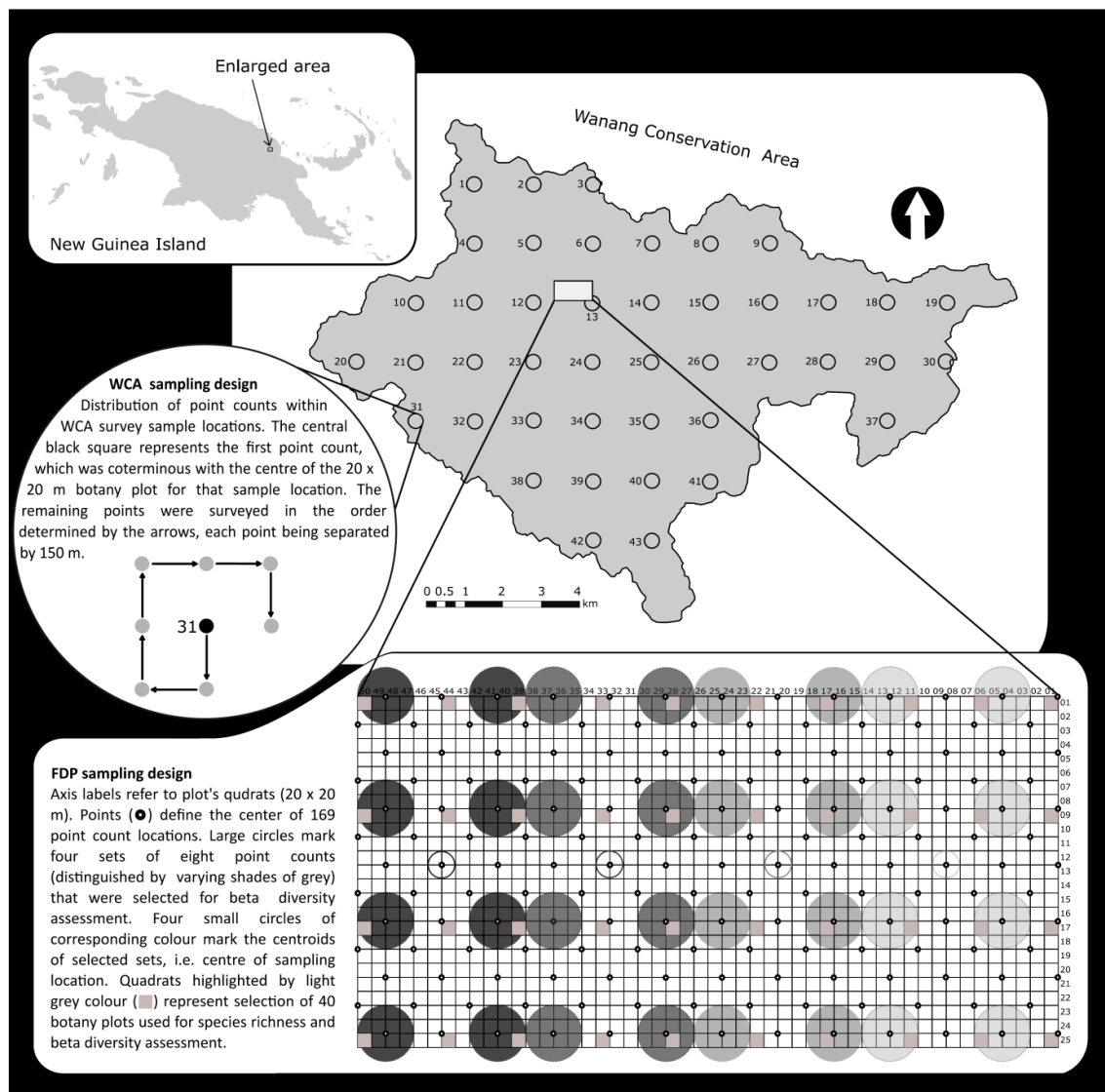


Figure 2.1. WCA map with 43 sampling locations and FDP represented by a rectangle adjacent to sampling location 13. Left and bottom insets display sampling design within WCA and FDP (respectively) for both woody plant and bird surveys and top left inset shows the geographic position of WCA within New Guinea Island. Bird surveys at sampling locations 1, 20 and 36 were omitted due to logistical constraints.

2.2.3 Bird surveys

Bird surveys were based on point counts. The FDP was surveyed using a regular grid of 169 points separated by 80 m along the horizontal and vertical lines parallel to the plot boundaries (Figure 2.1). Each point was used for one point count. Bird surveys in the WCA used the same 1.5 km grid as the vegetation surveys. 40 sample locations were sampled by eight point counts separated by 150 m, with the first point count being coterminous with the 20 x 20 m plot of the vegetation survey (Figure 2.1). This gave a total of 320 individual point counts.

Point counts followed the same protocol for both sets of surveys. Counts took place between 06.00 and 10.30 am, lasted 10 minutes and started after an interval of a few minutes following arrival at each point to minimise the effects of disturbance caused by arrival (Bibby et al. 2000). All individual birds seen or heard were recorded together with an estimate of their distance from the observer. Only birds estimated to be within 40 m of the observers were included in the analysis. In an effort to minimise multiple counts of the same individual, multiple conspecifics were recorded only if the observer could be sure they were different individuals (e.g. two birds singing simultaneously). Point counts were always conducted by two or three observers, one of whom was present across all surveys to minimize the effects of observer bias. During each point count, an audio recording was made using an Olympus LS-5 Linear PCM digital recorder. This enabled later identification of misidentified or poorly heard individuals. Field work took place from October 2014 to January 2015 in the WCA and from February to March 2015 in the FDP. Both surveys took place during the rainy season to minimise the effects of seasonal differences.

2.2.4 Data analysis

For both woody plants and birds, species richness for the FDP and WCA were compared using R version 3.4.2 (R Core Team 2013) and package *iNEXT* for rarefaction and extrapolation of species richness (Hsieh et al. 2016). For plants, 40 individual 20 x 20 m plots from within the FDP were selected to enable comparison of equivalent sampling effort with the WCA (Figure 2.1). Sample-based rarefaction and extrapolation curves for both plant and bird datasets were created using Hill numbers (with $q = 0$), i.e. species richness unbiased by abundances of individual species (Chao et al. 2014). A bootstrap method based on 999 random permutations of the data enabled the construction of confidence intervals and comparison of overlap at the maximum point for which sampling effort was equal (40 samples for plants; 169 samples for birds). In addition, the Chao 1 richness estimator (Chao et al. 2005) was calculated for each dataset to give an estimated value of asymptotic species richness.

For analysis of both plant and bird beta-diversity, data from the FDP and WCA were pooled. Plant beta-diversity was analysed using the 40 20 x 20 m plots from the FDP selected for the species richness analysis, providing a range of pairwise distances between plots from 0.1 to 1.12 km (Figure 2.1). When combined with the WCA plots, the maximum distance between plots was 13.8 km. For birds, individual sample locations combining eight point counts each were used as data points for the WCA. This data structure was mirrored in the FDP by creating four sets of eight adjacent point counts (spaced 160 m apart; Figure 2.1) used as equivalents of the WCA sample locations. The Bray-Curtis dissimilarity index and the Chao variant of the Jaccard dissimilarity index were then calculated for each pair of sample locations, using the “vegan” package in R (Oksanen et al. 2018). The choice of one abundance-based index (Bray-Curtis) and one presence-absence index (Chao-Jaccard) enabled us to explore the dominance effect by comparing the relative importance of common versus rare species in dictating overall community turnover. The community dissimilarity was correlated with distance by plotting the Bray-Curtis and Chao-Jaccard matrices against a between-site distance matrix, using a Mantel test (9999 permutations) with Pearson’s correlations.

In order to determine the relative importance of spatial and environmental variables in determining woody plant and bird community composition, we used Canoco 5 (Smilauer and Leps 2014) to perform a Principal Coordinates of Neighbouring Matrices (PCNM) analysis using Canonical Correspondence Analysis (CCA) for the woody plant dataset and Redundancy Analysis (RDA) with forward selection for the bird community dataset. Based on the length of the first Detrended Correspondence Analysis axis, Canoco 5 recommends either a unimodal (CCA) or linear (RDA) method. The PCNM approach enabled us to separate the effect of space predictors (represented by spatial eigenfunctions corresponding to spatial relationships among the sampling sites) from the effect of primary (environmental) predictors (Legendre and Legendre 2012). The analysis included nine steps: primary predictor test, primary predictor selection by CCA, principal coordinate analysis (PCoA), PCNM for all predictors, PCNM selection, spatial effects analysis, primary predictor effects analysis, joint effects analysis and removal of spatial effects (Smilauer and Leps 2014). Elevation of vegetation plots was tested as the environmental primary predictor of woody plant composition. In the case of bird community composition we included the following potential predictors in the analysis: canopy closure, tree basal area, total DBH of small (5 – 10 cm DBH) and large stems (> 40 cm DBH), diversity of trees (Simpson Index) and elevation of sampling location. Elevation was averaged over eight sample points for a given sampling location.

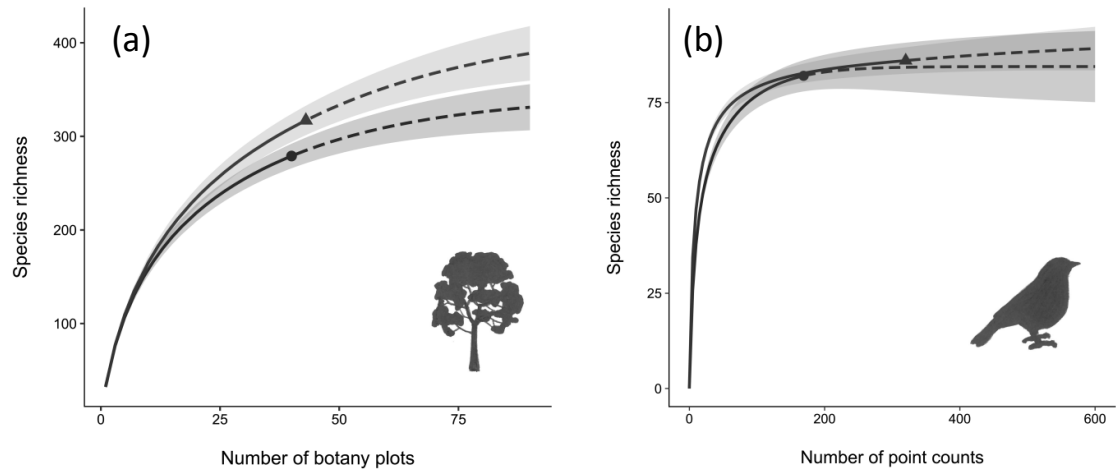


Figure 2.2. Woody plant (a) and bird (b) species richness represented by rarefaction curves for WCA (black triangle) and FDP (black circle). Solid lines show interpolated rarefaction curves. Dashed lines represent extrapolated rarefactions exceeding our sampling effort. Shaded areas represent $\pm 95\%$ confidence intervals. Species accumulation was calculated for plants across 20 x 20 m botanical plots, for a total of 43 (WCA) and 40 (FDP), and for birds by individual point count for a total of 320 (WCA) and 169 (FDP) points.

2.3 Results

2.3.1 Species richness of woody plant community

We recorded a total of 4,060 individual woody plants ≥ 5 cm DBH, representing 379 species, across both surveys. A total of 2,119 individual woody plants ≥ 5 cm DBH were recorded across the 43 sample locations of the WCA survey, representing a total of 317 species. The 40 plots taken from the FDP survey contained 1,941 individual woody plants ≥ 5 cm DBH from 279 species. A total of 217 species (57.3%) were present in both surveys. 68.5% of species and 90% of individuals found in the WCA were also present in the FDP, while 77.8% of species and 94.1% of individuals found in the FDP were present in the WCA. The rarefaction curves from both surveys do not appear to approach an asymptote, suggesting greater sampling effort is necessary in order to achieve accurate species richness estimates (Figure 2.2). Nevertheless, the Chao 1 richness indicator estimated asymptotic species richness values of 403 (WCA) and 339.1 (FDP). From observed and extrapolated species richness (Figure 2.2) a clear separation can be observed between species rarefaction curves for the two surveys. The lack of an overlap of 95% confidence intervals for the plant data indicates a significantly higher species richness across the WCA than in the FDP. However, despite the difference in species richness, woody plants from the two surveys show very similar dominance structure patterns (Figure 2.3).

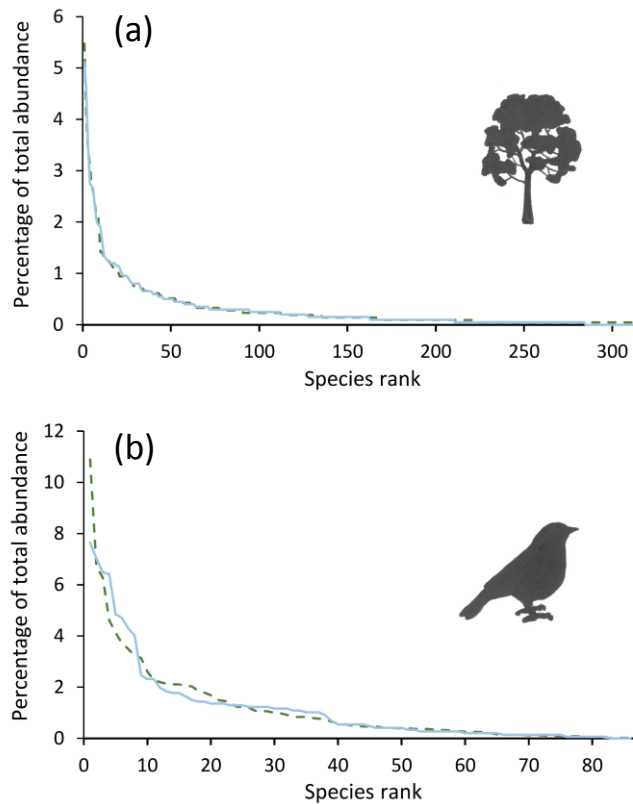


Figure 2.3. Woody plant (a) and bird (b) rank dominance for WCA (dashed line) and FDP (solid line). Curves show the percentage of all individuals represented by each species. N (plants) = 317 species (WCA) and 279 species (FDP). N (birds) = 86 species (WCA) and 82 species (FDP).

The results described above are supported by a comparison of the WCA dataset (40 plots) and the full FDP dataset (1,250 plots). The total species richness (452 species) in the latter dataset covering the entirety of the FDP is higher due to a strikingly more intense sampling effort. Nevertheless, the WCA dataset still comprises 53 (16.7%) unique species (7.3% of individuals) that did not occur in the full FDP dataset.

2.3.2 Species richness of bird community

We recorded a total of 6,389 individual birds of 93 species across both surveys. This included 4,976 individuals of 86 species from the 320 point counts in the WCA and 1,420 individuals of 82 species from the 169 point counts in the FDP. Community composition was similar between the two surveys. A total of 79 species (84.9%) were present in both surveys. 91.9% of species and 99% of individuals from the WCA were also present in the FDP, while 96.3% of species and 99.6% of individuals found in the FDP were present in the WCA. In contrast to plants, rarefaction curves showed no significant difference between the two datasets (95% CI) for 169 point counts, the highest sample size available for both WCA and FDP (Figure 2.2). This overlap persisted even

when using 84% confidence intervals (Appendix Figure A2.2), a technique which has been shown to robustly mimic 0.05 pairwise statistical tests when comparing species richness values (MacGregor-Fors and Payton 2013). Moreover, unlike woody plants, rarefaction curves for both bird survey datasets closely approach an asymptote (Figure 2.2). Extrapolation using the Chao 1 richness indicator produced estimated asymptotic species richness values of 91 (WCA) and 83.9 (FDP). Species rank abundance curves (Figure 2.3) are similar in shape for the two surveys, although the most common species represented a higher proportion of records at WCA (*Pitohui kirhocephalus*, 10.9% of records) than the FDP (*Meliphaga* sp., 7.6%).

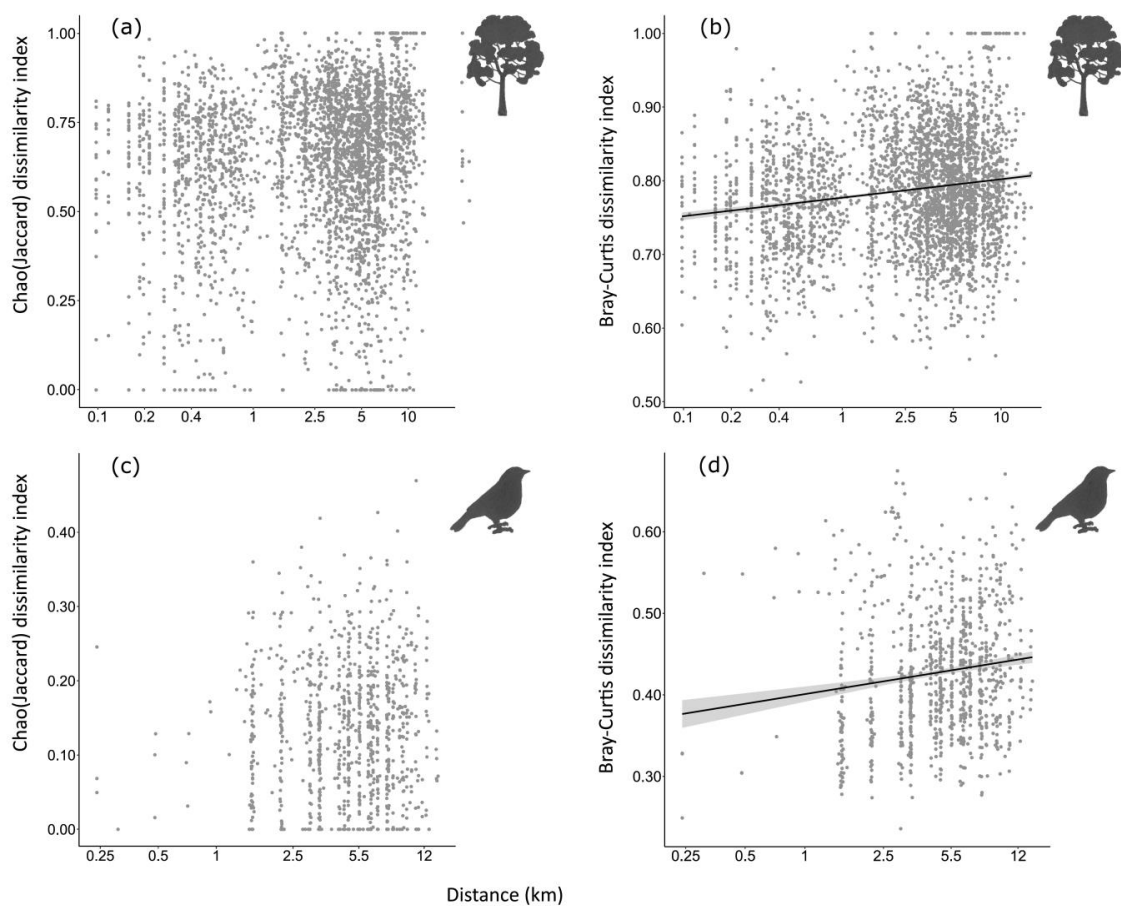


Figure 2.4. Pair-wise relationships of beta diversity indices and geographical distances between sampling sites. The relationship is shown for woody plants (a, b) and birds (c, d). We used two dissimilarity indices: Chao-Jaccard (a, c) and Bray-Curtis (b, d). Linear approximation with shaded area representing standard error was used for significant relationships (Mantel test, $p < 0.05$).

2.3.3 Beta-diversity

We found a non-significant (although marginal) relationship between pairwise distance and dissimilarity in plant community composition when measured using the Chao-Jaccard

dissimilarity index (Mantel test, 9999 permutations, $r = 0.09$, $p = 0.07$; Figure 2.4a). When using the Bray-Curtis index, the dissimilarity of plant communities significantly increased with geographic distance (Mantel test, 9999 permutations, Mantel $r = 0.14$, $p = 0.03$; Figure 2.4b). Similarly, when using the Chao-Jaccard dissimilarity estimator, we did not record a significant relationship between bird community dissimilarity and inter-site distance across the pooled WCA/FDP sample locations (Mantel test, 9999 permutations, Mantel $r = 0.03$, $p = 0.3$; Figure 2.4c). However, measuring beta diversity with the Bray-Curtis index did show a positive relationship between community dissimilarity and distance (Mantel test, 9999 permutations, $r = 0.13$, $p = 0.03$; Figure 2.4d).

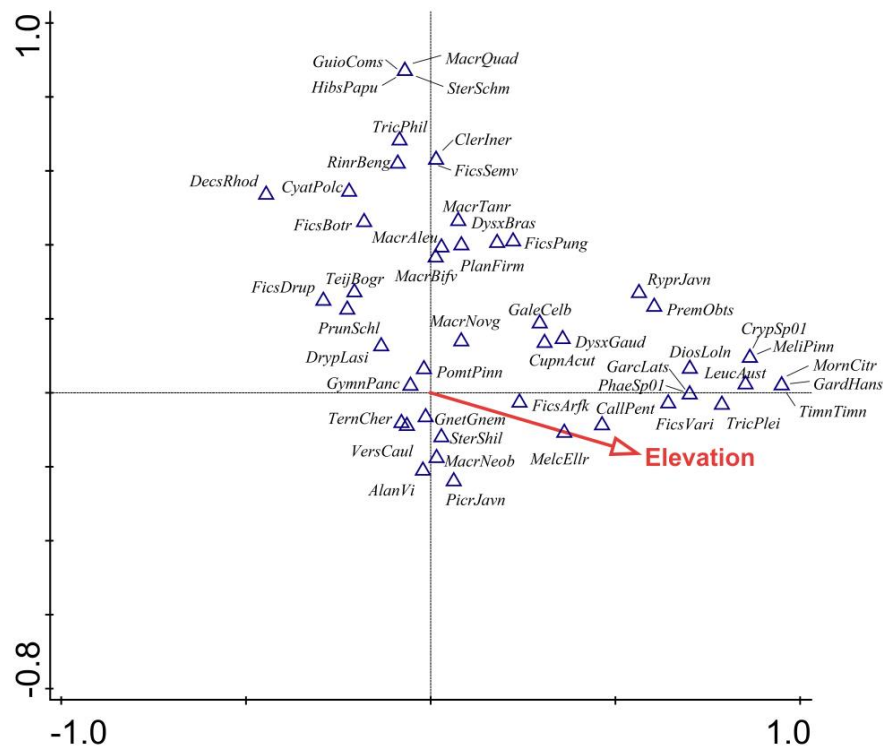


Figure 2.5. Canonical correspondence analysis (CCA) ordination diagram showing composition of woody plants (centroids with plant species codes) and influence of elevation as a primary predictor after the effect of space was filtered out (total variation = 10.079, axis 1 eigenvalue = 0.236, axis 2 eigenvalue = 0.195). The diagram displays 50 species with the highest fit value. Elevation was positively correlated with the first ordination axis (correlation coefficient = 0.43) and negatively correlated with the second ordination axis (-0.36). Species optima of several woody plant species (e.g. *Callicarpa pentandra*, *Ficus arfakensis*, *Ficus variegata* and *Melicope elleryana*) were found in plots located at higher elevations, i.e. on ridges. Other species such as *Drypetes lasiogynoides*, *Ficus drupacea*, *Gymnacranthera paniculata*, *Pometia pinnata* and *Prunus schlechteri* responded negatively to elevation and tended to occur more in valleys. Full species names for the species codes displayed are provided in Appendix Table A2.1.

2.3.4 Effect of environmental variables

A significant proportion of variation in woody plant species composition was explained by elevation of sampling locations (CCA; $F = 1.6$, $p < 0.01$, 22% of explained variation; Figure 2.5). Spatial structure of sampling locations, however, accounted for larger proportion of explained variation (77.1%). The primary (elevation) and space predictors shared 0.9% of explained variation and together they explained 9% of the total variation.

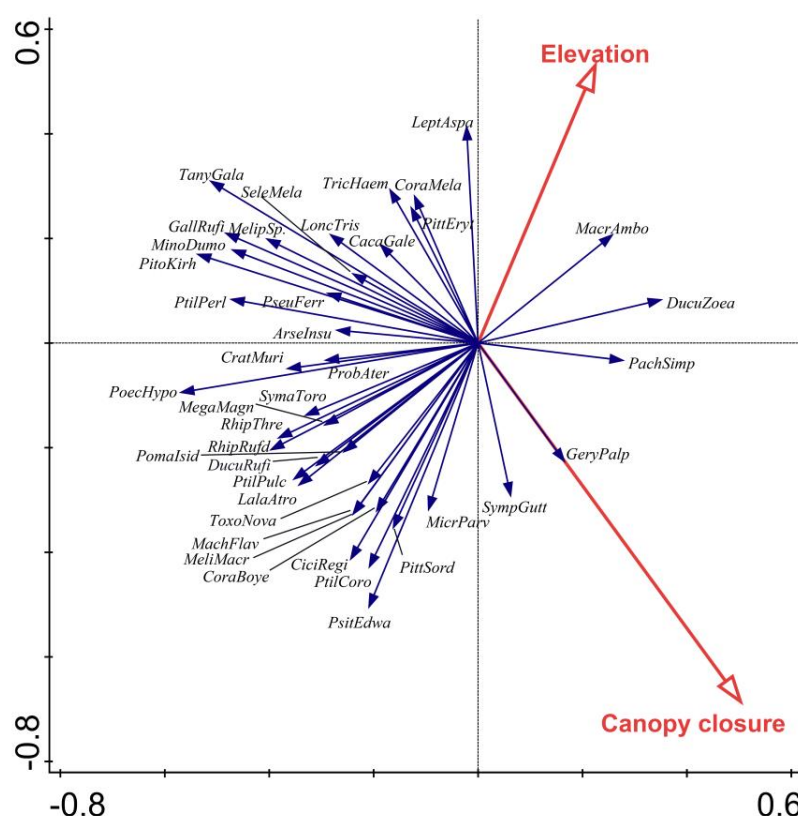


Figure 2.6. Redundancy analysis (RDA) ordination diagram showing composition of bird community (species arrows) in relation to elevation and canopy closure after the effect of space was filtered out (total variation = 9792.023, axis 1 eigenvalue = 0.121, axis 2 eigenvalue = 0.042). The 40 species with the highest fit value are displayed. Canopy closure was positively correlated with first ordination axis (correlation coefficient 0.47) and negatively with second ordination axis (-0.56). Elevation was positively correlated with the second ordination axis (0.36) and less so with first ordination axis (0.25). Number of individual trees was also a significant predictor of bird composition, but omitted from this diagram for ease of viewing. Common species (e.g. *Toxorhamphus novaguineae*, *Coracina boyeri*, *Cicinnurus regius* and *Ptilinopus coronulatus*) had highest abundances in sampling locations of lower elevation. *Leptocoma aspasia* and *Macropygia amboinensis* on the contrary tended to be more abundant at sampling sites of higher elevation. Simultaneously, the analysis distinguished species that avoided dense sites with high canopy closure (e.g. *Cacatua gallerita*, *Leptocoma aspasia*, *Lonchura tristissima*, *Tanyiptera galatea* and *Trichoglossus haematodus*). The only species that preferred sites with high values of canopy closure were *Gerygone palpebrosa* and *Symposiachrus guttula*. Full species names for the species codes displayed are provided in Appendix Table A2.2.

Forward selection found canopy closure, number of individual trees within plots and elevation to be the significant primary predictors of bird community composition across the pooled datasets (RDA; canopy closure: $F = 2.6$, $p < 0.01$; number of trees: $F = 2.0$, $p = 0.01$, elevation: $F = 2.0$, $p = 0.03$; Figure 2.6). The primary predictors accounted for 40.3% of explained variation, whereas space accounted for 51.0% of explained variation (8.7% of explained variation was shared between primary and space predictors). All predictors explained 29.9% of the total variation.

2.4 Discussion

The scale-dependent nature of diversity patterns has long been recognised in the field of ecology (Arrhenius 1921, Connor and McCoy 1979, Shmida and Wilson 1985, Huston 1999, Gaston 2000, Rahbek 2005). Studies exploring this relationship tend to draw a distinction between “local” diversity, determined mostly by species niche differentiation and direct inter-specific interactions, and “regional” diversity determined by species pools and evolutionary dynamics. However, few studies have focused on the species diversity patterns on spatial scales between these two extremes, within tens to thousands of km² within relatively uniform habitats. This study relates diversity patterns of woody plants and birds on this intermediate scale, represented here by 100 km² of a lowland rainforest, to the local patterns within a 50 ha forest plot.

2.4.1 Differences between plants and birds

The magnitude of bird species diversity and the rate of species accumulation with increasing sample size within the Wanang FDP was almost perfectly mirrored by that within the 10,000 ha WCA. The overlap in species composition between the data sets from 50 ha and 10,000 ha was also very high, suggesting that for bird diversity the FDP is representative of the wider area. Conversely, plant species richness was shown to be significantly higher across the WCA than within the selected plots from the FDP, although plant diversity within 50 ha still represented 88% of the species richness within 10,000 ha.

Bird species composition did not show any trends over the 10,000 ha area, i.e. there was no increase in Chao-Jaccard dissimilarity with increasing distance between the compared pairs of samples. However, there was a slow but significant change in the community composition taking account of species abundances with distance. This pattern, in combination with the relatively large proportion of variability in species composition explained by environmental variables, suggest that most of the variability in bird communities is fine-grained, within 1 km distances

and in response to vegetation structure and terrain. The contrasting results of the two indices suggest that any variability over the scale explored in this study is primarily driven by relatively few common species. Dissimilarity in woody plant species composition and community composition showed similar patterns to those of birds. Woody plants displayed a marginal but still non-significant increase in species dissimilarity with distance, while community dissimilarity accounting for species abundances was significant and similar to that of birds.

The difference in compositional dissimilarity patterns between plants and birds, while subtle, may be attributable to different ecological processes acting on the two taxa at the scale explored in this study. It is posited that dispersal limitation is a significant causal factor of species aggregation in tropical forest trees (Seidler and Plotkin 2006, Myers et al. 2013), with non-animal dispersed tree species appearing particularly dispersal-limited across spatial scales (Seidler and Plotkin 2006, Beaudrot et al. 2013). Meanwhile, evidence from tropical forest dynamics plots points to abiotic environmental filtering also being an important driver of tropical tree species distributions, at least at small (< 1 km) scales (Plotkin et al. 2002). However, our results suggest that distance between sampling locations likely accounts for a larger proportion of variability in woody plant species composition than environmental characteristics. As a highly mobile taxon, birds are less restricted in their dispersal than plants (Soininen et al. 2007), especially in unfragmented lowland habitats such as the one studied here (Van Houtan et al. 2007). Although the results of this study suggest bird species composition is related to habitat structure at fine scales, it shows very little variation across the (relatively environmentally homogenous) broader scale of the WCA. Taken together, these observations suggest that dispersal limitation, perhaps driven primarily by limited dispersal of non-fleshy fruited (i.e. non-bird dispersed) trees, is a key factor in explaining the distribution differences observed between the two taxa. However, a current lack of studies on lowland rainforest beta-diversity at this scale limits scope for comparative assessment.

2.4.2 Other studies

On comparing two separate 100 ha plots located within a 650 ha reserve in the Ecuadorian Amazon, Blake (2007) found bird species composition to be almost identical between plots, the only major variation being in individual species' distributions and abundances, reflecting small-scale differences in habitat structure and availability between plots. In a broader analysis of plots across French Guiana, Thiollay (2002) found that despite having sparse local populations, the vast majority of bird species had wide range sizes, thus masking any general determinant of

community structure. Species turnover between sites was found to be 29% on average, for inter-site distances 15 – 320 km, i.e. far higher than the distances analysed in this study.

In an analysis of plant beta-diversity from sites across Panama, Ecuador and Peru, Condit et al. (2002) showed that in the range of pairwise distances represented here (approximately 0 – 15 km), percentage of shared plant species between plots decreased in all three regions. In both Ecuador and Peru this decrease tended to level off beyond around 20 km, suggesting that in these cases local- and intermediate-scale variation plays a more important role in determining plant community composition than broader scale patterns. In a tropical dry forest in southern Mexico, Gallardo-Cruz et al. (2010) demonstrated a similar pattern of decreasing plant community similarity with increasing distance, in this case within a range of 0 – 6 km.

2.4.3 Summary

The results of this study and those described above highlight the varying importance of so-called intermediate-scale patterns in determining overall community composition for different taxa, and therefore in determining optimal sampling regimes. The relative homogeneity of bird communities across the WCA suggests that bird species richness and community composition across 10,000 ha of lowland rainforest may be accurately estimated by sampling within a 50 ha plot. This result is particularly notable given the lack of previous studies on birds in ForestGeo plots. Meanwhile, limiting plant surveys to 50 ha may miss a certain proportion of the broader community, due to the higher influence of local-scale variation on overall community composition in woody plants. However, the observed low beta-diversity of both woody plants and birds across the WCA provides support for the use of the ForestGeo Plot as a means of representing wider biodiversity for both taxa. Extending the study of intermediate-scale diversity patterns to important rainforest taxa such as insects will be necessary if we are to gain a fuller picture of biodiversity across spatial scales in lowland rainforests.

CHAPTER 3

Comparing facets of avian alpha- and beta-diversity along a tropical elevational gradient provides insights into community assembly processes

Abstract

Elevational patterns of bird species diversity are relatively well-studied, although less is known about the effects of elevation on other aspects of avian diversity. Functional and phylogenetic diversity, when compared with species patterns, have the potential to reveal information about the processes shaping community assembly both within and between elevations. We collected species, trait and phylogenetic data for bird communities spanning a tropical elevational gradient to determine whether elevational trends in taxonomic alpha- and beta-diversity were reflected by functional and phylogenetic trends. We then used null model analyses in order to infer what these comparisons reveal about community assembly mechanisms at the within- and between-site scales. Functional and phylogenetic alpha-dispersion (defined as functional and phylogenetic diversity relative to species diversity) decreased unimodally with elevation, and were characterised by lower than expected values (indicative of environmental filtering of bird communities) at all but the lowest elevation. Meanwhile, increasing species turnover (beta-diversity) with increasing distance between elevations was not mirrored by functional and phylogenetic turnover. Furthermore, functional and phylogenetic dissimilarity of bird communities were lower than expected for most between-site combinations. These results suggest that environmental filtering does not occur between elevations, and that the direct climatic effects of increasing elevation cannot alone account for the turnover observed in bird species communities. Indirect effects such as food availability may be more important. Finally, functional traits showed a strong phylogenetic signal, indicating that phylogenetic diversity may provide an effective proxy for functional diversity in the bird communities studied here.

Key Words: Elevation, functional diversity, phylogenetic diversity, community assembly, beta-diversity, birds, environmental filtering, niche differentiation, phylogenetic signal

3.1 Introduction

The focus on species as the principal metric by which diversity is quantified has come under scrutiny in recent years (McGill et al. 2006, Kraft et al. 2008, Villéger et al. 2012). It is now recognised that adherence to taxonomic diversity alone may mask underlying information which could be more useful for ecosystem functioning – for example, the health of an ecosystem or its resilience in the face of change (Elmqvist et al. 2003, Petchey and Gaston 2006). Increased focus on functional and phylogenetic diversity has helped to broaden the general definition of diversity and encompass such ideas (e.g. Faith 1992, Petchey and Gaston 2002, 2006, Violle et al. 2007, Devictor et al. 2010, Meynard et al. 2011, Silva and Brandão 2014, Maire et al. 2015).

Functional diversity may be defined as the diversity of morphological, physiological and ecological traits present in a community (Tilman 2001, Petchey and Gaston 2002, Devictor et al. 2010). As such, it reflects the ability of a community to maintain its functional capacity in the face of external pressures, such as habitat degradation or climate change (Folke et al. 2004, Meynard et al. 2011). In contrast, phylogenetic diversity encompasses the evolutionary relationships within a community accounting for phylogenetic distance between species (Crozier 1997, Hardy and Senterre 2007). It therefore reflects the evolutionary history and subsequent taxonomic uniqueness present within a community, and thus its ability to produce evolutionarily unique solutions in response to change (Forest et al. 2007, Meynard et al. 2011, Voskamp et al. 2017). It is commonly assumed that phylogenetic diversity may provide a reliable proxy for ecosystem function. Indeed, it has been hypothesised that protecting phylogenetic diversity may act to preserve the effective functioning of ecosystems (Webb et al. 2002). However, several studies have found very weak or no evidence for such a correlation, making such an assumption risky (Swenson et al. 2012, Purschke et al. 2013, Mazel et al. 2018). One way of testing this assumption is by measuring the phylogenetic signal in trait data (Blomberg et al. 2003, Münkemüller et al. 2012). If functional traits are strongly phylogenetically conserved, the use of phylogenetic diversity as a proxy for functional diversity is justified (Webb et al. 2002, Cavender-Bares et al. 2009, Swenson 2011, Baraloto et al. 2012). Such an approach could be useful in situations where functional trait values are not easily obtained or impossible to measure accurately, but where species' phylogenetic relationships are known.

An emerging area in which functional and phylogenetic diversity may prove especially useful is in disentangling the processes responsible for structuring of ecological communities (Kraft et al. 2008). The relative importance of different deterministic (niche-based) and neutral community assembly processes has been a topic of ongoing debate in recent years (Hubbell 2001, McGill 2003, Grime 2006, Thompson and Townsend 2006, Mouillot et al. 2007, Kraft et al. 2008, Vellend

et al. 2014). By contrasting taxonomic diversity patterns with those of phylogenetic and functional diversity, it is possible to make inferences about the relative importance of these processes in structuring communities (Mouillot et al. 2007, Emerson and Gillespie 2008, Kembel 2009, Spasojevic and Suding 2012, Purschke et al. 2013). Two niche-based processes in particular have been inferred in this way by previous studies. One is niche differentiation or limiting similarity, which should manifest as functional over-dispersion due to competition between coexisting species (Stubbs and Wilson 2004, Kraft et al. 2008). Conversely, functional clustering or under-dispersion may occur as a consequence of environmental filtering, in which barriers imposed by the abiotic environment limit the range of traits that may be expressed within it (Maaß et al. 2015, Seymour et al. 2015).

At the broader level, comparing patterns of taxonomic, functional and phylogenetic beta-diversity along environmental gradients has been suggested as another means of revealing the contributions of neutral versus deterministic community assembly processes (Stegen and Hurlbert 2011, Swenson et al. 2011, Villéger et al. 2012). Higher than expected functional turnover relative to species turnover between sites is indicative of environmental filtering, as changes in underlying environmental conditions lead to directional functional responses (Villéger et al. 2012). Moreover, this effect should be stronger between more environmentally divergent sites. Therefore, along environmental gradients with steadily changing climatic conditions we should expect a positive functional distance–decay relationship to indicate the presence of deterministic environmental filtering (Siefert et al. 2013).

The majority of the above mentioned studies are primarily concerned with plant and invertebrate communities. Meanwhile, comparatively little attention has been given to bird community assembly, particularly along elevational gradients (but see Dehling et al. 2014). Birds form an important functional component of tropical ecosystems, particularly in New Guinea where large predatory and seed-dispersing terrestrial mammals are largely absent (Mack 1998a). While bird communities have been studied in the context of an elevational gradient in New Guinea (Sam and Koane 2014, Sam et al. 2019), little is known of the ecological mechanisms responsible for the observed community patterns along the elevational gradient and whether these processes vary with elevation. This knowledge will be important if we are to effectively understand mechanisms driving bird species distributions and taxonomic diversity patterns.

This study proposes to measure taxonomic, phylogenetic and functional alpha- and beta-diversity of birds along an elevational gradient in Papua New Guinea, in order to answer a number of questions: i) Do functional and phylogenetic trends correlate closely with taxonomic trends? ii) What do the differences in alpha- and beta-diversity patterns reveal about community

assembly processes acting along the gradient? iii) How closely are functional traits phylogenetically conserved? The choice of a tropical elevational gradient is well-suited to this task because tropical mountains are characterised by rapid turnover in climatic and environmental conditions within a relatively small area, as well as high overall species diversity. In combination, these factors produce an ideal environment in which to study the differences between taxonomic, phylogenetic and functional patterns both within and between elevations (Dehling et al. 2014).

3.2 Methods

3.2.1 Study site

The study took place along the north-eastern slopes of Mt Wilhelm (4,509 m), in the northern watershed of the Central Range of Papua New Guinea (Figure 3.1). The study area, located in the Usino-Bundi district of southern Madang province, comprises six study sites separated by vertical intervals of 500 m ranging from 200 – 2,700 m above sea level (asl) (5° 44' S, 145° 20' E; 5° 49' S, 145° 09' E). The sites form part of a complete elevational rainforest transect which continues up to the tree line at 3,700 m asl, spanning a total of 30 km and 3,500 m in elevation (Sam and Koane 2014, Sam et al. 2019) (the highest two sites were omitted from the present study for logistical reasons). The habitats within the surveyed sites could be described as lowland alluvial forest (200 m asl), foothill forest (700 and 1,200 m asl) and lower montane forest (2,200 and 2,700 m asl) (Paijmans 1976). Average annual precipitation is 3,288 mm in the lowlands (200 m), rising to 4,400 mm at 3,700 m, with a distinct condensation zone around 2,200 and 2,700 m (Sam et al. 2019). Mean annual temperature decreases from 24.9° C at 200 m to 14.3° C at 2,700 m at a near constant rate of 0.42° C per 100 vertical metres.

3.2.2 Bird surveys

Bird surveys took the form of point counts. At each elevation site, we surveyed a 2,250 m transect comprising 16 points on three separate days. Each point was separated by 150 m in order to avoid making multiple records of individual birds. Transects predominantly followed those of Sam et al. (2019), and were selected to represent a range of microhabitats found at each site (e.g. ridges, valleys and creeks) while minimising deviation from the elevation represented. Surveys began at sunrise (approximately 05.30 am) and were completed by 11.00 am. Individual point counts lasted 15 minutes each, and commenced a few minutes after arriving at a point to reduce the effects of disturbance caused by arrival (Bibby et al. 2000). All birds

estimated to be seen or heard within a radius of 50 m were counted. To minimise multiple counts of one individual, we followed the protocol of Sam and Koane (2014): we only counted multiple conspecifics if two or more individuals could be heard singing simultaneously or from clearly different locations within a period of a few seconds. Point counts were always conducted by at least two observers. Points were located using Garmin GPSmap 62S handheld GPS units. Audio recordings of all point counts were made using an Olympus LS-5 Linear PCM digital recorder to enable later identification of any species not identified in the field. Point counts took place between February and July 2016.

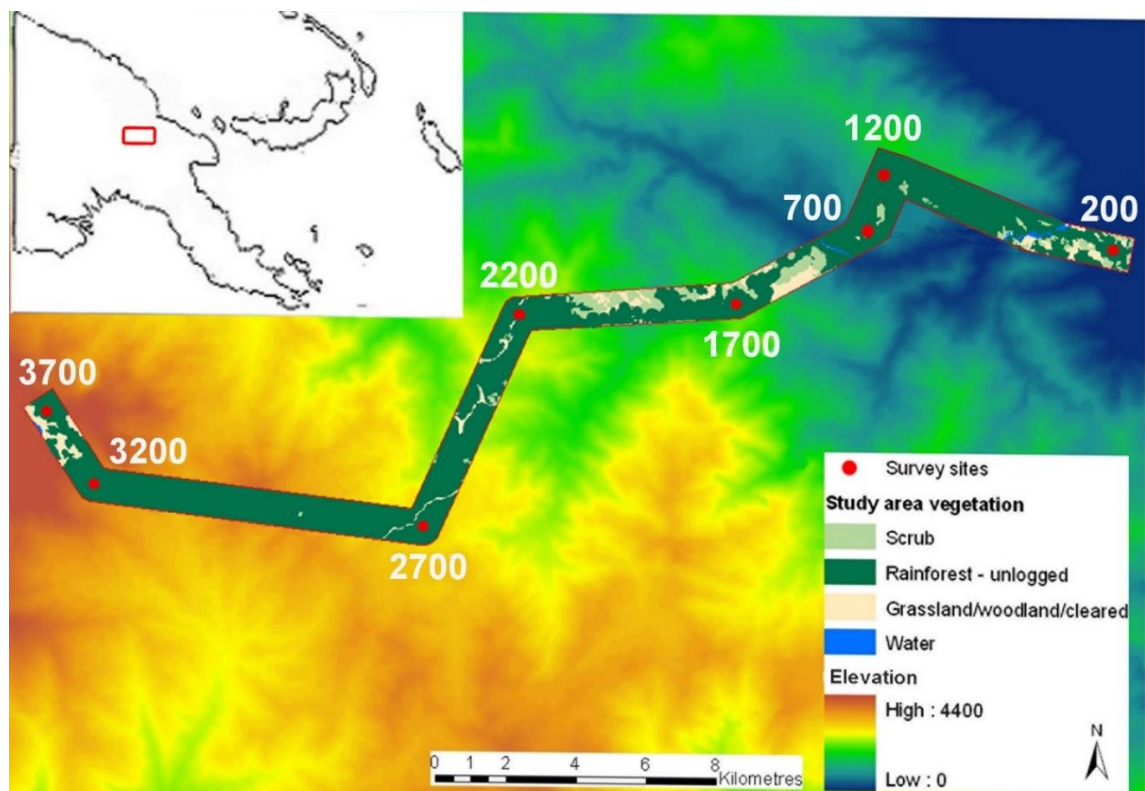


Figure 3.1. Map of the Mt Wilhelm elevational gradient in Papua New Guinea (red rectangle in insert), including the survey sites included in this study (200 – 2,700 m asl). Vegetation cover is displayed for a 2 km wide buffer zone surrounding the transect line. Figure used with permission from Sam et al. (2019).

3.2.3 Trait selection

The selection of traits to use in bird functional diversity analyses is subjective and there is still little consensus over the “correct” suite of traits to include in order to adequately represent birds as a functional group. We selected traits to represent a balance between morphological and behavioural aspects of avian ecology and to provide proxy measurements for a wide range of ecological functions that birds provide (see Table 3.1). The original list of traits was longer than the final list included here (see Appendix 3.1). In order to reduce redundancy in the suite

of traits used, we compared trait values using Pearson's correlations and removed any traits that showed values of positive or negative correlations higher than 0.7 (Appendix Figure A3.1).

Bird morphological traits (mass, bill width, Kipp's distance) for the species recorded were retrieved from a global database of avian functional traits (Pigot et al. in press). Additionally, a number of measurements were taken from museum specimens of birds collected from the Mt Wilhelm study sites themselves (Natural History Museum of Denmark, University of Copenhagen, March 2018), to ensure the trait values used adequately represented local assemblages. Traits related to feeding guild and diet used data from Sam et al. (2017), who analysed the diets of Mt Wilhelm bird species by using emetic tartar to induce regurgitation. In that study, food sources were broadly categorised into fruit, nectar, seeds, invertebrates and vertebrates, and their relative volumes in regurgitated material were used to categorise a primary and secondary (if present) food source for each species. Information on foraging substrate used by birds was taken from Pratt and Beehler (2015), and from our own observations. Using all sources stated above, we were able to obtain trait information on 184 species (96% of species recorded by us and 65% of bird species so far detected from the Mt Wilhelm gradient).

Table 3.1. Traits included in bird functional diversity analyses. Kipp's distance is defined as the distance between the tip of the longest primary and the first secondary feather measured on the folded wing. Bill width is defined as the width at the anterior edge of the nostrils (Pigot et al. 2016). Categorical traits with a number of levels were summed to 1 for analyses; for example an obligate frugivore scored 1 for fruit and 0 for all other food types, while a bird with both fruit and nectar in its diet scored 0.5 for each and 0 for the other three food types.

Trait		Type	Provides ecological information on:
Mass		Continuous	Range size and dispersal ability; resource quantity required
Kipp's Distance		Continuous	Flight performance; vertical niche within forest strata
Bill Width		Continuous	Dietary niche; type and size of food resource used
Food Source	Fruit	Categorical	
	Nectar	Categorical	
	Seeds	Categorical	
	Invertebrates	Categorical	
	Vertebrates	Categorical	
Foraging Substrate	Water	Categorical	Vertical niche within forest strata; type of food resource used
	Ground	Categorical	
	Vegetation	Categorical	
	Air	Categorical	

3.2.4 Phylogenetic information

In order to assess phylogenetic information on the bird species recorded along the gradient, we used the BirdTree global avian phylogeny developed by Jetz et al. (2012). This project represents the first attempt to produce a complete phylogeny of all 9,993 known extant bird species (Rubolini et al. 2015, García-Navas et al. 2018) and is based on two backbone taxonomies: those produced by Ericson et al. (2006) and Hackett et al. (2008). We used the BirdTree online platform (<http://birdtree.org>) to obtain phylogenetic information on bird species from the Mt Wilhelm gradient by subsetting the global phylogeny to include only the species present in our dataset.

3.2.5 Data analysis

All analyses were performed in R version 3.5.2 (R Core Team 2013). Because we were not able to obtain trait information from 5 species and lacked phylogenetic information for a further 2 species (Appendix Table A3.1), we subset our bird dataset to include only those species for which full trait and phylogenetic data were available. This subset was then used for all subsequent analyses using functional and phylogenetic data. The full dataset including all bird species was used only for calculating species alpha and beta-diversity.

Fitting generalised linear models

To test for changes in different variables with elevation, we created GLMs (variable ~ elevation) with selected error distributions. In each case we tested whether or not a polynomial relationship was significantly better than a linear relationship and refitted accordingly. We then checked models for over-dispersion and again refitted if necessary. For each test we additionally performed a Shapiro-Wilk test of normality on residuals (Shapiro and Wilk 1965). If residuals did not conform to a normal distribution, we refitted the model with values transformed as $x = \ln(x + 1)$. Finally, we performed significance tests based on the deviance between the null (~ 1) and final models.

Species alpha- and beta-diversity

Species alpha diversity was calculated as both total observed number of species (species richness) and using the Chao 1 richness estimator (Chao et al. 2005), which predicts asymptotic species richness given a hypothetical complete sampling effort. Species dissimilarity between elevations (beta-diversity) was calculated using the Bray-Curtis index between all possible elevation pairs, for a total of 15 pairwise comparisons. In addition, for each elevational pairwise comparison we separated beta-diversity into “nestedness” (loss of species between sites) and

“turnover” (replacement of species between sites) components using the “beta.pair.abund” function from the *betapart* package (Baselga et al. 2018).

Changes in traits with elevation

We calculated community weighed means (CWM) for each trait at every site and tested their relationship with elevation. Because Food Source and Foraging Substrate are categorical traits (Table 3.1), we calculated CWM for each of their levels, rescaled them to a relative value (the sum of all levels being equal to one) at each site, and subsequently tested the relationship of each level individually with elevation.

Functional alpha-diversity

Functional traits were first weighted such that categorical traits measured as a number of variables were not artificially inflated in importance (Laliberté and Legendre 2010). Gower’s distance (Gower 1971) was used to measure interspecific functional dissimilarity, as it has been shown to be tolerant of the inclusion of qualitative traits (Mouchet et al. 2008, Legendre and Legendre 2012). Using the function “gowdis” in the package *FD* (Laliberté et al. 2015), we created a species dissimilarity matrix from the species and trait datasets. Functional diversity was then calculated as Mean Pairwise Distance (MPD) within the community at each elevation (within-site MPD), using the “ses.mpd” function from the *picante* package (Kembel et al. 2010, 2018). We performed a null model analysis to test changes of MPD while accounting for species richness. A null distribution of MPD values was created by randomizing the species names in the dissimilarity matrix 999 times, while maintaining species occupancy rates and species richness for all sites along the gradient. We then calculated the Standardised Effect Size (SES) which measures the relationship between observed and expected MPD values using the following formula: $SES = \frac{(VAR_o - VAR_s)}{VAR_{sd}}$ where VAR_o is the observed value, VAR_s the mean simulated value, and VAR_{sd} the standard deviation of all simulated values.

Phylogenetic alpha-diversity

We produced 1,000 Markov Chain Monte Carlo (MCMC) trees using the Hackett et al. (2008) taxonomic backbone, which is the most recent high-level avian taxonomy available (Voskamp et al. 2017). We then used the “MaxCladeCred” function from the *phangorn* package (Schliep 2011) to obtain a maximum clade credibility (MCC) tree – i.e. the single tree with the highest possible product of clade probabilities from the MCMC subset (García-Navas et al. 2018) (Appendix Figure A3.2). Next, we used the “cophenetic.phylo” function from the *ape* package (Paradis et

al. 2018) to convert the MCC tree into a dissimilarity matrix. From this point, we calculated within-site MPD and null model analyses in the same way as for functional trait data, but in this case “distance” represented phylogenetic rather than functional distance between species.

We calculated all functional and phylogenetic analyses using two approaches: presence-absence weighted (in which each species provided a single data point for each trait) and abundance-weighted (taking species’ relative abundances into account).

Functional and phylogenetic beta-diversity

In order to calculate functional and phylogenetic beta-diversity, we used the “comdist” function from the *picante* package to calculate MPD between all pairs of sites (between-site MPD). This enabled us to test for a possible functional or phylogenetic distance-decay relationship between sites. We calculated null model analyses and SES using the same methods as for functional and phylogenetic alpha-diversity. As above, all analyses were conducted using both presence-absence weighted and abundance weighted data.

Phylogenetic conservatism

In order to detect any correlation between functional and phylogenetic patterns, we plotted the SES of functional diversity values of each site against that site’s SES for phylogenetic diversity. This was conducted for both within-site MPD and between-site MPD, to provide measures of phylogenetic conservatism at the scale of both alpha- and beta-diversity. Additionally, we used Blomberg’s K statistic (Blomberg et al. 2003) to test for the phylogenetic signal present in each of the three recorded continuous functional traits (body mass, bill width and Kipp’s distance), using the “multiPhylosignal” function in the *picante* package.

3.3 Results

We recorded a total of 5,245 individuals of 191 bird species across the six survey sites (Appendix Table A3.1). Observed species richness was very similar to that predicted by the Chao 1 richness estimator in all plots (Figure 3.2a), suggesting well sampled communities in all sites. The fitted model for species richness showed a decreasing trend with increasing elevation (GLM_{SpeciesDiversity}: deviance = 12.62, DF = 1,4, $p < 0.01$; Figure 3.2b). Abundance-weighted diversity, measured using MPD, displayed unimodal and broadly decreasing trends with increasing elevation (Figure 3.2b) for both functional (GLM_{FD}: deviance = 0.003, DF = 2,3, $p < 0.01$) and phylogenetic diversity (GLM_{PD}: deviance = 0.002, DF = 2,3, $p < 0.01$). Size-related traits, measured individually using CWMs, all showed unimodal decreasing trends with elevation (Figure 3.3, Appendix Table A3.2).

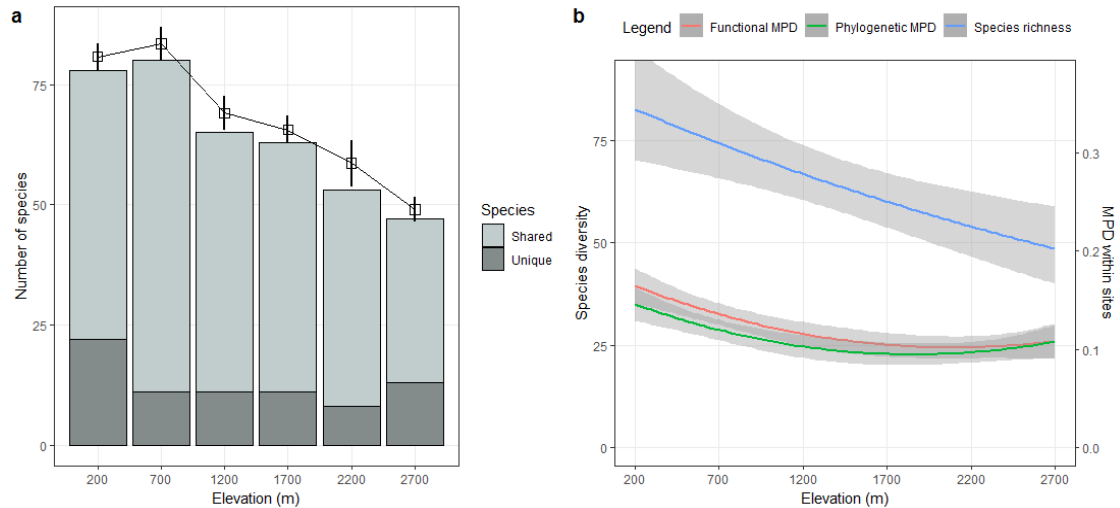


Figure 3.2. Overall bird alpha diversity patterns along the Mt Wilhelm elevational gradient. (a) Taxonomic diversity is represented as species richness (bars) and Chao 1 species richness estimates (squares; vertical lines represent 95% confidence intervals). Bars are divided into species unique to a site (dark grey) and those shared with at least one other elevation (light grey). (b) The relationship between species richness and elevation (left axis; blue line) is plotted alongside functional diversity (right axis, measured as within-site functional Mean Pairwise Distance; red line) and phylogenetic diversity (right axis, measured as phylogenetic MPD; green line). Grey bands represent 95% confidence intervals.

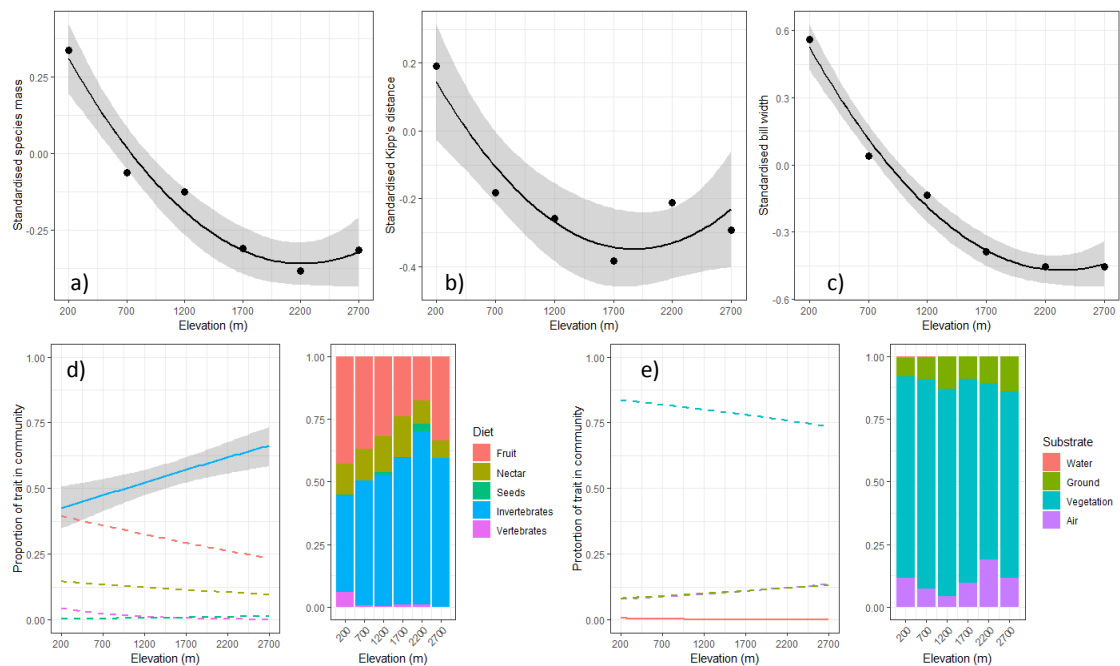


Figure 3.3. Community weighted means (CWM) for each individual trait included in functional diversity analyses of Mt Wilhelm birds. Mean species mass (a), Kipp's distance (b) and bill width (c) are represented by black circles, together with fitted line and 95% confidence intervals (represented by grey bands). Species diets show a significant elevational trend only for invertebrates (d). The only significant elevational trend in foraging strategy is a decrease in water-feeding birds with increasing elevation (e).

The proportion of insectivorous species increased with elevation ($\text{GLM}_{\text{FSinv}}$: deviance = 0.16, DF = 1,4, $p = 0.02$). Foraging strategy showed little elevational variation (Figure 3.3, Appendix Table A3.2), with the only significant change being a decrease in aquatic-feeding birds with elevation (primarily attributable to a lack of kingfisher species occurring above 1,200 m, corresponding to a decrease in riparian habitat at higher elevations).

Functional and phylogenetic diversity showed very similar trends with elevation after accounting for species richness (i.e. functional and phylogenetic dispersion) (Figure 3.4). Abundance-weighted data in both cases show a general pattern of clustering, except at 200 m where both functional and phylogenetic diversity are similar to null expectations (Figure 3.4). Both patterns show the highest level of clustering at 1,700 m, and are significantly unimodal with elevation ($\text{GLM}_{\text{FD-SES}}$: deviance = 6.71, DF = 2,3, $p < 0.01$; $\text{GLM}_{\text{PD-SES}}$: deviance = 6.18, DF = 2,3, $p < 0.01$; Appendix Table A3.2). When considering presence-absence weighted data, the trend becomes significantly monotonically declining with elevation for both functional and phylogenetic dispersion ($\text{GLM}_{\text{FD-SES}}$: deviance = 10.988, DF = 1,4, $p < 0.01$; $\text{GLM}_{\text{PD-SES}}$: deviance = 12.597, DF = 1,4, $p < 0.05$; Appendix Table A3.2). In both functional and phylogenetic diversity, species were over-dispersed at 200 m and clustered only at the three highest elevations (Figure 3.4).

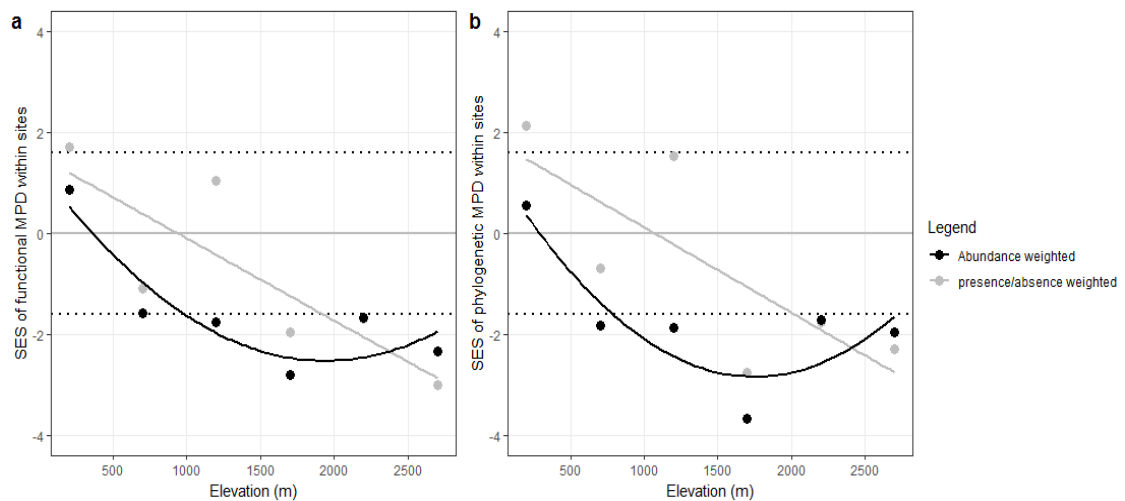


Figure 3.4. Results of null model analyses showing bird functional (a) and phylogenetic (b) dispersion at each of the six survey sites. Black circles represent abundance weighted functional and phylogenetic dispersion (measured as standardised effect sizes of within-site MPD), with the fitted line displaying a unimodal decreasing trend with elevation. Grey circles represent functional and phylogenetic dispersion as above but presence-absence weighted – i.e. each species contributing equally to SES.MPD scores. Here the fitted line shows a monotonic decrease with elevation. SES values above the upper horizontal dotted lines indicate functional or phylogenetic over-dispersion (significantly higher than expected FD/PD given species diversity) while values below the lower dotted lines indicate significant functional or phylogenetic clustering (lower than expected FD/PD given species diversity).

Species beta-diversity showed a clear increase with increasing elevational distance between plots, which appears to be driven primarily by species turnover as opposed to nestedness (Figure 3.5a), with all relationships being significant (GLM_{Bray-Curtis}: $F = 35.46$, $DF = 1,13$, $p < 0.01$; GLM_{Nestedness}: $F = 12.64$, $DF = 1,13$, $p < 0.01$; GLM_{Turnover}: $F = 32.78$, $DF = 1,13$, $p < 0.01$; Appendix Table A3.2). In contrast, increasing elevational difference does not yield a significant increase in dissimilarity between plots for either functional (GLM_{FD-beta}: deviance = 0.001, $DF = 1,13$, $p = 0.07$; Figure 3.5b) or phylogenetic data (GLM_{PD-beta}: deviance = 0.001, $DF = 1,13$, $p = 0.06$; Figure 3.5c). The lack of a distance-decay trend is also present in both functional and phylogenetic beta-dispersion, represented by the SES of MPD between sites (GLM_{FD-betaSES}: deviance = 2.50, $DF = 1,13$, $p = 0.21$; GLM_{PD-betaSES}: deviance = 1.70, $DF = 1,13$, $p = 0.28$; Appendix Figure A3.3, Appendix Table A3.2). A general trend of functional and phylogenetic clustering between sites is also apparent, with 10 out of 15 site pairs showing SES values significantly lower than random for both functional and phylogenetic data (Appendix Figure A3.3, Appendix Table A3.3). This pattern of under-dispersion includes all adjacent site pairs, with the exception of 200 – 700 m (Appendix Figure A3.4). This suggests that neighbouring sites are more functionally and phylogenetically similar than would be expected given species beta-diversity, a trend which is particularly apparent at 1,200 – 1,700 m, where a sudden and marked increase in species dissimilarity occurs (Appendix Figure A3.4).

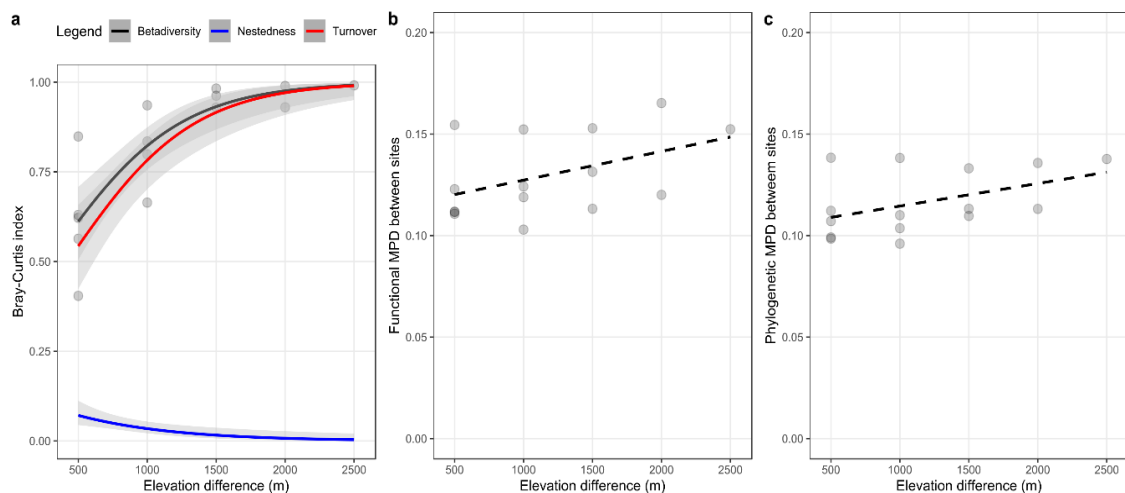


Figure 3.5. Taxonomic, functional and phylogenetic beta-diversity of birds along the Mt Wilhelm gradient. Taxonomic diversity (a) is measured as Bray-Curtis dissimilarity between sites (grey circles) and shows a positive distance-decay relationship with increasing distance between sites (black line). When separated into turnover and nestedness components, turnover also increases with distance (red line) while nestedness decreases with distance (blue line). Grey bands represent 95% confidence intervals. Functional (b) and phylogenetic (c) beta-diversity are measured as between-site MPD (grey circles), neither of which show a significant trend with increasing distance between sites.

Bird functional trait data showed a high level of evolutionary conservatism. SES values for phylogenetic diversity show a strong positive correlation with those for functional diversity both within sites (GLM_{WithinSites}: deviance = 7.67, DF = 1,4, $p < 0.01$, Figure 3.6a) and between sites (GLM_{BetweenSites}: deviance = 18.75, DF = 1,13, $p < 0.01$, Figure 3.6b). Additionally, individual continuous traits showed strong evidence of phylogenetic signal, measured using Blomberg's K statistic (Blomberg et al. 2003). Phylogenetic signal was particularly strong for body mass ($K = 2.93$, $p < 0.01$), although bill width ($K = 1.6$, $p < 0.01$) and Kipp's distance ($K = 1.61$, $p < 0.01$) both also showed higher than expected phylogenetic signal under a Brownian motion model of evolution ($K = 1$).

3.4 Discussion

3.4.1 Overall diversity patterns

We found bird species richness on Mt Wilhelm to decline linearly with increasing elevation. Such a trend is consistent with globally observed trends in bird species richness with increasing elevation (McCain 2009), including those observed in the study area (Sam et al. 2019). Overall, bird functional and phylogenetic diversity patterns also showed a decline with increasing elevation, but these patterns were unimodal, showing a relatively steeper initial decline before levelling out towards higher elevations. Thus, while initial species declines with elevation were accompanied by a corresponding loss in ecosystem function, at higher elevations any further loss of species had increasingly little functional impact. This suggests that lowland assemblages include phylogenetically distinct species with more unique trait combinations than those found at higher elevations, where phylogenetic and functional redundancy is more prevalent.

3.4.2 Alpha-diversity patterns and community assembly

When considering all individuals in communities, we found functional and phylogenetic diversity to be lower than expected, given species richness at all sites except 200 m. Such pattern suggests that variation in bird species traits is relatively constrained across most of the gradient, and does not show evidence of limiting similarity due to interspecific competition for resources. The results indicate a moderate effect of environmental filtering in structuring bird communities at all sites above 200 m. However, when considering presence-absence data, we found a slightly different pattern of monotonically decreasing functional and phylogenetic dispersion with elevation. In this instance only the highest three elevations showed lower functional and phylogenetic diversity than expected, while 200 m was functionally and phylogenetically over-dispersed.

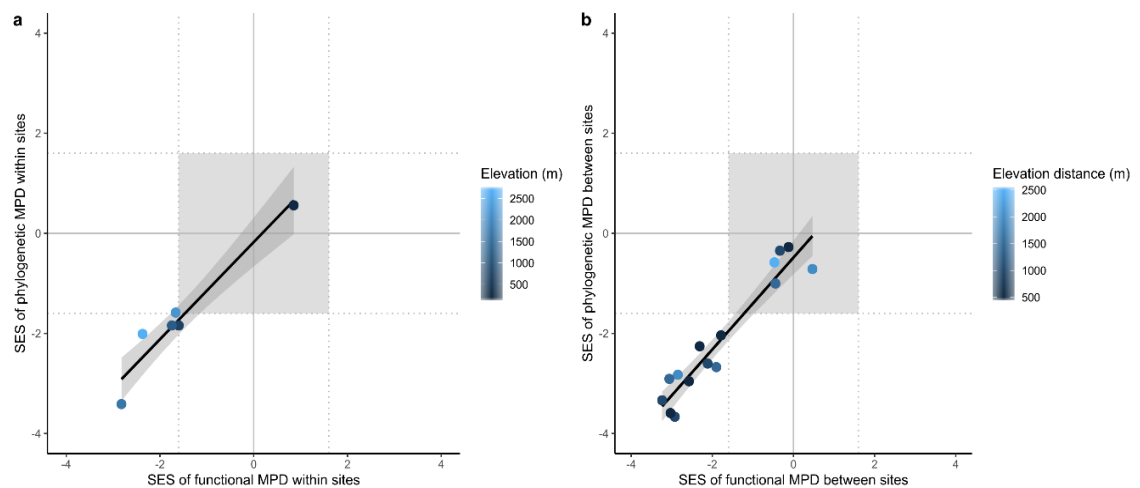


Figure 3.6. Relationship between functional and phylogenetic alpha- (a) and beta-diversity (b) patterns for Mt Wilhelm birds. (a) Standardised effect sizes of functional within-site MPD values are plotted against those of phylogenetic within-site MPD. Sites are represented by circles, with circle colour corresponding to elevation. (b) SES of functional between-site MPD are plotted against phylogenetic between-site MPD. Here each circle represents a single pairwise comparison between two elevations, with colour corresponding to the distance between the compared elevations. In both plots, the black line displays a significant positive correlation (grey bands represent 95% confidence intervals). Sites/pairwise comparisons below and to the left of the grey box are characterised by phylogenetic and functional clustering, while those inside the box are not significantly over- or under-dispersed.

The discrepancy between abundance weighted and presence-absence weighted data suggest that the lower overall functional and phylogenetic dispersion observed in the former is likely driven primarily by relatively few common species with close phylogenetic relationships and similar trait values. Meanwhile, rare species seem to contribute a disproportionate amount to overall functional and phylogenetic diversity, especially at low and mid-elevations. These findings support previous research highlighting both the functional (Mouillot et al. 2013; fish and plants, Jain et al. 2014; plants, Leitão et al. 2016; fish, trees and birds) and phylogenetic (Isaac et al. 2007; mammals, Mi et al. 2012; plants) importance of rare species. A notable example of the functional importance of rare birds in particular has been observed in Pacific islands where the loss of rare large frugivores may lead to functional collapse of seed dispersal networks (Wotton and Kelly 2011).

The general pattern of decreasing functional and phylogenetic dispersion with increasing elevation makes sense if we assume that colder and relatively harsher environments should impose stronger environmental filters than warmer ones (Graham et al. 2014). Tropical mountains such as Mt Wilhelm are characterised by rapid climatic turnover, with more than 10° C separating the highest and lowest sites in this study. The conditions at higher elevations may

present environmental filters which constrain the range of traits that may be expressed, whereas warmer environments may be characterised by more functionally and phylogenetically diverse assemblages (Machac et al. 2011, Hoiss et al. 2012, Graham et al. 2014, He et al. 2018). A similar trend was observed by Dehling et al. (2014), who studied frugivorous bird communities along an elevational gradient in the Peruvian Andes. They found that while lowland assemblages were functionally and phylogenetically dispersed, assemblages above 1,200 m asl were more clustered. However, in the area of study, Sam et al. (2019) found that bird species richness is driven more by habitat complexity and by abundance of food resources than by climate per se. This suggests that environmental filtering at mid and high elevations likely results from a reduction in physical niche space associated with simpler habitat structure and reduced food availability, rather than being directly imposed by species' climatic tolerances. This is supported by the fact that the species lost with increasing elevation tend to be functionally unique. For example, many large-gaped frugivores are characterised by having a lowland distribution (Pratt and Beehler 2015), while highland assemblages lack equivalent species. Such a trend may be related to the higher availability of large fruits in lowland areas (Muñoz et al. 2017, also see Chapter 5 of this thesis).

3.4.3 Beta-diversity patterns and community assembly

At the broader scale of inter-elevation comparisons, we found functional and phylogenetic dissimilarity between sites to be broadly lower than expected, given the species dissimilarity. We also found no evidence of increasing functional and phylogenetic distance between sites with increasing vertical distance between them. This contrasts with species data which showed a strong vertical distance-decay relationship. Unlike within-site patterns, these data do not support environmental filtering, which we would expect to cause higher than expected functional differences between sites (Swenson et al. 2011). Furthermore, we should expect the effects of environmental filtering to be stronger with increased climatic distance between sites, leading to a positive functional distance-decay relationship (Siefert et al. 2013).

When focusing on neighbouring pairs of sites separated by 500 m in elevation, a clear mid-elevational shift in the bird community can be observed: species turnover is markedly higher between 1,200 m and 1,700 m than between any other pair of neighbouring sites. Indeed, these two elevations represent the respective upper and lower elevational limits of a large number of species along the gradient (Sam et al. 2019). However, this pattern of high turnover is not replicated by functional and phylogenetic data, both of which show a particularly low dissimilarity between these two elevations after accounting for the high level of species

dissimilarity. This suggests that species' replacements with increasing elevation represent a non-random subset of the overall species pool characterised by closer phylogenetic relationships and more similar trait values than expected under random replacement. This reinforces the idea that species turnover along the gradient is not primarily due to deterministic responses, for example to climatic factors, but may be explained in other ways.

One possible explanation for the observed pattern is that lowland and highland bird assemblages have different evolutionary histories (Weir 2006). For example, it has been shown for certain New Guinean genera spanning large elevational ranges that highland lineages are more ancient (Jönsson et al. 2014, Garg et al. 2019), perhaps preventing the upward expansion of their lowland counterparts. Diamond (1973) noted a similar mid-elevational shift to that observed at Mt Wilhelm in several bird taxa across New Guinea and postulated that a number of genera may have undergone separate radiations in lowland and highland areas. He argued that competitive exclusion at mid elevations subsequently prevents the elevational overlap of the now distinct but closely related species. Indeed, the concept of separate radiations has been proposed as a reason for the differences observed in lowland and highland assemblage structure in South American birds (Weir 2006, Dehling et al. 2014). In our data and that of Sam et al. (2019), a total of 7 genera (*Charmosyna*, *Ducula*, *Gerygone*, *Lonchura*, *Manucodia*, *Meliphaga*, and *Xanthotis*) contain both species occurring between 200 m – 1,200 m and between 1,700 m – 2,700 m, but lack species spanning across 1,200 m – 1,700 m. The preponderance of closely related species across the elevational gradient is certainly consistent with the hypothesis that separate radiations may have occurred in highland and lowland assemblages, leading to phylogenetically and functionally similar species occurring in both.

Another potential explanatory factor for the lower than expected functional beta-diversity along the elevational gradient concerns species' ecological roles. The occurrence of a high proportion of generalist species with relatively wide individual niches should lead to functionally equivalent species occurring at different elevations. This should in turn manifest as low functional beta-diversity, even if species turnover between sites is high. Although not on an elevational gradient, such a trend was observed by Villéger et al. (2012) among tropical estuarine fish communities. In our data, approximately one third of species display multiple values for each of the two behavioural traits of dietary niche and foraging substrate (60 and 63 species respectively). This relatively widespread dietary and habitat generalisation could in part account for the observed low functional beta-diversity, especially if the species involved are characterised by high individual abundances.

3.4.4 Phylogenetic conservatism

We found both a strong correlation between bird phylogenetic and functional diversity and correspondingly high levels of phylogenetic signal in species trait data, suggesting a strong effect of evolutionary conservatism in dictating birds' functional trait expression. This high degree of trait conservatism is unusual in birds, for which existing evidence is decidedly mixed (Böhning-Gaese and Oberrath 1999, Gómez et al. 2010, Khaliq et al. 2015, Mazel et al. 2018), although it may be higher among birds in the tropics than elsewhere (Khaliq et al. 2015).

The high degree of phylogenetic conservatism in bird traits also helps to explain the low functional turnover of birds along the gradient (Baraloto et al. 2012). The observed high incidence of congeneric species occurring in both lowland and highland assemblages means that closely related species are found across a wide elevational range. Because traits are conserved within genera, similar trait combinations are thus expressed across a similarly wide elevational range, despite changing climatic conditions along the gradient. If traits are related to the niches occupied by birds then this pattern naturally leads to functional similarity across elevations (Emerson and Gillespie 2008). The observed low functional dispersion in highland assemblages may also be attributable to phylogenetic conservatism if, despite the availability of unused functional niche space, highland assemblages are characterised by a lack of phylogenetically unique species.

3.4.5 Summary

This study found a number of differences between species richness and turnover patterns and those of functional and phylogenetic alpha- and beta-diversity. The results suggest that environmental filtering affects species assemblage structure at a local scale but not at the level of inter-elevation comparisons. The decelerating decline in bird functional and phylogenetic diversity with elevation relative to species richness, and the relatively slow functional and phylogenetic turnover between elevations, combine to suggest that increasing elevation (and decreasing temperature) alone is not enough to account for changes in bird communities observed along Mt Wilhelm. This supports the conclusions of Sam et al. (2019) who found the indirect effects of food availability and habitat complexity to be more important drivers of bird species richness than temperature alone along the same gradient. Meanwhile, phylogenetic conservatism of functional traits was strong for the bird communities studied, suggesting that phylogenetic diversity may provide an effective proxy for ecosystem function in tropical bird assemblages.

CHAPTER 4

Fruit traits reflect adaptation to dispersers along an elevational gradient

Abstract

The relationship between fruiting plants and their frugivorous dispersers is a central component of tropical ecology. Tropical mountains form hotspots of global diversity and fruit traits have the potential to influence disperser communities across elevations. However, the ranges of traits expressed by fruits have rarely been explored in detail, especially along elevational gradients. Here we present fruit trait data from a community of fruiting plants along an elevational gradient in Papua New Guinea, focusing on the relationship between elevation and four fruit traits related to dispersal by frugivores: diameter, seed to pericarp ratio, colour and presentation (i.e. location of displayed fruits on the trunk or on the branches). Additionally we use phylogenetic information to test the “dispersal syndromes” hypothesis: that combinations of fruit traits have evolved in accordance with the preferences and sensory abilities of different frugivore guilds. We found fruit diameter to be lower at higher elevations, while seed to pericarp ratio did not change with elevation. Fruit colour showed few strong elevational trends, although colours typically attributed to attracting avian dispersers were more prevalent at higher elevations. The proportion of ramiflorous species (bearing fruits from branches) increased with elevation. All fruit traits except presentation showed little evidence of phylogenetic signal. Finally, we found fruits displaying colours attributed to mammal frugivory to be larger than “bird colour” fruits. We also found evidence for the correlated evolution of fruit size and colour, in support of the dispersal syndromes hypothesis.

Key Words: Fruit traits, elevation, dispersal syndromes, frugivory, gape limitation, phylogeny

4.1 Introduction

It has long been known that the ability of a plant to disperse its seeds constitutes an important

factor determining its survival (Janzen 1970, Connell 1971, Howe and Smallwood 1982, Beckman and Rogers 2013). In response, fruits have evolved into a variety of different forms in order to maximise seed dispersal ability in differing environments. In tropical regions for example, an estimated 70 – 90% of plant species have evolved fleshy fruits which are adapted to dispersal by vertebrate frugivores (Muller-Landau and Hardesty 2005). The frugivory mutualism thus has important implications for the evolution of fruit traits in tropical plants – traits related to accessibility and potential attractiveness to frugivores are of clear importance in determining potential fitness. An obvious example relates to fruit size: it is known that while larger seeds confer evolutionary advantages related to seedling survival (Mack 1998b, Pizo et al. 2006, Lopes Souza and Fagundes 2014), a plant's animal dispersers are limited in the maximum size of seed they can consume. This sets an upper limit on the size of fruits a plant can produce if it is to be successfully dispersed (Wheelwright 1985).

One area in which the study of tropical fruit traits related to dispersal may prove particularly informative is on mountains. Elevational gradients in the tropics are characterised by steady but rapid changes in climatic conditions across relatively small geographical distances. This typically leads to high species turnover of both plant species and their potential dispersers, and a corresponding high turnover of functional traits along tropical elevational gradients. The interaction between elevation and fruit trait profiles thus has the potential to influence local assemblages of frugivorous species occurring at different elevations (Burns 2013, Dehling et al. 2014, Bender et al. 2018) and, by trophic cascade effects, whole ecosystems. Nevertheless, while changes in many plant functional traits across elevational gradients are well studied (Swenson and Enquist 2007, Swenson et al. 2011, Hulshof et al. 2013, Read et al. 2014, Asner et al. 2017), surprisingly little is currently known about how fruit traits change with elevation on a community scale (but see Chen et al. 2016, Lu et al. 2019). On one hand this is understandable – data on fruit traits are often less readily available than for other plant characteristics. Fruits may be physically difficult to reach, and most plants fruit only intermittently and for relatively short periods. However, if we are to fully understand the functional roles of plants in tropical forests then knowledge of fruit traits is key.

Of course, individual fruit traits do not exist in isolation. Numerous studies have attempted to detect the presence of “dispersal syndromes” – combinations of fruit traits occurring together more frequently than expected by chance, based on the differing sensory and fruit-handling abilities of frugivore guilds (Gautier-Hion et al. 1985, Herrera 1992, Fischer and Chapman 1993, Lomáscolo et al. 2008, 2010, Flörchinger et al. 2010). For example, birds have acute colour vision and are generally unable to handle fruits with their limbs, meaning gape size commonly limits

the maximal size of fruits they can consume (Wheelwright 1985, Alcántara and Rey 2003). Mammals are typically larger than birds and have teeth and forelimbs able to manipulate fruits, meaning they can consume and disperse larger fruits. However, outside of the simian primates, mammals generally lack colour vision and rely more on olfactory cues to find fruits (Nevo et al. 2018). If trait matching occurs between fruits and their frugivore dispersers, we may expect to observe evidence of dispersal syndromes related to fruit colour and size. Bird-dispersed fruits should be smaller than mammal-dispersed fruits and should display colours that contrast strongly with a background of bark and foliage (Schmidt et al. 2004, Lomáscolo et al. 2008). Mammal-dispersed fruits may be more dullly coloured, as visual contrast is of limited importance for primarily nocturnal mammalian foragers. As mammals are not gape-limited, mammal-dispersed fruits may also be larger on average than bird-dispersed fruits, and should display a greater range of sizes.

Current evidence for dispersal syndromes is varied, with some studies supporting the hypothesis (e.g. Lomáscolo et al. 2008, 2010) and others rejecting it (e.g. Fischer and Chapman 1993). An alternative non-adaptive hypothesis is phylogenetic inertia, whereby fruit size and colour are determined by the size and colour of ancestral species, and frugivores disperse fruits according to pre-determined preferences for certain combinations in a process known as ecological fitting (Janzen 1985, Jordano 1995, Flörchinger et al. 2010). If dispersal syndromes occur based on trait combinations selected for by dispersers, then we should expect to see evidence of correlated evolution of the traits in question, and the appearance of these traits independently in different clades. Meanwhile the phylogenetic inertia hypothesis should predict phylogenetic clustering of these traits, indicative of shared evolutionary histories.

In this study, we use a fruit trait dataset from a continuously forested elevational gradient in Papua New Guinea to answer the following questions: i) How do four key fruit traits related to dispersal by vertebrates (diameter, seed to pericarp ratio, colour, presentation of fruits on branches versus the trunk) change with elevation? ii) Can fruits along the elevational gradient be categorised into dispersal syndromes based on size and colour? iii) To what extent are fruit traits phylogenetically conserved? New Guinea lacks primates and thus has an exclusively nocturnal mammalian fauna, meaning the prominent frugivores can be divided fairly neatly into a diurnal avian guild and a nocturnal mammalian one comprising bats, marsupials and rodents. This makes a New Guinean elevational gradient an ideal location to study the adaptations of fruits to dispersal by varying frugivore taxa.

4.2 Methods

4.2.1 Study site

The study was conducted along the north-eastern slopes of Mt Wilhelm (4,509 m), in the northern watershed of the Central Range of Papua New Guinea. The study area is located in the Usino-Bundi district of southern Madang province and comprises six study sites separated by 500 m elevation, ranging from 200 – 2,700 m above sea level (asl) (5° 44' S, 145° 20' E; 5° 49' S, 145° 09' E). The sites represent the lower portion of a complete rainforest transect spanning from the lowland floodplains of the Ramu River to the treeline at 3700 m asl (Sam et al. 2019). The habitats at the surveyed sites range from lowland alluvial forest (200 m asl) through foothill forest (700 and 1,200 m asl) to lower montane forest (2,200 and 2,700 m asl) (Paijmans 1976). Mean annual temperature recorded using data loggers decreases from 24.9° C at 200 m to 14.3° C at 2,700 m. Average annual precipitation measured by local weather stations is 3,288 mm at 200 m asl, rising to 4,400 mm at 3700 m asl, with a distinct condensation zone around 2,500 – 2,700 m asl (Sam and Koane 2014, Marki et al. 2016, Sam et al. 2019).

4.2.2 Data collection

Fruit surveys

We collected data on fruiting plants and their fruits using transect surveys (March – July 2016). 10 transects were created at each elevation, each 20 m wide and 500 m in length. This provided a total of 10 hectares of sampled area per elevation. Surveyors walked the transect route, searching carefully for any fruiting woody plants or fallen fruits. Fruiting plants were recorded only if the base of the stem occurred at least partially within the transect. When a fruiting plant was located, we collected data on plant location, diameter at breast height (DBH), growth form and taxonomy (identifying to species level where possible). When necessary, leaf voucher specimens were collected and photographs of stems taken to allow subsequent detailed identification. We also collected information on the method of fruit presentation: either cauliflorous (fruiting directly from the stem) or ramiflorous (fruiting from the branches). In the case of fallen fruits encountered on the ground, we located the most likely source plant using binoculars when necessary. In most cases this was not difficult as the plant was still displaying fruits. To calculate canopy closure, canopy photographs were taken vertically from breast height at intervals of 20 m along each transect using a Panasonic Lumix DMC TZ55 camera.

We collected up to 10 ripe fruits at random from each fruiting plant we encountered. In cases where fewer than 10 ripe fruits were reachable, we collected as many as safely possible. In cases

where fruits were completely unreachable we estimated mean fruit length and width and the colour of ripe fruits, using binoculars when needed.

Fruit measurement

We measured fruits as soon as possible after their collection to ensure that fruit traits were recorded before the onset of decomposition. Fruit dimensions were measured to the nearest 0.1 mm using digital calipers. Fruit diameter was defined as the secondary (longest orthogonal to the primary) axis, regardless of the fruit's morphological characteristics such as stem location or the orientation of seeds. Fruits were weighed using digital scales to the nearest 0.01 g. Fruit colour was defined subjectively using the basic colour categories of “red”, “orange”, “yellow”, “green”, “blue”, “purple”, “pink”, “brown”, “black” and “white”. For bicoloured fruits, only the dominant colour (covering > 50% of the fruit surface) was used in analyses. After fruit measurements were made, a subset of up to five fruits from each fruiting plant sample were dissected and the seeds removed. The number of seeds in each fruit was recorded, as was the total seed weight and pericarp weight (using digital scales as above). This enabled a broad calculation of “seed to pericarp ratio”, as the proportion of fruit weight attributable to seed weight.

4.2.3 Analyses

To enable interspecific analyses of fruit traits across elevations, we first calculated the mean trait values per species at each elevation. For species occurring across multiple elevations we calculated separate mean values for each elevation at which it was recorded, to allow for any potential intraspecific variation in fruit traits depending on elevation. In addition, we calculated fruit traits weighted by number of individual fruiting plants at each elevation.

Analyses of fruit traits across elevations

We used generalised linear models (GLMs) to test for the effect of elevation on a number of fruit traits, for both species and abundance weighted data, in R version 3.5.2 (R Core Team 2013). The GLM for fruit diameter used Gaussian error distributions and included plant DBH as a fixed effect. The GLM for the proportion of fruit weight attributable to seed weight used binomial error distributions. To test the effect of elevation on the proportion of fruiting plants bearing fruits of different colours and different presentation types, we used separate GLMs for each colour and for each presentation type, using binomial error distributions. We additionally tested for the effect of elevation on fruit colours when grouped into two “types” (see “Fruit Syndromes” below), again using a GLM with binomial error. Tukey pairwise comparisons (calculated using the “emmeans” function in *emmeans* package; Lenth et al. 2018) were used to

adjust p-values during multiple comparisons.

Canopy closure

Canopy closure was assessed in Matlab version 2019b (Mathworks 2019) by measuring the mean percentage cover of foliage in 60 canopy photos from each elevation, using code developed by Korhonen and Heikkinen (2009).

Phylogenetic analyses

For phylogenetic analyses of fruit traits, we used a global phylogeny adapted by Smith and Brown (2018) from GenBank release 218 (<ftp://ftp.ncbi.nlm.nih.gov/genbank>) and Open Tree of Life synthetic tree (taxonomy version 3; <https://tree.opentreeoflife.org/about/synthesis-release/v9.1>). The phylogeny was subjected to hierarchical analysis with individual phylogenies constructed for major clades, and using a backbone provided by Open Tree of Life version 9.1. The adapted phylogeny used here (labelled “ALLOTB”) can be found at https://github.com/FePhyFoFum/big_seed_plant_trees/releases. We used the “prune.sample” function in the R package *picante* (Kembel et al. 2010) to subset this global phylogeny to include only species found in our dataset from the Mt. Wilhelm study sites.

To determine whether the categorical traits of colour and presentation were clustered or randomly distributed across the phylogeny, we used a null model analysis. We first calculated the mean phylogenetic distance (MPD) between individuals of each colour and of each presentation type, and then compared this to a distribution of values generated by shuffling the tip labels across the phylogeny 999 times. We then assessed the deviation of observed and null values. Null models were implemented using functions in the package *picante*. For the continuous traits of fruit diameter and seed proportion, we used Pagel’s lambda (λ) (Pagel 1999a) to test for phylogenetic signal in the trait data. Pagel’s λ uses phylogenetic data to assess whether a trait has evolved independently of phylogeny (low phylogenetic signal) or if it conforms to an evolutionary model expected under Brownian motion (high phylogenetic signal) (Molina-Venegas and Rodríguez 2017).

Fruit syndromes

The fruit syndrome hypothesis predicts correlated evolutionary change in fruit size and colour according to dispersal guild (Lomáscolo et al. 2008). To test the hypothesis that fruit traits corresponding to dispersal by birds and mammals evolved together, we first divided fruits into binary size and colour categories corresponding to each dispersal syndrome. Fruits were divided by colour into “Type A” (green, brown, orange or yellow) and “Type B” (red, black, blue, purple,

pink or white), according to Janson's (1983) classification. Fruits were divided by size based on mean fruit diameter for all fruiting plant species recorded in our data. We performed Pagel's likelihood ratio test of binary correlations (Pagel 1994, 1999b), using the subset of fruiting plant species for which phylogenetic data was available, on the two binary categories of colour (Type A vs. Type B) and size (large vs. small), using the "fitPagel" function in the package *phytools* (Revell 2012, 2019). Pagel's test compares the goodness of fit of a model of correlated evolution to one of independent evolution, taking into account phylogenetic branch lengths.

To test whether Type A fruits were larger overall than Type B fruits (regardless of phylogeny), we performed a Mann-Whitney U test (Mann and Whiney 1947) using fruit diameter per fruiting plant as the response variable. To test whether variation in fruit diameter was greater for Type A fruits than for Type B fruits, we used a Fligner-Killeen test, which is a non-parametric test for assessing the homogeneity of variances (Fligner and Killeen 1976).

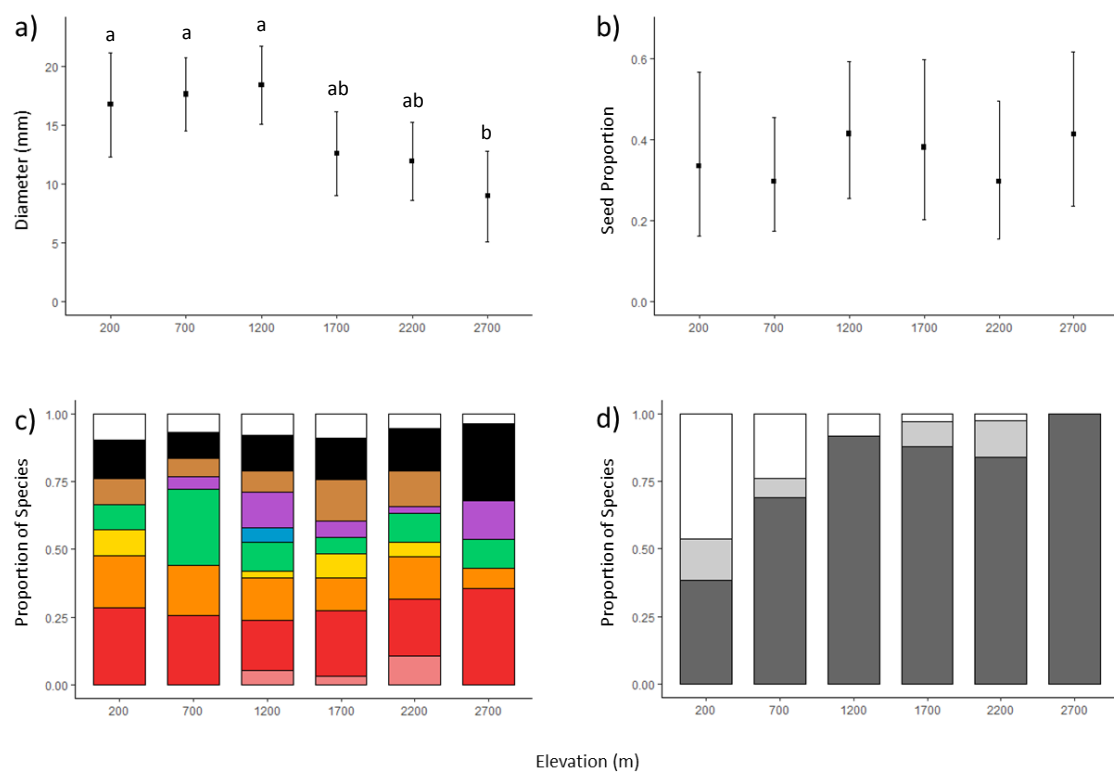


Figure 4.1. Effect of elevation on four fruit traits related to dispersal by frugivores, weighted by plant species. a) Mean fruit diameter per fruiting plant species is represented by squares, with error bars displaying 95% confidence intervals (CIs). Letters above points denote significant differences after adjusting for multiple comparisons using Tukey pairwise tests. b) Mean proportion of fruit weight attributable to seed weight for fruiting plant species at each elevation, with 95% CIs. c) Proportion of fruiting plant species displaying fruits of each colour (top to bottom: white, black, brown, purple, blue, green, yellow, orange, red and pink) at each elevation. d) Proportion of fruiting plant species bearing cauliflorous fruits (white bars), ramiflorous fruits (dark grey bars) and a combination of both presentation types (light grey bars) at each elevation.

4.3 Results

We collected and measured ripe fruits from a total of 1,062 fruiting plants across all elevations, representing 167 species and morpho-species (Appendix Table A4.1). Of these, 83 species were sufficiently identified to be used in phylogenetic analyses. Outside of phylogenetic analyses, we used data from all fruiting plant species and morpho-species.

Mean fruit diameter showed a significant decrease towards higher elevations when weighted both by species ($p < 0.01$; Figure 4.1a) and individual fruiting plants ($p < 0.01$; Appendix Figure A4.1a). Fruit diameter was also positively correlated with fruiting plant DBH ($p < 0.01$; Appendix Figure A4.2). The mean proportion of fruit mass attributable to seeds did not change with elevation ($p = 0.86$; Figure 4.1b). Fruit colour showed differing patterns depending on whether weighted by species or individual, although most colours were represented at all or nearly all elevations. Five colours (red, orange, green, black and white) were represented at all elevations (Figure 4.1c, Appendix Figure A4.1c). Using species-weighted data, most individual fruit colours did not show strong elevational trends (Table 4.1, Appendix Table A4.2), although green fruits peaked at 700 m and purple fruits at 2,700 m. In contrast, fruit colour divided by type showed a

Table 4.1. Results of generalised linear models testing the effect of elevation on fruit diameter, seed to pericarp ratio, fruit colour and presentation type for fruiting plant species along the elevational gradient. Significant ($p < 0.05$) individual pairwise interactions between elevations are presented, after correcting for multiple comparisons using Tukey pairwise comparisons. Significance values for all pairwise comparisons are displayed in full in Appendix Table A4.2.

Parameter	Category	Deviance	p-value	Significant Pairwise Interactions
Fruit Diameter		2338.1	<0.01	700-2700; 1200-2700
Seed Proportion		1.89	0.86	None
Colour	Red	9.89	0.08	None
	Orange	11.99	0.03	None
	Yellow	21.69	<0.01	None
	Green	21.79	<0.01	700-1700; 700-2200
	Blue	8.62	0.13	None
	Purple	45.47	<0.01	700-2700; 1700-2700; 2200-2700
	Pink	37.13	<0.01	1700-2200
	Brown	18.35	<0.01	None
	Black	15.68	<0.01	1700-2700
	White	2.7	0.75	None
Colour Type		35.73	<0.01	700-2700; 1200-2700; 1700-2700
Presentation	Cauliflorous	36.79	<0.01	None
	Ramiflorous	55.09	<0.01	200-700; 200-1200; 200-1700; 200-2200; 200-2700; 700-2700

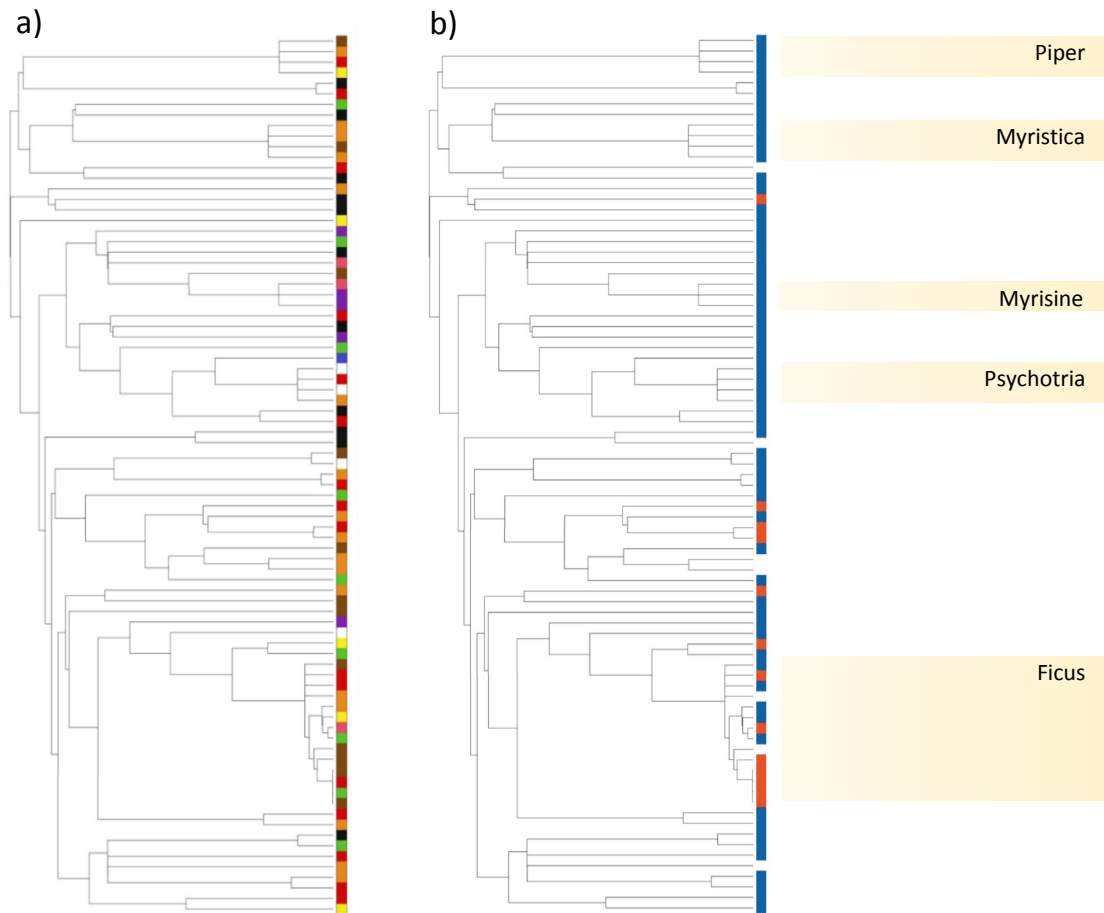


Figure 4.2. Phylogenies of the 83 fruiting plant species for which phylogenetic data was available, including data on the predominant colour of fruits from each species (a) and the presentation method of fruits (b). Blue squares in (b) represent ramiflorous fruiting species, while orange squares are cauliflorous species. Species without squares attributed to them indicate a combination of ramiflory and cauliflory within a single species. Genera represented by more than two species are displayed to the right.

significant trend – the proportion of species bearing Type B coloured fruits increased with elevation ($p < 0.01$). Fruit presentation similarly showed a clear trend with elevation: less than 40% of fruiting species were exclusively ramiflorous at 200 m, increasing to 100% at 2,700 m ($p < 0.01$; Figure 4.1d). We observed a similar increase with elevation in individual-weighted data ($p < 0.01$; Appendix Figure A4.1d). Finally, canopy closure showed a significant decreasing trend with increasing elevation ($p < 0.01$; Appendix Figure A4.3).

Phylogenetic analysis on the categorical traits of fruit colour and presentation showed broadly contrasting patterns. Of all fruit colours, null model analysis found only brown fruits to be significantly phylogenetically clustered (SES.MPD = -2.21, $p = 0.03$), while purple fruits showed a near-significant pattern (SES.MPD = -1.36, $p = 0.07$). All other colours showed patterns that did

not differ from random expectations (Figure 4.2a, Appendix Table A4.3). Fruit presentation however showed evidence of significant phylogenetic clustering: cauliflorous fruits were clustered significantly more than expected under null models (SES.MPD = -7.12, $p < 0.01$; Figure 4.2b). For the continuous traits of fruit diameter and seed to pericarp ratio, we found little evidence of phylogenetic clustering. Fruit diameter showed a low phylogenetic signal ($\lambda = 0.29$, $p = 0.02$), while seed to pericarp ratio showed a similarly low, although in this case non-significant, result ($\lambda = 0.32$, $p = 0.34$).

Both phylogenetic and non-phylogenetic analysis revealed significant relationships between fruit colour and size. We observed a significant phylogenetic association between large and small fruits and Type A and Type B coloured fruits respectively (likelihood ratio = 14.33, $p < 0.01$; Appendix Figure A4.4), showing evidence of correlated evolution of fruit colour and size. Regardless of phylogeny, we found Type A coloured fruits to have significantly greater median diameter than Type B fruits (median_{Type A} = 14.06 mm, median_{Type B} = 10.2 mm, $W = 6026$, $p < 0.01$; Figure 4.3), and to show a greater variation in size (Fligner-Killeen median $\chi^2 = 18.04$, $p < 0.01$; Figure 4.3). The mean diameters of each fruit type were 17 mm (Type A) and 12.8 mm (Type B).

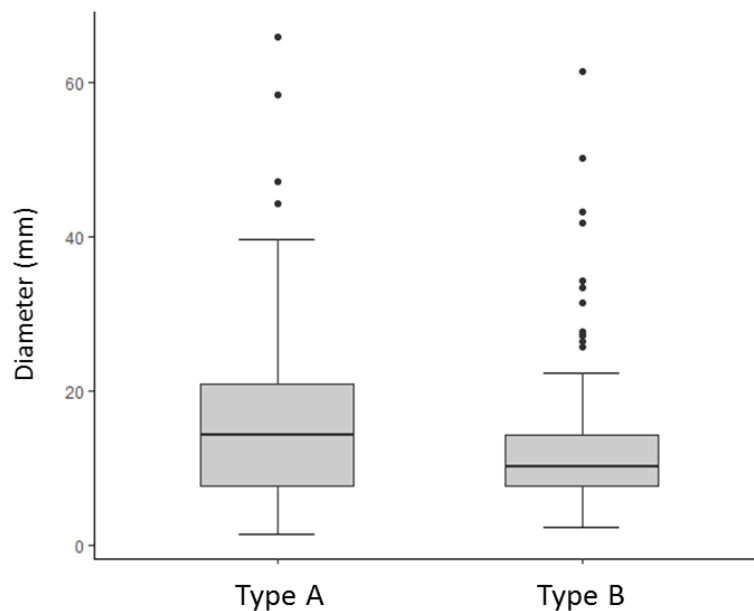


Figure 4.3. Relationship between fruit “type” and fruit diameter for all fruiting plant species and morpho-species recorded along the Mt Wilhelm gradient. Type A fruits include green, yellow, orange and brown fruits. Type B fruits include red, pink, purple, blue, black and white fruits (Janson 1983). Grey boxes span the first and third quartiles of fruit diameter and the horizontal line within each box represents the median diameter. Vertical lines indicate maximum and minimum observations falling within 1.5 times the interquartile range. Remaining observations are displayed as black circles.

4.4 Discussion

In this study we investigated four fruit traits relevant to dispersal by vertebrate frugivores (fruit diameter, seed to pericarp ratio, colour and presentation) along an elevational gradient in Papua New Guinea. To our knowledge this represents the first comprehensive summary of fruit traits across a fruiting plant community spanning a forested tropical elevational gradient. We also used data from fruit colour and size to test evidence in support of the dispersal syndromes hypothesis.

4.4.1 Fruit traits and elevation

Diameter

We found mean fruit diameter to decrease towards higher elevations, after a plateau between 200 and 1,200 m. Seed to pericarp ratio of fruits did not change across elevations, suggesting a similar decrease in seed volume per fruit towards higher elevations. Our result mirrors a trend observed by Almeida-Neto et al. (2008), who found fruit diameter to be lower at higher elevations among 135 forest communities in the Brazilian Atlantic rainforest. A number of potential factors could explain the observed pattern: i) A decrease in productivity with decreasing temperature at higher elevations limits the production of large fruits. ii) Fruit size is constrained by plant size, which in turn decreases with elevation. iii) Denser canopies at low elevations lead to lower light conditions on the forest floor, presenting a stronger evolutionary advantage to large-seeded plants (Foster 1986, Walters and Reich 2000). iv) A lack of large-gaped frugivores at high elevations prevents the seed dispersal of large-fruited plants. These hypotheses are not mutually exclusive and our data likely reflect a combination of factors; here we briefly discuss each one.

As temperature decreases monotonically with elevation, we may expect a similarly steady decrease in fruit diameter if productivity is a dominant factor in determining seed size. However, Almeida-Neto et al. (2008) found that differences in fruit diameter with elevation were primarily not attributable to temperature: low-elevation communities had greater mean fruit diameter than did higher-elevation communities with identical annual temperature values (i.e. those from warmer areas). Coupled with the observation from our data that fruit size does not follow a monotonic decrease with elevation, the evidence suggests that productivity alone cannot account for the pattern in fruit diameter observed here. Regarding the question of whether fruit size is constrained by plant size, we found fruit diameter to be positively correlated with fruiting plant DBH. However, elevation still explained changes in fruit size after accounting for DBH.

Canopy closure decreased towards higher elevations, allowing more light to reach the forest floor. While this supports the hypothesis that lower light levels at low elevations could promote the need for larger seeds, it is difficult to explicitly attribute seed size to differing light levels without conducting controlled experimental studies. Previous such studies have found weak evidence for the interaction (e.g. Leishman and Westoby 1994). Furthermore, in a survey of seed weight across the Neotropics (Rockwood 1985), elevation was not found to affect seed weight in 6 out of 7 plant families. While we found no elevational change in the mean total seed weight per fruit, we lack data on individual seed size, meaning our data cannot fully resolve this issue.

The relationship between disperser size and fruit size is complex and it is difficult to determine a cause-effect relationship between the two: does a lack of large fruits at high elevations prevent large frugivores from feeding effectively, or does a lack of large-gaped dispersers at high elevations prevent large-fruited species from establishing? While it may prove impossible to untangle cause and effect with the current evidence, the association between fruit size and frugivore size is clear. Indeed, trait matching between fruits and frugivore dispersers has been noted by a number of studies (Burns 2013, Dehling et al. 2014, Muñoz et al. 2017, Bender et al. 2018). Our data, showing a low-elevation plateau in fruit diameter followed by a decline towards high elevations, is consistent with a change in the frugivore community observed between lowland and highland forest. In the area of study, Sam et al. (2019) noted a mid-elevational shift in which many large-gaped frugivores such as the Papuan hornbill *Rhyticeros plicatus* and the majority of pigeon species are confined to forests from 200 – 1,200 m, a trend also recorded in Chapter 3 of this thesis. Furthermore, the relative importance of frugivory by mammals, which are not gape-limited and may consume larger fruits than birds, declines with elevation. McCain (2007a, 2007b) recorded a decrease in mammal species diversity with increasing elevation in Papua New Guinea, and a relative decline in mammalian (especially bat) frugivory rates with elevation was observed in the study area (Chapter 5). Such a trend has also been noted in other regions (Almeida-Neto et al. 2008).

Colour

There were few clear trends in specific fruit colours along the elevational gradient. Nevertheless, some colours showed significant variation in prevalence between elevations: the proportion of species bearing green fruits peaked at 700 m, while purple and black fruits showed a peak at 2,700 m. Although no relationship is apparent between fruit colour and specific avian colour preferences along the gradient (Chapter 5), the dispersal syndrome hypothesis would predict a higher prevalence of “bird syndrome”- coloured fruits (red, pink, purple, blue, black, white) with

the increased relative importance of avian frugivory at higher elevations. Such a trend was indeed observed in this study. Fruit colour may also reflect an adaptation to abiotic factors (Burns 2015, Valenta et al. 2018). Anthocyanins, which are pigments responsible for blue, deep red, purple and black colours in fruit, additionally serve an important role in protecting plants from abiotic stressors such as photo-oxidation, heat and drought. Thus their presence in other plant tissues and in fruits may be coupled, meaning fruit colours characterised by high anthocyanin content could be simply a by-product of this effect (Stournaras and Schaefer 2017). Indeed, Zoratti et al. (2015) found anthocyanin concentrations in berries to increase with elevation and light intensity, suggesting that high light levels favour their production. Such a pattern could explain the prevalence of purple and red fruits at higher elevations in our study sites, where the canopy is more open and a greater proportion of the forest receives direct sunlight. Additionally, fruits reflecting light mainly in the ultraviolet part of the spectrum are more protected from ultraviolet radiation (Hakala-Yatkin et al. 2010), which could provide an adaptive explanation in particular for the prevalence of purple fruits at 2,700 m where the canopy is most open.

Presentation

We found elevation to have a significant effect on the presentation method of fruits. Cauliflorous fruits were relatively common at 200 m but steadily declined with elevation and were absent at 2,700 m. Such a pattern is consistent with a decline in mammalian frugivory with increasing elevation. Unlike birds, which approach fruits from the air and typically require a branch on which to perch while feeding, arboreal mammals may easily access fruit presented on the main stem of a fruiting plant. Bats, meanwhile, are known to preferentially forage on fruits borne away from foliage, including cauliflorous fruits (Whittaker and Jones 1994). Mammalian diversity in New Guinea is known to peak at low to mid elevations, especially bat diversity which drops rapidly with elevation (McCain 2007a, 2007b). Indeed, frugivory rates by bats in particular show a sharp decrease above mid elevations in the area of study (Chapter 5). It should be noted however that cauliflory also showed significant phylogenetic clustering in this study, meaning the effects of phylogenetic inertia cannot be discounted in structuring the observed patterns. Nevertheless, as with fruit diameter, the decrease in cauliflory with elevation suggests a relatively greater importance of avian frugivores at higher elevations, as observed by Almeida-Neto et al. (2008).

4.4.2 Fruit syndromes

Our results support the dispersal syndrome hypothesis. Across elevations, we demonstrated a

clear relationship between fruit “type” (groups of colours commonly attributed to dispersal by either mammals or birds) and fruit diameter. We found Type A fruits (brown, green, yellow and orange) to be larger than Type B fruits (red, pink, purple, blue, black and white) and to show a greater variation in diameter. Both of these factors are consistent with adaptation to dispersal by mammalian versus avian frugivores. Gape limitation sets an upper limit on the size of fruits that birds can consume, while mammals more commonly consume fruits piecemeal (Lomáscolo et al. 2008). Additionally, mammalian frugivores are larger on average than birds and have wider digestive tracts (Sallabanks and Courtney 1992). Therefore we should expect mammal-dispersed fruits to be larger on average than bird-dispersed fruits, while showing a greater range in sizes due to the greater range of feeding techniques employed by mammals (Howe 1986) and the lack of a lower size limit on consumable fruits.

The association between fruit colour type and diameter was shown to occur in separate clades across the phylogeny of fruiting plants, suggesting correlated evolution of size and colour type. This is despite very little evidence of phylogenetic clustering of individual fruit colours. Indeed, specific fruit colours are known to be evolutionarily labile. In a wide-ranging study of avian frugivory in a subtropical Andean forest, Ordano et al. (2017) found only weak phylogenetic effects on fruit chromatic contrast and conspicuousness of fruiting displays. A similarly broad study on fruit traits in the Brazilian Atlantic forest found no significant phylogenetic signal in fruit colour, although it was present in several other fruit traits (Cazetta et al. 2012). Stournaras et al. (2013) found little indication of phylogenetic constraints on fruit colour at local and global scales, despite fruit colour being limited by other factors such as chemical constraints. The fact that individual fruit colours are spread randomly across the phylogeny, but that colour still correlates with fruit size at the broader level of “fruit type”, supports the hypothesis that fruit colours have adapted independently to dispersal by different frugivore guilds. Thus we can discount the hypothesis of phylogenetic inertia as a means of explaining observed fruit colour/size combinations.

4.4.3 Summary

This study is the first to measure a range of fruit traits relevant to dispersal by frugivores across a community of fruiting plants along a tropical elevational gradient. Fruit traits such as size, colour and presentation are undoubtedly important in determining frugivory by different guilds. Therefore the range of traits displayed by fruits has the potential to influence disperser communities at different elevations, and by extension seed dispersal and ultimately plant community assembly across elevational gradients. The shifting distributions of plants and

frugivores resulting from climate change has the potential to disrupt these relationships, and should be a focus of further study (Mokany et al. 2014).

CHAPTER 5

Bird preferences for fruit size, but not colour, vary in accordance with fruit traits along a tropical elevational gradient

Abstract

Birds constitute one of the most important seed-dispersal agents globally, especially in the tropics. The feeding preferences of frugivorous birds are therefore potentially of great ecological importance. A number of lab-based and observational studies have attempted to ascertain the preferences of certain bird species for certain fruit traits. However, relatively little attention has been paid to community-wide preferences of frugivorous birds and the potential impact this may have on fruit traits on a broader scale. Here we used artificial fruits of different colours (green, purple and red) and sizes (19 mm, 13 mm and 7 mm diameter) to investigate community-wide fruit trait preferences of birds at three sites along an elevational gradient in Papua New Guinea. We recorded attack rates on artificial fruits as visible impressions made by a bird's beak during a feeding attempt. We also measured the sizes and colours of real fruits at each site, and the abundance and gape widths of frugivorous birds, allowing for comparisons between bird feeding preferences and bird and fruit traits. The total number of attacks on artificial fruits at each elevation showed a strikingly similar pattern to that of understory frugivore abundance. Red and purple fruits were universally preferred to green, and attacked at similar rates to one another, regardless of elevation, and despite strong elevational patterns in real fruit colour. However, elevation had a significant effect on fruit size preferences. A weak, non-significant preference for large fruits was recorded at 700 m, while medium fruits were strongly preferred at 1,700 m and small fruits at 2,700 m. These patterns mirror those of both real fruit size and bird gape width along the gradient, suggesting the potential for selective pressure of birds on fruit size at different elevations.

Key words: Fruit size, fruit colour, seed dispersal, frugivory, artificial fruits, elevation, gape width, abundance

5.1 Introduction

Seed dispersal is a key factor determining tree community assembly (Levin et al. 2003, McConkey et al. 2012, Harrison et al. 2013). It is estimated that 70 – 90% of tropical tree species bear fleshy fruits that are primarily dispersed by vertebrate frugivores (Muller-Landau and Hardesty 2005, Chen et al. 2016), and that birds represent the majority of these frugivores in most tropical regions (Willson et al. 1989, McConkey and Drake 2002, Corlett 2017). Feeding preferences of birds thus have the potential to be a significant selective pressure on the evolution of fruit traits (Lord 2004, Eriksson 2016), as seed dispersal is known to be related to plant fitness (Howe and Smallwood 1982, Beckman and Rogers 2013, Snell et al. 2019). However, the preferences of birds for different fruit traits in different environments is poorly known.

Birds are known to select fruits visually, primarily using cues such as colour and size (Corlett 2011, Schaefer and Ruxton 2011, Duan et al. 2014). According to zoological classifications of fruit syndromes, bird-dispersed fruits are typically categorised as brightly coloured (Janson 1983, Gautier-Hion et al. 1985, Lomáscolo et al. 2008). However, it is not fully understood why birds choose certain fruit colours over others. Some evidence points to fruit colour cues signalling high nutritional reward (Schaefer et al. 2008, 2014, Cazetta et al. 2012). Alternatively, an important factor may simply be conspicuousness, i.e. fruits that contrast against a background of foliage are more likely to be noticed by birds (Schmidt et al. 2004, Ordano et al. 2017, Nevo et al. 2018). Direct selection for specific colours based on innate preferences of birds has found little support (Willson et al. 1990).

Fruit size preferences of birds may similarly represent a combination of a choice and physical limitations. Unlike mammalian frugivores, birds usually swallow fruits whole (Lomáscolo et al. 2008), meaning their gape size limits the maximal diameter of fruits they can consume (Wheelwright 1985, Corlett 1998, 2017). This imposes an upper limit on the size of seed that a given bird can disperse, although not a lower limit (Wheelwright 1985). Nevertheless, there is some evidence suggesting that larger birds tend to preferentially feed on larger fruits (Sobral et al. 2010a, 2010b, Burns 2013, Chen and Moles 2015). The matching of traits in this way (e.g. fruit size and bird body/gape size) has recently gained attention for its apparent importance in structuring species interaction networks, particularly mutualistic ones such as frugivory (Dehling et al. 2014, González-Castro et al. 2015, Garibaldi et al. 2015, Muñoz et al. 2017, Bender et al. 2018).

Determining the importance of fruit traits attractive to birds is a major challenge due to the covariation of traits in uncontrollable ways (Levey and Grajal 1991). The use of artificial fruits is

one way to independently manipulate fruit traits. Analyses using artificial fruits have been largely limited to laboratory experiments in which birds feed on gelatine- or dough-based fruits under artificial conditions (Willson et al. 1990, Levey and Grajal 1991, Sallabanks 1993, Puckey et al. 1996, Duan et al. 2014). However, it is known that birds under laboratory conditions may exhibit unnatural feeding behaviours (Alves-Costa and Lopes 2001). Additionally, the existing studies were generally limited to a few individuals of one to four focal bird species, which limits their broader applicability. If we are to understand the evolutionary implications of bird feeding preferences on a community level, experiments need to be conducted at the community scale.

Field-based approaches using artificial fruits constructed from waterproof modelling clay offer a solution to this problem. Birds readily attack these fruits but rarely swallow them (Alves-Costa and Lopes 2001). Fruits may thus be deployed in the field for a number of days and exposed to the entire frugivore community. Furthermore, the marks left in the fruits reveal some information about the feeding behaviour of the birds that attempted to eat them. The fruits are easy to produce in large numbers and traits such as size and colour can be precisely and individually manipulated. Few studies have used artificial modelling clay fruits in this way (Alves-Costa and Lopes 2001, Galetti et al. 2003, Cazetta et al. 2012, Vollstädt et al. 2017), and to our knowledge none have used them to experimentally test avian frugivore preferences of fruit traits (especially size) across environmental gradients.

Tropical mountains provide an opportunity to study bird preferences for fruit traits in different natural environments. Plant and bird communities are known to change with elevation, as do their traits (Swenson et al. 2011, Dehling et al. 2014). For example, the mean body size and abundance of avian frugivores are known to reduce with increasing elevation (Terborgh 1977, Sam et al. 2017), while mean fruit size and fruit colour similarly show changing patterns with elevation (Guo et al. 2013, Zoratti et al. 2015, Lu et al. 2019, Chapter 4 of this thesis).

Here we attempt to determine avian frugivore preferences for fruit size and colour at different elevations (low, mid and high: 700, 1,700 and 2,700 m above sea level, respectively) along a tropical elevational gradient in Papua New Guinea. This is made possible by determining the number of feeding attempts on artificial modelling clay fruits of different size (small, medium and large: 7 mm, 13 mm and 19 mm diameter respectively) and colour (green, purple and red). We compare this to the relative size and colour prevalence of real fruits, and the gape width of frugivorous birds present at each site. We hypothesise that: i) Birds prefer fruit sizes and colours that are naturally common at a given elevation, and preferences reflect bird gape limitation ii) The number of feeding attempts on artificial fruits decreases with increasing elevation because

a relatively higher abundance of frugivores, which we expect in lowlands, should naturally lead to higher rates of frugivory (Smith and McWilliams 2014).

5.2 Methods

5.2.1 Study sites

We conducted the study along the north-eastern slopes of Mt Wilhelm (4,509 m), in the northern watershed of the Central Range of Papua New Guinea (Appendix Figure A5.1). The study area is located in the Usino-Bundi district of southern Madang province and comprises three study sites separated by 1,000 m elevation, ranging from 700 – 2,700 m above sea level (asl) (5° 43.6' S, 145° 15.5' E; 5° 48.9' S, 145° 09.3' E). The sites represent part of a complete rainforest transect running from the lowland floodplains of the Ramu River to the treeline (Sam and Koane 2014). The habitats at the surveyed sites range from foothill forest (700 m asl) to lower montane forest (2,700 m asl) (Paijmans 1976). Mean annual temperature recorded using data loggers decreases from 21.97° C at 700 m to 14.34° C at 2,700 m. Average annual precipitation measured by local weather stations is 3,288 mm in the lowlands, rising to 4,400 mm at the tree line, with a distinct condensation zone around 2,500 – 2,700 m asl (Sam and Koane 2014, Marki et al. 2016, Sam et al. 2017, 2019).

5.2.2 Artificial fruit exposures

Spherical artificial fruits (hereafter “fruits”) were prepared from non-toxic modelling clay (Koh-I-Noor Hardtmuth, Ceske Budejovice, Czech Republic; Sam et al. 2015) in three different colours (green, red and purple) and three different sizes (19 mm, 13 mm and 7 mm diameter – hereafter “large”, “medium” and “small” respectively), giving a total of nine unique size/colour combinations. Colours and sizes were selected based on the observed prevalent characteristics of ripe fruits at each of the three survey sites. At each site, 180 artificial fruits of each colour/size combination were simultaneously exposed in six clusters of 30 fruits, during August and September 2017. This gave a total of 1,620 exposed fruits at each elevational study site (30 fruits * 6 clusters * 3 colours * 3 sizes). Each fruit cluster was exposed on a separate individual host tree. Host trees were ca. 10 m apart from each other, with fruits placed between two and three metres above the ground. Fruits were attached to the host tree using florist’s wire. The fruits were no closer than 10 cm to each other, and no further than 1 m from the end of the branch (Ferber et al. 2016). Host trees were selected based on two criteria: having enough branches to allow the attachment of 30 fruits within the required height, and not currently displaying any

fruits of their own or showing evidence of recent fruiting (e.g. decaying fruits on the ground). A minimum of 10 m separated each fruit cluster.

Fruits were checked for evidence of potential attack 72 hours after initial exposure. At this point, any damaged or removed fruits were replaced. After a further 72 hours, the fruits were again checked and removed, giving a total of 144 hours (six days) of exposure time (and thus 1620×2 surveys = 3,240 surveyed fruits per elevation). During both the intermediate check and the final collection, any bitten, pecked or removed fruits were noted, including attacked fruits that had fallen to the ground. The taxonomic identity of the attacker was ascertained based on characteristics of the impressions left in the modelling clay (Alves-Costa and Lopes 2001). These were categorised broadly as: bird, arboreal mammal, bat, and arthropod. For bird-attacked fruits, additional information was collected on the feeding technique attempted by the attacker, based on physical characteristics of the impressions left on the fruit (see below for details).

We assigned categories to all bird-attacked fruits (Appendix Figure A5.2): i) Held: These fruits had clearly been grasped on opposite sides, suggesting the attacker was capable of swallowing the fruit. ii) Intermediate: These fruits showed imprints of upper and lower mandibles but whose maximal distance apart was less than the fruit's diameter. iii) Pecked: These fruits showed only a single hole, characteristic of pecking.

5.2.3 Bird surveys

Bird abundance data was collected using point counts (February – July 2016). At each of the three elevations, we surveyed a 2,250 m transect comprising 16 points separated by 150 m. Transects predominantly followed those of Sam and Koane (2014). Surveys began at sunrise (approximately 05.30 am) and were completed by 11.00 am. We replicated the surveys of all points three times, on three different days. Individual point counts lasted 15 minutes and commenced a few minutes after arriving at a point to minimise the effects of disturbance caused by arrival (Bibby et al. 2000). We recorded all birds seen or heard within a radius of 50 m. To minimise multiple counts of one individual, we followed the protocol of Sam and Koane (2014): that is, we only counted multiple conspecifics if two or more individuals could be heard singing simultaneously or from clearly different locations within a period of a few seconds. Points were located using Garmin GPSmap 62S handheld GPS units.

For the analytical purposes of this study, we considered only species richness and abundance of obligate frugivores that are known to feed primarily in the forest understory. Obligate frugivores are known to form a disproportionately important component of plant-frugivore networks in tropical forests (Palacio et al. 2016, de Assis Bomfim et al. 2018). First, birds were classified into

feeding guilds based on data from Sam et al. (2017), who analysed the diets of Mt Wilhelm bird species by using emetic tartar to induce regurgitation. Birds were classified as understory frugivores based on information on foraging height from Pratt and Beehler (2015) and our own observations. Gape width measurements were taken from museum specimens of birds collected from the Mt Wilhelm study sites and stored in the Natural History Museum of Denmark, University of Copenhagen. Gape width (defined as the distance between the points where the two mandibles join at the base of the beak) was measured on male and female adult birds to the nearest 0.1 mm using digital calipers.

5.2.4 Fruit surveys

Data on size and colour of real fruits at each elevation were collected using transect surveys of fruiting woody plants (March – July 2016). We created 10 transects at every elevational study site, each measuring 20 * 500 m, to give a total of 10 hectares surveyed per elevation. We collected fruits (both from branches and fallen onto the ground) from all fruiting trees present within the transects. We identified fruiting plants to species level where possible. Collected fruits were measured along their secondary axis, giving a measure of mean fruit diameter per individual plant. The secondary axis was used because this represents the minimal dimensions restricting possible dispersal by gape-limited frugivores such as birds (Mazer and Wheelwright 1993). Each collected fruit was photographed, and its colour noted. For bicoloured fruits, both colours were noted, although only the most dominant colour (covering > 50% of the fruit's surface) was used in analyses.

5.2.5 Data analysis

All data analyses were performed using R version 3.5.2 (R Core Team 2013). To test the hypothesis that preferences of birds for certain fruit traits would differ depending on elevation, we modelled the proportion of attacked fruits as a function of fruit size, fruit colour, elevation and their interactions using a generalised linear model (GLM) with binomial error structure and a logit link. Backwards elimination procedure was then used to sequentially simplify the model for each variable that was not significant. The importance of the eliminated variable was determined using likelihood ratio tests. Parameters of the final model were considered significant at $p < 0.05$ and Tukey pairwise comparisons (“emmeans” function in package *emmeans*; Lenth et al. 2018) were used to adjust p-values during multiple comparisons.

In order to test the effect of elevation on the proportion of fruits held in the beak by birds and thus their potential seed dispersal success, we used a GLM with binomial error structure to

investigate the effect of fruit size, fruit colour, elevation and their interactions on the proportion of fruits that had been “held” only (as defined above) while excluding those not held (i.e. “pecked” + “intermediate attack”). As above, backwards elimination and likelihood ratio tests were used to select an appropriate model, and Tukey pairwise comparisons were used to adjust p-values during multiple comparisons. We used ‘held’ as a response variable in our model.

Data analysis on bird and fruit characteristics was carried out as follows:

- 1) To determine the differences in frugivore gape size across elevations, we used a GLM with Gaussian error distributions; gape size of each recorded species was our response variable. To characterise the effects of elevation on the upper limit of gape size, we used a linear quantile regression, using the *quantreg* package in R (Koenker et al. 2019). We selected the 95th quantile to approximate the upper limit of gape width. In addition, we compared community-weighted mean gape size across elevations using a separate GLM with Gaussian error distributions using abundance-weighted data in which the response variable was individual gape size.
- 2) To determine the variation in fruit size across elevations, we used a GLM with Gaussian error distributions; mean fruit diameter per fruiting plant species was our response variable. We again used quantile regression (selecting the 95th quantile) to approximate the upper limit of fruit diameter. As with gape size, we performed a separate GLM with Gaussian error distributions using data weighted by abundance of individual fruiting plants.
- 3) To determine the abundances of natural fruit colours represented in this study (green, purple and red) across elevations, we used three separate GLMs, each with binomial error distributions. The three response variables were the proportion of all individual fruiting plants that bore green, purple and red fruits respectively.
- 4) To determine the differences in understory frugivore abundances across elevations, we used a GLM with Poisson error distributions; understory frugivore abundance at each point was our response variable.

5.3 Results

We exposed a total of 9,720 artificial fruits along the whole elevation gradient, during which 510 fruits were attacked by birds and 241 fruits were attacked by other taxa: arboreal mammals (83 fruits), bats (30) and arthropods (128) (Appendix Table A5.1). Eleven fruits were missing entirely and were excluded from analyses.

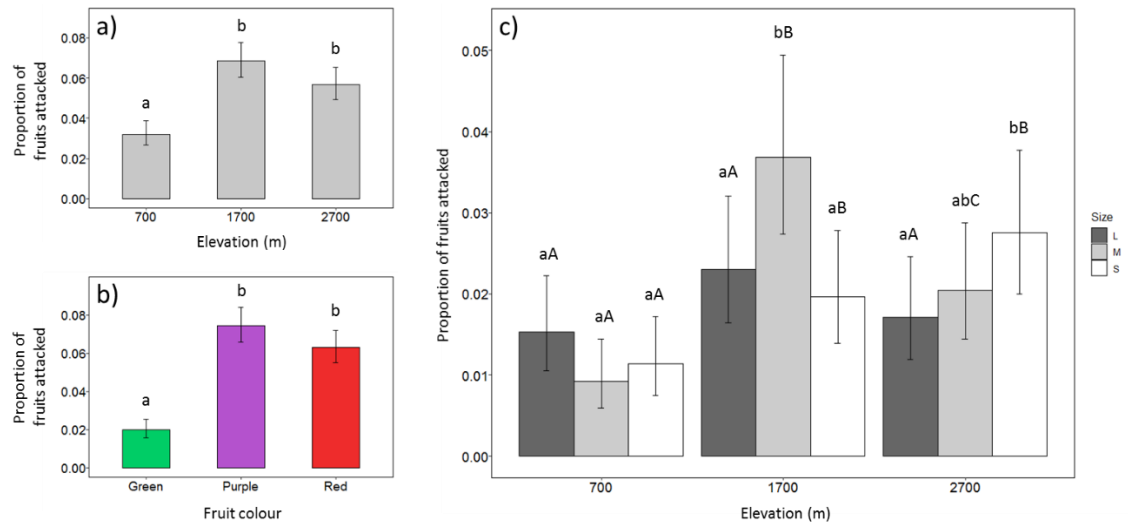


Figure 5.1. Mean proportion of artificial fruits (per 30-fruit cluster) showing evidence of bird feeding attempts across elevations (a), fruit colour (b) and for fruit sizes at each elevation (c). Overall attack rates on different-sized fruits were similar across the gradient, so not displayed here. Error bars represent 95% confidence intervals in all cases. Letters above bars denote the significance of multiple comparisons between attack rates, after adjusting using Tukey pairwise comparisons. In part (c), dark grey bars represent large fruits, light grey bars represent medium fruits and white bars represent small fruits; Letters represent significantly different attack rates on fruits of each size category at a given elevation (lower case), and between each elevation for a given size category (upper case).

Avian attack rates on fruits were significantly lower at 700 m in comparison with attack rates at 1,700 m and 2,700 m, but attack rates at 1,700 m and 2,700 m were similar (Figure 5.1a; Table 5.1). Along the whole gradient, purple and red fruits were attacked more than green fruits, but similarly to each other (Figure 5.1b, Table 5.1). Elevation had little to no effect on the relative attack rates by birds on different coloured fruits ($p = 0.15$; Table 5.1). Green fruits were consistently the least attacked (Figure 5.1b). Purple fruits were significantly more attacked than red fruits only at 1,700 m ($p = 0.05$). There was similarly little interaction between colour and size of attacked fruits, although this interaction was near-significant ($p = 0.06$; Table 5.1). Green fruits were again least attacked across size categories, and attack rates on green fruits did not differ with fruit size. Attack rates on purple and red fruits were similar for all fruit sizes.

Considering data from along the whole gradient, there was no difference between attack rates of different sized fruits ($p = 0.28$). However, elevation in its interactions with fruit size had a significant effect on the number of attacked fruits (Table 5.1). Birds showed no preference in relation to fruit size at 700 m asl and attacked medium sized fruits significantly more often than small and large fruits at mid-elevations (1,700 m). Finally, small fruits were attacked significantly more often than large fruits at 2,700 m ($p = 0.03$), with medium fruits showing an intermediate attack rate (Figure 5.1c).

Table 5.1. Results of generalised linear model (GLM) for bird attack rates on artificial fruits including fixed effects of fruit size (L = large, M = medium, S = small), fruit colour (G = green, P = purple, R = red) and elevation (m), and their interactions. Deviance values are presented for each fixed effect and each pairwise/triple interaction between effects. Estimate and standard error of multiple comparisons are presented for fixed effects and interactions that were significant at $p < 0.05$. p-values for multiple comparisons are adjusted using Tukey pairwise comparisons. Significant results are presented in bold. Results of the GLM for the subset of fruits held in the beak by birds are in Appendix Table A5.2.

Parameter	Deviance	P value	Multiple Comparisons	Estimate	SE	Adjusted p-value
Size	2.56	0.28				
Colour	123.22	<0.01	G vs. P	-1.38	0.14	<0.01
			G vs. R	-1.2	0.15	<0.01
			P vs. R	0.18	0.1	0.16
Elevation	48.28	<0.01	700 vs. 1700	-0.79	0.13	<0.01
			700 vs. 2700	-0.61	0.13	<0.01
			1700 vs. 2700	0.19	0.11	0.18
Size:Colour	9.25	0.06				
Size:Elevation	25.1	<0.01	700:L vs. 700:M	0.51	0.25	0.1
			700:L vs. 700:S	0.3	0.24	0.41
			700:M vs. 700:S	-0.21	0.26	0.71
			1700:L vs. 1700:M	-0.48	0.17	0.01
			1700:L vs. 1700:S	0.16	0.19	0.67
			1700:M vs. 1700:S	0.64	0.17	<0.01
			2700:L vs. 2700:M	-0.18	0.2	0.64
			2700:L vs. 2700:S	-0.49	0.19	0.03
			2700:M vs. 2700:S	-0.31	0.18	0.21
Colour:Elevation	6.71	0.15				
Size:Colour:Elevation	7.1	0.53				

When restricting attack rates only to fruits that were held in the beak (indicating potential dispersal), we found the interaction between fruit size and elevation to again be the most important interaction, although in this case it was marginally significant overall ($p = 0.05$). Multiple comparisons of “held” fruit size within elevations showed a pattern similar to that of overall attack rates, but with some noteworthy differences. At 700 m, holding rates did not differ between fruit sizes. Medium fruits were held significantly more than large fruits at 1,700 m, but at a similar rate to small fruits. At 2,700 m, small fruits were held significantly more than medium fruits, which were in turn held significantly more than large fruits (Figure 5.2; Appendix Table A5.2).

Mean gape width of understory frugivore species showed a decreasing, although non-significant, trend with elevation ($p = 0.27$; Appendix Table A5.3). This decrease appears to be primarily driven by a significant loss of large-gaped frugivores with increasing elevation (95th percentile, $p = 0.04$; Figure 5.3a). Meanwhile, community-weighted mean gape size decreased

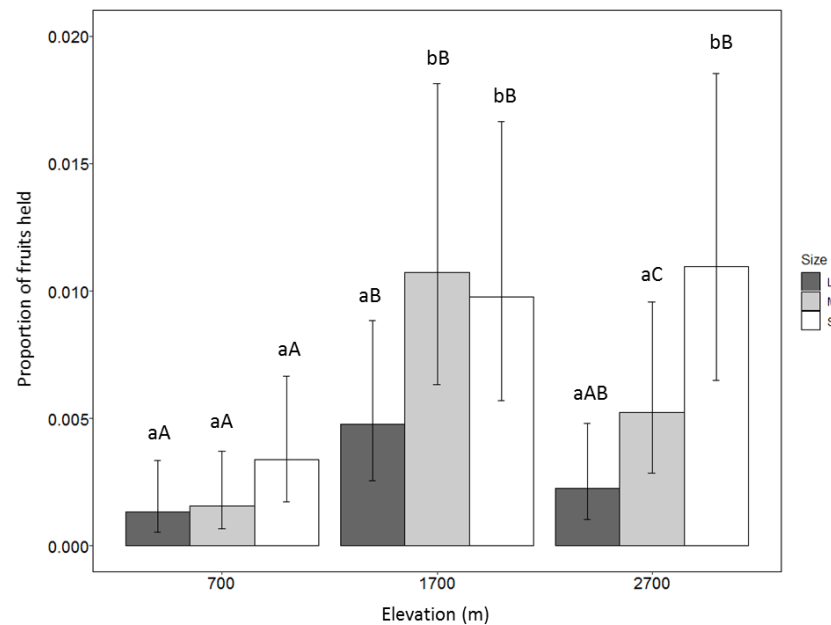


Figure 5.2. Mean proportion of differently sized artificial fruits per 30-fruit cluster held in the beak by birds at three elevations. Dark grey bars represent large fruits, light grey bars medium fruits and white bars small fruits. Error bars represent 95% confidence intervals. Letters above bars denote the significance of multiple comparisons between grabbing rates, after adjusting using Tukey pairwise comparisons. Letters represent significantly different grabbing rates on fruits of each size category at a given elevation (lower case) and between each elevation for a given size category (upper case).

significantly with elevation (Appendix Figure 5.3a). The mean diameter of fruits per fruiting plant species decreased steadily and significantly with increasing elevation ($p < 0.01$; Figure 5.3b, Appendix Table A5.3), and again appears to be driven primarily by a decrease in maximal rather than minimal fruit size (95th percentile, $p < 0.01$). Mean fruit diameter weighted by individual fruiting plant also showed a significant decrease with elevation (Appendix Figure A5.3b). The relative abundances of plants naturally bearing green and purple fruits changed significantly with elevation ($p < 0.01$), although this was not the case for plants bearing red fruits ($p = 0.52$, Appendix Table A5.3). Plants bearing green fruits were most common at 700 m (Figure 5.4a), while those bearing purple fruits were most common at 2,700 m (Figure 5.4b). At 1,700 m, plants bearing red fruits showed the highest abundance of the three fruit colours included in this study (Appendix Figure A5.4c).

Elevation had a significant effect on the abundance of frugivorous understory birds ($p < 0.01$; Figure 5.5, Appendix Table A5.3). Indeed, understory frugivore abundance showed a markedly similar pattern to that of overall attack rates on artificial fruits (Figure 5.1a, Figure 5.5). As with attack rates, frugivore abundance was highest at 1,700 m and 2,700 m, and significantly lower at 700 m.

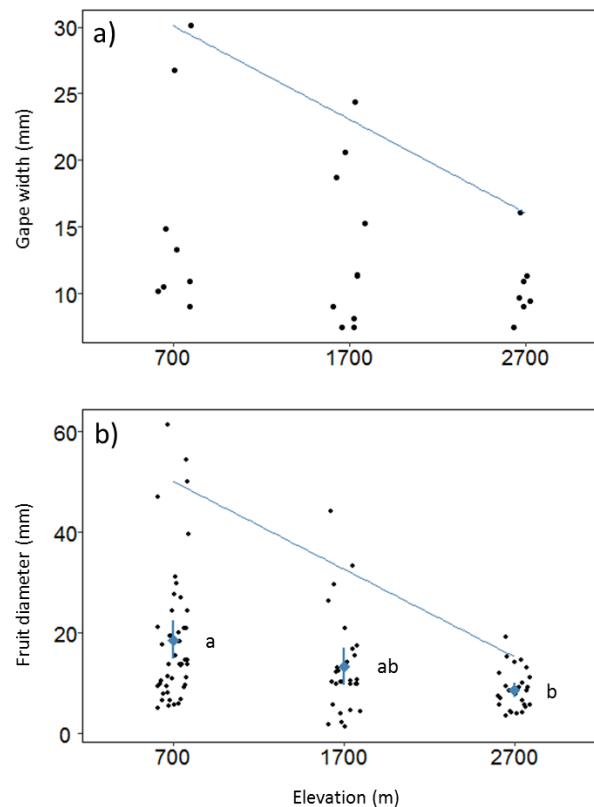


Figure 5.3. Gape widths of understory frugivores (a) and fruit diameter of fruiting plants (b) at each of three elevations. (a) Mean adult gape width of each obligate frugivorous bird species recorded at an elevation is represented by black circles ($N = 8$ species at 700 m, 10 at 1,700 m and 7 at 2,700 m). The diagonal blue line represents the 95th linear quantile. (b) Black circles here denote the mean diameter of ripe fruits (as measured along a fruit's secondary axis) for a given plant species at each elevation. The overall elevational mean fruit diameter, weighted evenly per plant species, is denoted by blue diamonds, with error bars representing 95% confidence intervals. As with gape width, the diagonal blue line represents the 95th linear quantile. Letters denote statistically significant differences in overall mean fruit diameter between elevations ($p < 0.05$), after adjusting using Tukey pairwise comparisons. Community-weighted mean values of frugivore gape width and fruit diameter are displayed in Appendix Figure A5.3.

5.4 Discussion

The variation in ornithochoric fruit traits (e.g. size, colour) across climatic gradients has received increased attention in recent years (Chen et al. 2016, Lu et al. 2019), but our understanding about the changes in bird preferences remains poor. This is the first study that experimentally showed that birds prefer smaller fruits (7 mm diameter vs 13 and 19 mm fruits) at higher elevations, intermediate sized fruits (13 mm) at mid-elevation and have no size preference at lower elevations. Birds preferred red and purple fruits to green fruits, and their colour preferences did not shift with elevation. We found that frugivory rates increased with elevation, in contrast to a previous study in Tanzania by Ferger et al. (2016) that showed a decrease in

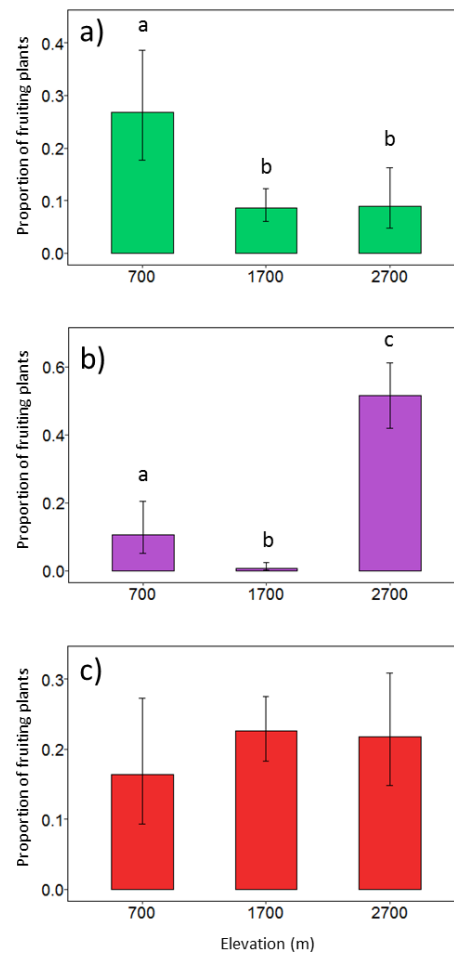


Figure 5.4. Relative abundance of fruiting plants at each elevation for the fruit colours represented in this study, represented as a proportion of the total number of fruiting trees at each elevation. Mean proportions are displayed for green (a), purple (b) and red (c) fruits. Error bars represent 95% confidence intervals. Letters above bars denote significant differences between elevations ($p < 0.05$), after adjusting using Tukey pairwise comparisons.

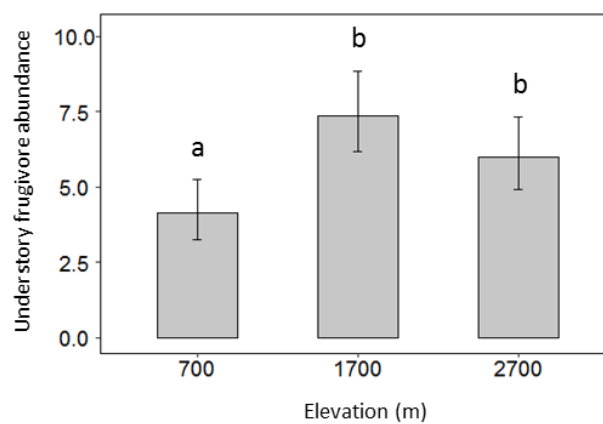


Figure 5.5. Abundance of frugivorous birds occurring in the understory at each elevation, measured as the mean abundance of obligate understory frugivores recorded (seen or heard) per point count. Error bars represent 95% confidence intervals. Letters above bars denote the significance of multiple comparisons, after adjusting using Tukey pairwise comparisons.

frugivory rates with elevation. However, both studies found that frugivory rates increase with frugivore abundance. Therefore, contrasting patterns between studies could be because of contrasting frugivore abundances across elevation gradients in New Guinea compared to Tanzania, or variation in habitat types (dry forests vs rainforests) where the experiments were conducted.

In our study, we report community-level preferences for fruit traits among a dispersal guild (frugivorous birds) and relate them to the actual traits of fleshy fruits present at three sites along an elevational gradient in tropical Papua New Guinea. In total we exposed 9,720 artificial fruits of which 510 fruits were attacked by birds and 241 fruits were attacked by other taxa (arboreal mammals, bats and arthropods). The attack rate of 5.3% by birds and 2.5% by other taxa after six days is comparable to results of other studies. In large forest fragments of Brazilian Atlantic forests, birds were responsible for attacks on 5% of artificial fruits after 96 hours (Galetti et al. 2003). In central Amazonia, birds feeding attempts were recorded on 10% of fruits in 6 days (Arruda et al. 2008). A higher proportion of attacks was detected in a continuous Brazilian forest, where birds pecked ca. 11% of fruits after 3 days (Alves-Costa and Lopes 2001). Similarly to the above-mentioned studies, we found a significant effect of colour and habitat on the number of attacks on the fruits.

5.4.1 Overall attack rates

We recorded lower overall attack rates on fruits at 700 m than at higher elevations. Considering that frugivory increases with increasing frugivore abundance (Smith and McWilliams 2014), such a trend initially seems to contradict existing data suggesting that frugivorous bird abundance generally decreases with increasing elevation (Terborgh 1977, Sam et al. 2017). However, the placement of artificial fruits within a few metres of the ground means this study specifically provides a representation of understory frugivory. Data from the same sites surveyed in this study show that abundances of avian obligate frugivores foraging within the understory only (i.e. excluding canopy feeders) actually correlates closely with frugivory rates recorded between elevations. This data suggests that at lower elevations, the forest canopy hosts the majority of frugivory interactions, whereas understory frugivory becomes relatively more important as elevation increases and the canopy becomes more open (Sam et al. 2019).

5.4.2 Fruit colour and elevation

Overall, we found that birds attacked red and purple fruits more often than green fruits. However, attack rates on red and purple fruits were not significantly different from one another.

A preference for red over green fruits has been commonly recorded by studies on avian frugivory (Janson 1983, Wheelwright and Janson 1985, McPherson 1988, Arruda et al. 2008, Lomáscolo et al. 2008, Amico et al. 2011, Duan et al. 2014). Data on purple fruits is less easy to ascertain, as purple fruits are commonly combined with other colours such as black and blue in such studies. This study is therefore to our knowledge the first to explicitly compare relative preferences of birds for purple fruits.

Unlike fruit size, elevation did not affect the attack rates on different coloured fruits. Furthermore, bird colour preferences did not correspond with the colour of the most common fruits at each elevation. This suggests that birds are exerting little selective pressure on fruit colour at a community level, and that other factors are more important than frugivory in determining fruit colour.

That our results show little preference between purple and red fruits regardless of elevation and fruit size suggests a lack of innate preferences between these colours at the community level. We also observed universally low attack rates on green fruits, including no preference at 700 m where green fruits are relatively common. However, it should be noted here that the abundance of green fruits in lowlands may reflect a higher abundance of mammalian frugivores (such as bats) at these elevations. Indeed, our data found a higher attack rate by mammals on green fruits at 700 m (2.7%) than any other colour/elevation combination (Appendix Table A5.1). Nevertheless, green fruits contrast less with a background of foliage than red or purple fruits, and as primarily visual foragers birds are likely to see red or purple fruits more clearly against such a background (Nevo et al. 2018). Our data are therefore consistent with a stochastic explanation for fruit colour choice; i.e. birds randomly selecting fruits that are most noticeable to them. This finding lends support to the hypothesis that noticeability is the most important factor in determining fruit colour choice of bird communities, as has been demonstrated for certain species (Schmidt et al. 2004).

The lack of evidence for selective pressure by dispersers suggests that other factors are likely to account for the differences in fruit colours observed between elevations. For example, many plant traits (including fruit traits) are known to show evidence of phylogenetic signal, whereby closely related plants may display similar traits regardless of environmental factors or selection pressures between trophic levels (Jordano 1995, Blomberg et al. 2003). However, fruit colour specifically has been shown by several studies to be evolutionarily labile (Cazetta et al. 2012, Stournaras et al. 2013, Ordano et al. 2017), perhaps due to the high versatility of the biosynthetic pathways for plant pigments (Rausher 2008). Alternatively, fruit colour may reflect an

adaptation to abiotic, rather than biotic factors (Burns 2015, Valenta et al. 2018). Anthocyanins, which are responsible for blue, purple and red colours in fruit, have been found to vary as a function of decreasing latitude and increasing elevation (Zoratti et al. 2015), suggesting that high light levels favour their production. Such a pattern could explain the prevalence of purple and red fruits at higher elevations in our study sites, where the canopy is more open, and a greater proportion of the forest receives direct sunlight.

5.4.3 Fruit size and elevation

We found avian community-level fruit size preferences to be consistent with a decreasing trend in frugivorous bird gape size with elevation, suggesting community-scale trait matching. We also found an association between fruit size preferences and the diameter of actual fruits along the elevational gradient, suggesting a potential selective effect of frugivores' fruit size preferences on fruit diameter. To our knowledge, this study constitutes the first experimental evidence of bird preferences for fruit size on a community scale.

Trait matching should predict sites with large-gaped birds to show higher attack rates on large fruits and vice-versa (Dehling et al. 2014). While this trend was apparent at higher elevations, we found only weak evidence of frugivores feeding preferentially on large fruits at 700 m. This is despite the diameter of the large artificial fruits being based on the mean diameter for real fruits measured at that elevation. There are a few possible explanations for this. Firstly, some of the largest fruits recorded at 700 m are likely to be mammal-dispersed rather than bird-dispersed, meaning the mean size of bird-dispersed fruits could actually be lower than was measured. Secondly, our data show that while maximal frugivore gape size indeed decreases with increasing elevation, small-gaped frugivores are still present at low elevations. Thus, a lack of a clear community preference for large fruits at 700 m is consistent with the community displaying a wide range of gape sizes, even if large birds individually tend to preferentially select larger fruits (Burns 2013).

If we are to consider the frugivory mutualism from the perspective of plants, the feeding behaviour employed by frugivores is important (Rey and Gutierrez 1996). A bird that swallows a fruit whole is far more likely to provide a seed dispersal function than the one that pecks it (Simmons et al. 2018). Dispersal of seeds results in lower density-dependent mortality of seedlings and thus is an important component of plant fitness (Howe and Smallwood 1982, Beckman and Rogers 2013). Therefore, fruit swallowing is likely to act as a positive selective pressure on fruit traits, whereas pecking is not. When considering a subset of artificial fruits that were held in the beak and thus potentially able to be dispersed, frugivore gape range and fruit

size preferences show a strikingly similar pattern across elevations. As maximal frugivore gape size decreases with increasing elevation, so too does the maximal size of fruits held in the beak, while the minimal gape size and minimal held fruit size (small) do not change. Our results therefore suggest that “community gape limitation” is a factor limiting maximal fruit size. In terms of selective pressure, an upper size limit of fruits is more important than a lower size limit in determining a plant’s chance of dispersal success. This mirrors the pattern of individual gape limitation, whereby large-gaped frugivores are able to disperse small fruits but not vice-versa (Wheelwright 1985).

The patterns described here highlight a trade-off faced by fleshy-fruited plants in tropical forests that can be broadly considered in terms of “quality” versus “quantity”, representing the classic *r/K* selection spectrum (MacArthur and Wilson 1967). Large fruits allow the production of large seeds, which are associated with enhanced seedling survivorship at low light intensities such as those found on the forest floor (Foster 1986). Large seeds produce seedlings with greater vigour (Pizo et al. 2006, Lopes Souza and Fagundes 2014) and are more tolerant to predation by rodents and beetles (Harms and Dalling 1997, Mack 1998b). However, small fruits can be produced in greater numbers than large fruits for the same energy cost. Additionally, as our results demonstrate, having large fruits limits potential avian dispersal agents to only a subset of the bird community, whereas having smaller fruits does not (Wheelwright 1985, Muñoz et al. 2017). While large frugivores, typically having large range sizes, may provide “high quality” long-distance dispersal (Wotton and Kelly 2012), limiting potential dispersers in this way represents a risky strategy for plants, especially at sites with naturally low abundances of large frugivores (such as high elevations).

5.4.4 The use of artificial fruits

Artificial fruits represent a useful tool for ascertaining feeding preferences of frugivorous birds at the community level without resorting to invasive techniques which may affect birds’ behaviour. However, there are a few limitations to the approach. Unlike lab-based studies, community-based approaches such as this do not identify individual feeding interactions, which would enable more direct functional comparisons between fruits and their dispersers. Additionally, our study, in common with others using similar methodologies, is limited by the placement of artificial fruits relatively close to the ground. This neglects information on the feeding preferences of canopy feeding frugivores, which form a very important component of avian frugivory especially in lowland rainforest (Shanahan and Compton 2001, Schleuning et al. 2011). An extension of our experimental methodology to encompass canopy as well as

understory frugivory, while logistically difficult, would doubtless provide a more complete picture of avian community-level fruit preferences.

5.4.5 Summary

This study represents the first attempt to record community-wide preferences of frugivorous birds for fruit traits along an elevational gradient. We have shown that at the community scale, birds do not preferentially select artificial fruits corresponding to the colour of prevalent real fruits. This lack of a correspondence suggests that avian colour preferences are broad and inflexible and thus unlikely to be able to select for specific fruit colours. In contrast, we showed fruit size preferences of birds do correspond to real fruit size along the gradient, and that preferences are consistent with the gape limitation hypothesis. A result is that progressively smaller fruits are preferred with increasing elevation. Furthermore, this pattern extends to fruits held in the beak by birds and thus able to be dispersed, suggesting the potential for birds to act as a selective pressure on fruit size. This result demonstrates a trade-off for plants between maximising seed size and maintaining the likelihood of dispersal, especially at high elevations. Nevertheless, further experimental study is needed if we are to untangle explicitly whether a lack of large fruits at high elevations is a result of selection by birds or due to other factors such as environmental constraints.

CHAPTER 6

General Conclusions

6.1 Summary of findings

The aims of this thesis were to understand the processes driving bird diversity patterns and their functional relationships with food resources and environment, in lowland and montane rainforests in New Guinea. Over the course of four chapters I have used a combination of observational and experimental methodologies across a lowland forest and an elevational gradient in order to address these aims, as detailed below.

- In **Chapter 2**, I studied bird and woody plant beta-diversity across a 10,000 ha area of lowland rainforest in Papua New Guinea. Bird beta-diversity was very low: species composition did not change with increasing distance between sites from 0.25 – 14 km apart, while change in community composition (accounting for species abundances) increased marginally with inter-site distance. Species richness of birds was identical for a 50 hectare plot and the surrounding 10,000 ha of forest, suggesting that bird diversity at intermediate spatial scales is well-represented by local-scale diversity within this relatively climatically homogenous habitat. Plant species richness showed a more divergent pattern between spatial scales: local-scale richness was significantly lower than that recorded across the wider 10,000 ha area with similar sampling effort. Beta-diversity of plants, however, showed a similar pattern to that of birds. Overall, bird community composition was shown to be driven by a combination of spatial and environmental factors, while for plants spatial factors were more important, reflecting a greater importance of dispersal limitation. Overall the results highlight the differing importance of local- and intermediate-scale patterns in determining wider diversity in different taxa, and suggest that intensively surveyed small-scale forest dynamics plots may be suitable for assessing wider-scale bird diversity in lowland habitats.
- In **Chapter 3**, I investigated patterns of avian diversity along an elevational gradient on Papua New Guinea, focusing on the relationships between taxonomic, functional and phylogenetic diversity. High alpha-diversity at low elevations was matched by high

functional and phylogenetic diversity. However, while bird species richness decreased monotonically with increasing elevation, functional and phylogenetic diversity showed a unimodal trend, flattening out at higher elevations and showing functional and phylogenetic clustering. This suggests that mid and high elevation assemblages are driven more by environmental filtering than by niche-based processes. The loss of functional diversity with increasing elevation may be due in part to a loss of large frugivorous species outside lowland assemblages. Beta-diversity patterns, in contrast with alpha-diversity patterns, did not show evidence of environmental filtering occurring between communities. Functional and phylogenetic turnover were both lower than expected given species turnover and did not show a distance-decay relationship with increasing elevational distance between sites. Such a pattern may be explained by separate evolutionary histories of highland and lowland assemblages, or by widespread generalism in the traits measured. The close relationship between functional and phylogenetic trends indicated a strong influence of phylogenetic conservatism in determining the trait values expressed. This suggests that phylogenetic relationships of the bird communities studied may provide an effective proxy for ecosystem functioning, highlighting the importance of protecting phylogenetically distinct species.

- In **Chapter 4**, I examined four fruit traits related to dispersal by frugivores (diameter, seed to pericarp ratio, colour and presentation) along the elevational gradient in Papua New Guinea, and tested for evidence of dispersal syndromes by studying the correlated evolution of fruit colour and diameter. Fruit diameter was lowest at higher elevations, while seed to pericarp ratio did not show an elevational trend. Fruit colours lacked strong elevational trends other than a peak in green fruits at 700 m and in black and purple fruits at 2,700 m. As a result overall, colours known to be attractive to birds were more prevalent at 2,700 m than at other elevations. Fruit presentation type showed a significant elevational trend: ramiflorous fruiting species increased from less than half of all species at 200 m to 100% of species at 2,700 m. Presentation showed evidence of phylogenetic signal, while all other fruit traits measured did not. A lack of phylogenetic signal in both fruit colour and diameter, coupled with significant phylogenetic and non-phylogenetic associations between large/"mammal colour" fruits and small/"bird colour" fruits, provided evidence supporting the dispersal syndromes hypothesis.
- In **Chapter 5**, I used a field experiment involving artificial fruit exposures to investigate fruit size and colour preferences of frugivorous bird communities at three sites along

the Mt Wilhelm elevational gradient. Bird preferences for fruit colour did not show an elevation-dependent trend and thus did not reflect prevalent fruit colours found at each elevation. Therefore it is unlikely that birds have a selective effect on specific fruit colours, which are likely to be driven more by environmental factors such as light availability. In contrast to colour, the sizes of fruits preferred by birds did change with elevation. All sizes were attacked similarly at 700 m asl, although large fruits were weakly preferred. At 1,700 m, medium-sized fruits were the most frequently attacked, and small fruits were preferred at 2,700 m. The fruit size preferences of birds, especially at the higher two elevations, thus correspond to the mean diameters of fruits recorded along the gradient, as described in Chapter 4. In addition, bird gape width showed a similar decreasing pattern with elevation as did fruit diameter, as a loss of large frugivores with increasing elevation limits the maximum gape sizes occurring at higher elevations. The results suggest that gape limitation at the community scale is a potentially important factor in limiting the sizes of fruits at higher elevations, and that birds may act as a selective pressure on fruit size along elevational gradients.

6.2 Broader ecological context

This thesis has explored a number of aspects relating to avian diversity on elevational gradients. The results shed light on the importance of incorporating a range of measures of diversity which a traditional focus on species richness may overlook. A casual glance at the bird communities recorded along the Mt Wilhelm transect seems to reveal a simple pattern of decreasing species richness with increasing elevation, in common with numerous other studies on tropical avian diversity (Terborgh 1977, Jankowski et al. 2013, Dehling et al. 2014, Ferger et al. 2014, Sam et al. 2019). However, this apparently simple pattern masks a complex array of processes occurring below the surface. Community turnover is marked by an abrupt shift at mid-elevations, with lowland assemblages defined predominantly by niche-based dynamics and those at higher elevations increasingly constrained by environmental conditions. Across elevations, qualitative differences in intertrophic interactions between birds and their food sources serve to add further complexity to the picture. Indeed, the loss or gain of certain functionally important species with changing elevation has the potential to create knock-on effects on ecosystem functioning, which may in turn inform our understanding of the changes in ecological processes occurring along elevational gradients.

While birds in their interactions with other organisms perform a wide range of ecological

functions, the functional role that has received the most attention in this thesis is frugivory. The relationships between avian frugivores and their preferred fruit resources is of particular importance in the context of tropical rainforests, where frugivores make up a higher proportion of bird species than in other biomes (Kissling et al. 2009) and where the majority of plant species bear fleshy fruits (Muller-Landau and Hardesty 2005). Seed dispersal by birds clearly represents a fundamentally important ecosystem service that dictates tropical forest community assembly, particularly in areas such as New Guinea where the mammalian frugivore guild is relatively depauperate.

The evidence for dispersal syndromes found in this study suggests that birds have been instrumental in the evolution of fruit traits on Mt Wilhelm, as has been demonstrated elsewhere for certain groups of fruiting plants (Lomáscolo et al 2008, 2010). Furthermore, in the context of elevational gradients, this study has demonstrated that bird fruit preferences at the community level have the potential to have an evolutionarily selective effect on fruit size at different elevations. The prevalence of smaller-fruited plants at higher elevations may therefore at least in part reflect the inability of small highland bird species to disperse larger fruits. The converse effect, that is, the selection for smaller avian frugivores at higher elevations due to smaller average fruit size, is not necessarily discounted by our results, although the asymmetrical nature of gape limitation means that birds are likely to inherently pose a stronger selection pressure on fruit size than the other way round (larger-gaped birds may still survive by consuming fruits smaller than their gape size, while larger fruits cannot be dispersed if there are no dispersers with gapes large enough) (Simmons et al. 2018). Nevertheless, elevational migration, known to occur in some bird species in the study area (Sam and Koane 2014) may still serve to enable larger-fruited plants access to higher elevations via the digestive tracts of migrating birds.

The association between frugivore gape size and fruit diameter observed at the community level in this study represents an extension to the concept of fruit-frugivore trait matching. Trait matching has been observed at the level of individual frugivory interactions by a number of studies (Dehling et al. 2014, Muñoz et al. 2017, Bender et al. 2018), including those focusing specifically on gape size and fruit diameter (Burns 2013), where it has also sometimes been termed “size coupling”. Such a matching of traits need not necessarily translate to community-scale effects – after all, high levels of generalism between birds and fruits could ostensibly serve to muddy the picture as more and more species are involved, and the frugivory mutualism has indeed been described as a “diffuse coevolution” characterised by generalised interactions (Levey 1987, Schleuning et al. 2011, Sankamethawee et al. 2011). This is particularly true in the tropics, where frugivore diversity and fruit availability are high year round (Chama et al. 2013),

and contrasts with other mutualistic interactions such as pollination, whose interaction networks show high levels of specialization (Maglianesi et al. 2014). Therefore the detection of fruit-frugivore trait matching at the community level here is notable, and suggests that the factors determining size-coupling between fruits and birds are occurring across scales.

6.3 Study limitations and future research

A limitation inherent to studies on functional diversity is the lack of a fully satisfactory way to represent the complexity of species' functional niches using a finite set of traits (Voille et al. 2007). Bias is always introduced in the process of selecting which traits to use and in their relative weighting, and a small variation at this stage may lead to a large difference in functional diversity values obtained (Petchey and Gaston 2006, Bernhardt-Romermann et al. 2008). While efforts have been made in this study to minimise the effects of bias and to select a range of traits that reflect as fully as possible the functional roles performed by birds, it is impossible to ensure that the traits used reflect the full breadth of ecological space occupied by the birds of Mt Wilhelm. It is also certainly the case, especially in an understudied avian fauna such as that encountered in New Guinea, that many relevant ecological and life history traits of many bird species are simply not well-known enough to enable their quantification in this way. For example, it has been proposed that clutch size may represent an important quantifiable trait relating to population demographics (Voille et al. 2007). However, data on clutch size was not available for the majority of species recorded on the Mt Wilhelm transect. This example demonstrates the importance of natural history in informing ecological research, particularly when attempting to define the ecological niches of species.

The broader applicability of the findings of this study were also limited on a number of fronts by an inability to access the forest canopy. While a common limitation of studies undertaken in tropical rainforest, it nevertheless leaves open avenues for further research in cases where budget and time allow for improved methods of canopy access. For example, results of the fruit surveys undertaken in Chapter 4 were likely to have been biased towards fruits presented within easy visual distance of ground-based observers. It was frequently difficult to spot fruits high in the canopy, particularly at lower elevations (200 – 1,200 m) where the canopy is high and in many cases hidden from view behind understory foliage. If the fruit traits measured in this study vary in any consistent way between forest strata, then this observer bias could have resulted in skewed data with regards to the traits in question, especially at lower elevations. An additional advantage of improved visibility of canopy fruits is that it would allow the estimation of fruit

abundance at each elevation. This would allow the weighting of fruit traits by the relative abundance of fruits displaying these traits (rather than simply by the number of individual trees bearing these fruits), thus potentially better reflecting the actual prevalence of fruit traits at each elevation. It would also allow the estimation of fruit crop size and biomass at each elevation, which are factors known to be important components of frugivory interactions (Flörchinger et al. 2010, Albrecht et al. 2012). However, incorporating abundance measures into fruit trait data would also require year-round surveys, as fruit abundance is likely to be temporally variable (Ramírez and Kallarackal 2015), and a single snapshot of fruit abundance may be highly skewed by the chance occurrence of masting events.

Canopy fruits may be better represented if surveys make use of technological solutions. For example, drones fitted with high-quality cameras have in recent years started being employed to survey forest canopies from above (Koh and Wich 2012), and in combination with ground-based surveys in order to detect arboreal animals such as monkeys (Kays et al. 2019). While the relatively small size of fruits means that direct estimation of abundance is unlikely to be possible using this kind of survey, canopy imaging could potentially be used as a means of detecting important canopy fruiting trees that could then be focused on with subsequent careful ground-based observations.

Another aspect of this thesis that would have benefitted from access to the forest canopy is the experimental data on fruit trait preferences of birds presented in Chapter 5. As mentioned in the discussion of Chapter 5, the existing experimental setup neglects frugivory interactions occurring at mid and upper forest strata, due to the limitations imposed by conducting the experiments within 3 m of ground level. This is significant because many important avian frugivores, including the fruit doves and imperial pigeons in New Guinea, are predominantly canopy-feeding species (Pratt and Beehler 2015). Expanding the current setup in order to expose artificial fruits at higher strata would undoubtedly provide a more complete view of avian frugivory patterns with elevation than is currently available, and could be achieved using canopy access techniques. This would also potentially allow for assessments of niche separation within bird communities in a single forest by comparing relative frugivore preferences across forest strata.

Notwithstanding the lack of canopy feeding data, this study has demonstrated the effectiveness of artificial fruits as a means of assessing avian feeding preferences, and further studies could expand on this methodology by manipulating artificial fruits to vary in a greater number of traits, for example incorporating fruit shape and smell. Additionally, the data on frugivory by non-avian frugivores, while touched on briefly here, could be expanded upon significantly. As proven in

this study, artificial fruits are attacked not only by birds but by a variety of mammals and insects. Further studies using artificial fruits could provide a more complete view of ecosystem-wide frugivory occurring across taxa, thus enabling better-informed ecological assessments of the changes in fruit traits observed across environmental gradients. Indeed, the data already obtained in this study could form a suitable starting point for such assessments.

Finally, while artificial fruit exposures provide information on broad fruit trait preferences of bird communities at different elevations, the current study does not allow the individual-level trait matching of specific avian frugivore species with their preferred fruits, as seen in other studies previously mentioned (Burns 2013, Dehling et al. 2014, Bender et al. 2018). Direct observations of frugivory interactions would provide a better understanding of individual fruit-frugivore relationships, helping to reveal the importance of aspects of frugivory such as gape limitation at a more granular level. This would also allow comparison of the processes dictating both individual-level and community-level trait matching. Such observations may be conducted either by conducting watches on target fruiting plant species or artificial fruit clusters, or remotely by means of camera traps. The relationship between trait matching and the observed functional diversity patterns at different elevations also requires further exploration, particularly considering functional beta-diversity of birds and fruits.

6.4 Implications for conservation

The results of this thesis highlight the complex relationships that birds share with their environment along elevational gradients. The presence of a bird at a particular elevation is likely to be a result of a combination of factors spanning from its evolutionary history to climatic tolerances, availability of spatial niches and food resources. In turn, birds may act as a powerful force in driving elevational trends in rainforest community assembly through processes such as seed dispersal. As I hope this thesis has demonstrated, an approach focusing on bird functional traits and those of their food resources has the ability to shed light on the factors affecting both bird communities and their intertrophic relationships.

A clear example of the importance of functional traits on intertrophic dynamics concerns the relationship between bird gape size and fruit size. Along the Mt Wilhelm elevational gradient, a loss of large-gaped frugivores with elevation was strongly associated with a loss of large-fruited plants. The closeness of this relationship has potential implications for the conservation of both of these groups. It is known that large frugivores in tropical forests tend to have larger range sizes and thus larger area requirements than smaller species (Price et al. 1999). Additionally they

may be particularly attractive to hunters (Strahl and Grajal 1991), both for subsistence and – in the case of New Guinea – sometimes for feathers used in ceremonial activities (Mack and Wright 1998). The combined result is that large frugivores tend to be more vulnerable to extinction from hunting and habitat fragmentation than smaller species (Dominy and Duncan 2005, Galetti et al. 2013, Vidal et al. 2013).

As they stand, the forests of New Guinea are relatively intact. However, this may not remain the case for long – between 2002 and 2014, 7.3% of Papua New Guinea’s accessible forests (mostly in the lowlands) were logged or cleared, and 14.9 million hectares of remaining forest occurs inside logging concessions (Bryan and Shearman 2015). The continued degradation of lowland forest habitat could potentially have a severe impact on large frugivores in PNG’s lowlands. This could in turn create knock-on effects whereby a lack of large-gaped frugivores leads to inadequate dispersal of large-fruited plants that depend on them. Such a pattern is known to have occurred after the extinction of many frugivorous Pleistocene megafauna across the globe (Guimarães et al. 2008), and has been observed after more recent avian extinctions on Polynesian islands (McConkey and Drake 2002, Wotton and Kelly 2011) and in Brazil (Galetti et al. 2013). Therefore if seed dispersal services are to be maintained across New Guinea’s forests, the protection of large frugivores should form a focus of conservation efforts.

Focusing on elevational gradients, the functional dynamics between fruits and frugivores may be an important factor to consider in the context of elevational range shifts under future climate change (Mokany et al. 2014). Surface temperatures across the tropical Pacific are projected to increase by 2 – 3° C by the end of the century (Lough et al. 2011). In addition, El Niño activity (which in New Guinea typically produces drought conditions) has increased over the past 50 – 100 years (Vecchi and Wittenberg 2010). Here tropical mountains such as Mt Wilhelm stand to be particularly affected by rising temperatures and fluctuating rainfall, due to the strong temperature and precipitation gradient that exists across elevation in the tropics. Birds in the region are known to respond to changing climatic conditions by shifting their ranges across elevations (Sam and Koane 2014). However, as fundamentally more sessile organisms, plants are unlikely to react as quickly, potentially leading to a functional mismatch between fruits and frugivores (Nowak et al. 2019). From the data presented here, it is also clear that large-gaped frugivorous birds are less restricted in their fruit size requirements than are large-fruited plants on frugivore gape size. A shift or contraction of large-gaped frugivore species’ ranges away from the lowest elevations may lead to a similar pattern of reduced plant dispersal effectiveness in the lowlands as that described under scenarios of habitat degradation above.

At higher elevations, climate change scenarios predict that species will be forced towards the tops of mountains as their available niche space shifts (Freeman et al. 2018). As this thesis has shown, bird community assembly at mid and high elevations in New Guinea is primarily filtered by the environment, suggesting highland assemblages are especially vulnerable to any changes in environmental conditions such as rising temperatures. As species shift upwards, available land area decreases and populations may become more fragmented (Spehn and Körner 2005). Indeed, available habitat for some species may be lost altogether on lower mountain ranges where the mountaintops are already below the treeline. High mountains such as Mt Wilhelm may therefore become important refuges for increasing numbers of montane species in the future, and their protection should form another priority of conservation efforts.

6.5 Concluding remarks

The forests of New Guinea remain relatively unknown, and have undoubtedly yet to reveal many “treasures” to Wallace’s modern day counterparts. Their high species endemism and huge carbon reserves make them a vital global resource, although one that is facing a greater number of external pressures than ever before. In this thesis I have provided some insights into the factors affecting bird diversity across the island and their relationships with the forests they inhabit, both in lowland and montane environments. I hope that I have made some contribution towards better understanding and thus more effectively protecting New Guinea’s forests in the future.

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APPENDICES

Appendix: Chapter 2

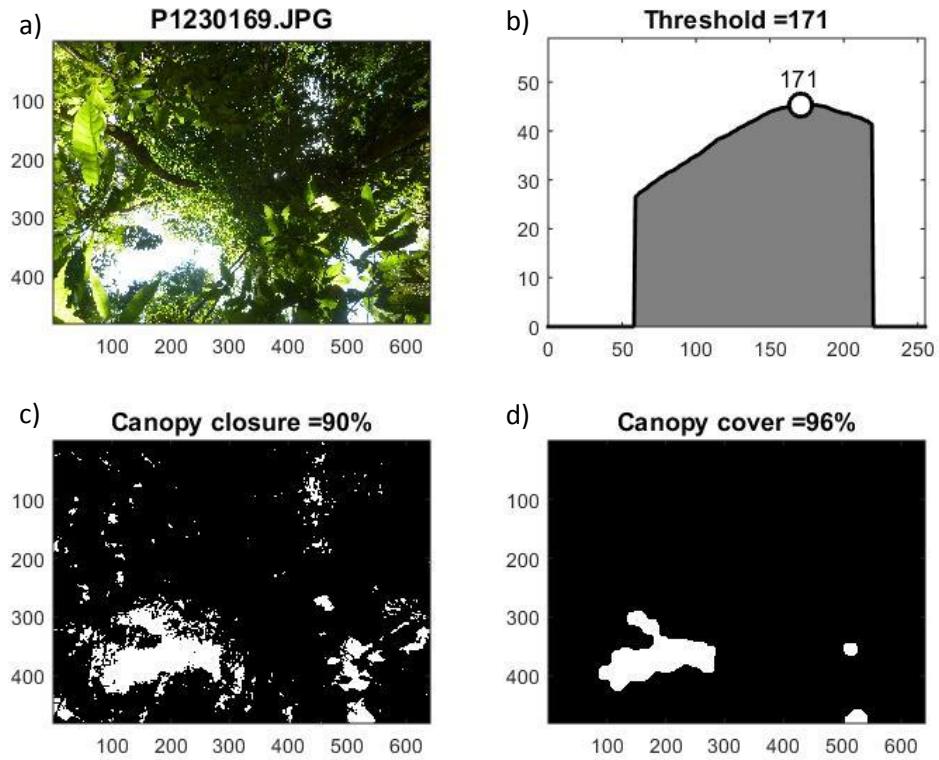


Figure A2.1. Example of canopy photo analysis using Matlab 2015's Image Processing Toolbox (Mathworks 2015) and code developed by Korhonen and Heikkinen (2009). The original photo (a) is converted into a black and white Bitmap image according to a threshold brightness value (b). The produced image (c) is assessed according to the relative proportion of black versus white pixels, defined as canopy closure. Canopy cover (d) was not assessed in the current study.

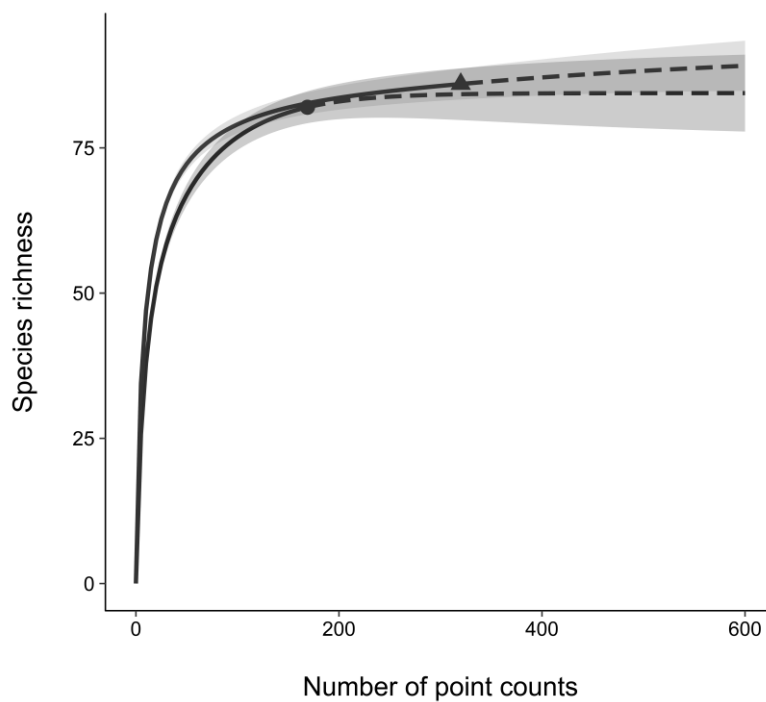


Figure A2.2 Bird species richness as shown in Figure 2.2, in this case represented by rarefaction curves for WCA (black triangle) and FDP (black circle) with $\pm 84\%$ confidence intervals (shaded areas). Solid lines show interpolated rarefaction curves. Dashed lines represent extrapolated rarefactions exceeding our sampling effort. Species accumulation was calculated by site (individual point count location) for a total of 320 (WCA) and 169 (FDP) sites.

Table A2.1 Woody plant species names corresponding to species codes displayed in Figure 2.5. Morphospecies are presented in the cases of *Cryptocarya sp.01* and *Phaeanthus sp.01* where identification to species level was not possible.

Species Code	Species Name
AlanVi	<i>Alangium villosum</i>
CallPent	<i>Callicarpa pentandra</i>
ClerIner	<i>Clerodendrum inerme</i>
CrypSp01	<i>Cryptocarya sp.01</i>
CupnAcut	<i>Cupaniopsis acuticarpa</i>
CyatPolc	<i>Cyathocalyx polycarpa</i>
DecsRhod	<i>Decaspermum rhodoleucum</i>
DiosLoln	<i>Diospyros lolin</i>

DrypLasi	<i>Drypetes lasiogynoides</i>
DysxBras	<i>Dysoxylum brassii</i>
DysxGaud	<i>Dysoxylum gaudichaudianum</i>
FicsArfk	<i>Ficus arfakensis</i>
FicsBotr	<i>Ficus botryocarpa</i>
FicsDrup	<i>Ficus drupacea</i>
FicsPung	<i>Ficus pungens</i>
FicsSemv	<i>Ficus semivestita</i>
FicsVari	<i>Ficus variegata</i>
GaleCelb	<i>Galearia celebica</i>
GarcLats	<i>Garcinia latissimi</i>
GardHans	<i>Gardenia hansemanii</i>
GnetGnem	<i>Gnetum gnemon</i>
GuioComs	<i>Guioa comesperma</i>
GymnPanc	<i>Gymnacranthera paniculata</i>
HibsPapu	<i>Hibiscus papuadendron</i>
LeucAust	<i>Leucosyke australis</i>
MacrAleu	<i>Macaranga aleuritoides</i>
MacrBifv	<i>Macaranga bifoventata</i>
MacrNeob	<i>Macaranga neobritannica</i>
MacrNovg	<i>Macaranga novoguineensis</i>
MacrQuad	<i>Macaranga quadriglandulosa</i>
MacrTanr	<i>Macaranga tanarius</i>
MelcEllr	<i>Melicope elleryana</i>
MeliPinn	<i>Meliosma pinnata</i>
MornCitr	<i>Morinda citrifolia</i>
PhaeSp01	<i>Phaeanthus sp.01</i>
PicrJavn	<i>Picrasma javanica</i>
PlanFirm	<i>Planchonella firma</i>
PomtPinn	<i>Pometia pinnata</i>
PremObts	<i>Premna obtusifolia</i>
PrunSchl	<i>Prunus schlechteri</i>
RinrBeng	<i>Rinorea bengalensis</i>
RyprJavn	<i>Ryparosa javanica</i>

SterShil	<i>Sterculia shillinglawii</i>
SterSchm	<i>Sterculia schumanniana</i>
TeijBogr	<i>Teijsmanniodendron bogoriense</i>
TernCher	<i>Ternstroemia cherry</i>
TimnTimn	<i>Timonius timon</i>
TricPhil	<i>Trichadenia philippinensis</i>
TricPlei	<i>Trichospermum pleiostigma</i>
VersCaul	<i>Versteegia cauliflora</i>

Table A2.2 Bird species names corresponding to species codes displayed in Figure 2.6. Two species from the genus *Meliphaga* are presented in the case of *MeliSp.* where it was usually not possible to distinguish between the two species.

Species Code	Species Name
Arselnsu	<i>Arses insularis</i>
CacaGale	<i>Cacatua galerita</i>
CiciRegi	<i>Cicinnurus regius</i>
CoraBoye	<i>Coracina boyeri</i>
CoraMela	<i>Coracina melas</i>
CratMuri	<i>Crateroscelis murina</i>
DucuRufi	<i>Ducula rufigaster</i>
DucuZoea	<i>Ducula zoeae</i>
GallRufi	<i>Gallicolumba rufigula</i>
GeryPalp	<i>Gerygone palpebrosa</i>
LalaAtro	<i>Lalage atrovirens</i>
LeptAspa	<i>Leptocoma Aspasia</i>
LoncTris	<i>Lonchura tristissima</i>
MacrAmbo	<i>Macropygia amboinensis</i>
MachFlav	<i>Machaerirhynchus flaviventer</i>
MegaMagn	<i>Megaloprepia magnifica</i>
MeliMacr	<i>Melidora macrorrhina</i>
MeliSp.	<i>Meliphaga analoga</i> / <i>M. Aruensis</i>
MicrParv	<i>Microdynamis parva</i>

MinoDumo	<i>Mino dumontii</i>
PachSimp	<i>Pachycephala simplex</i>
PitoKirh	<i>Pitohui kirhocephalus</i>
PittEryt	<i>Pitta erythrogaster</i>
PittSord	<i>Pitta sordida</i>
PoecHypo	<i>Poecilodryas hypoleuca</i>
Pomalsid	<i>Pomatostomus isidorei</i>
ProbAter	<i>Probosciger aterrimus</i>
PseuFerr	<i>Pseudorectes ferrugineus</i>
PsitEdwa	<i>Psittaculirostris edwardsii</i>
PtilCoro	<i>Ptilinopus coronulatus</i>
PtilPerl	<i>Ptilinopus perlatus</i>
PtilPulc	<i>Ptilinopus pulchellus</i>
RhipRufd	<i>Rhipidura rufidorsa</i>
RhipThre	<i>Rhipidura threnothorax</i>
SeleMela	<i>Seleucidis melanoleucus</i>
SymaToro	<i>Syma torotoro</i>
SympGutt	<i>Symposiachrus guttula</i>
TanyGala	<i>Tanyiptera galatea</i>
ToxoNova	<i>Toxorhamphus novaeguineae</i>
TricHaem	<i>Trichoglossus haematodus</i>

Appendix: Chapter 3

A3.1 Morphological Trait Measurement and Trait Selection

Morphological traits in the global database were obtained from a combination of live mist-netted birds and preserved museum skins. Traits were measured to the nearest 0.01 mm. Where possible, measurements were taken from at least four individuals per species (two from each sex; mean total = 8 individuals) (Pigot et al. 2016). Morphological traits included in preliminary analyses were: mass, bill culmen length, bill width, gape width, wing chord length, Kipp's distance and tail length. Behavioural Traits were: food source, foraging substrate, foraging height, nest location and clutch size. The latter two traits were removed due to having a high number of missing values. Remaining traits (morphological and behavioural) were subjected to Pearson's correlations (see figure S1 below for traits included in final analyses).

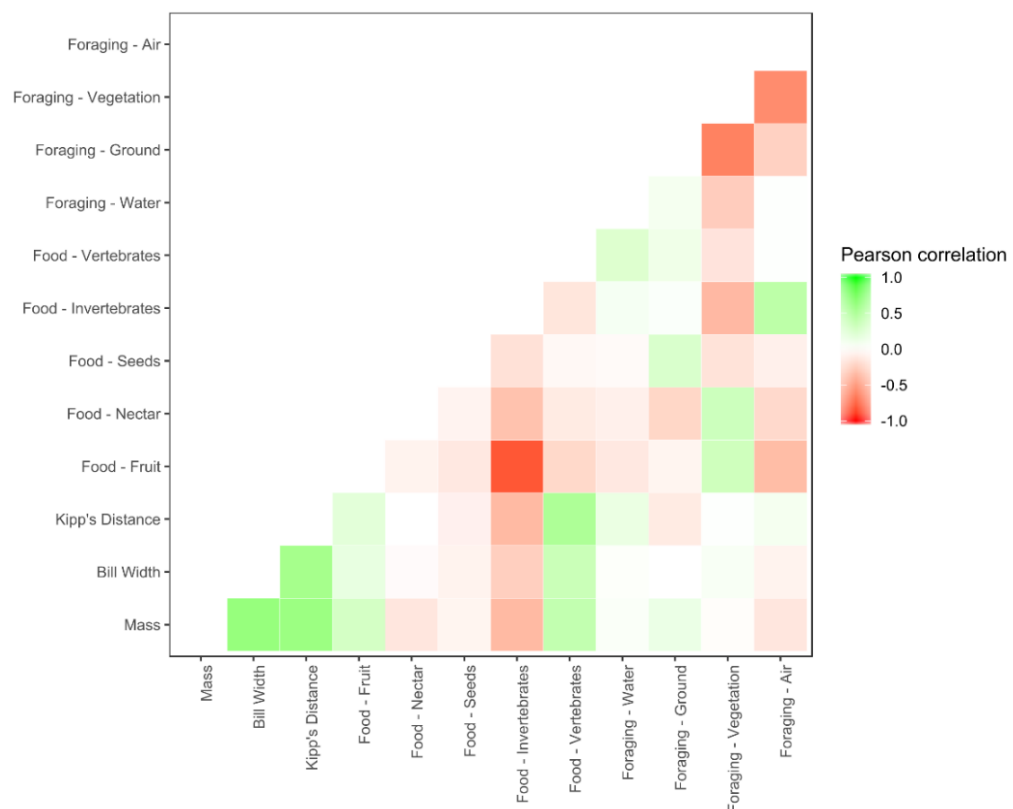


Figure A3.1. Pearson correlation matrix for traits included in final functional diversity analyses. Green squares represent positive correlations between traits/trait levels and red squares represent negative correlations. Traits were excluded if they included correlations with multiple other traits above/below a threshold value of ± 0.7 . Of the final traits included (mass, bill width, Kipp's distance, food source and foraging substrate, only one correlation exceeded this threshold: Food (invertebrates) vs. Food (fruit) at -0.81: this was permitted because it is a within-trait correlation.

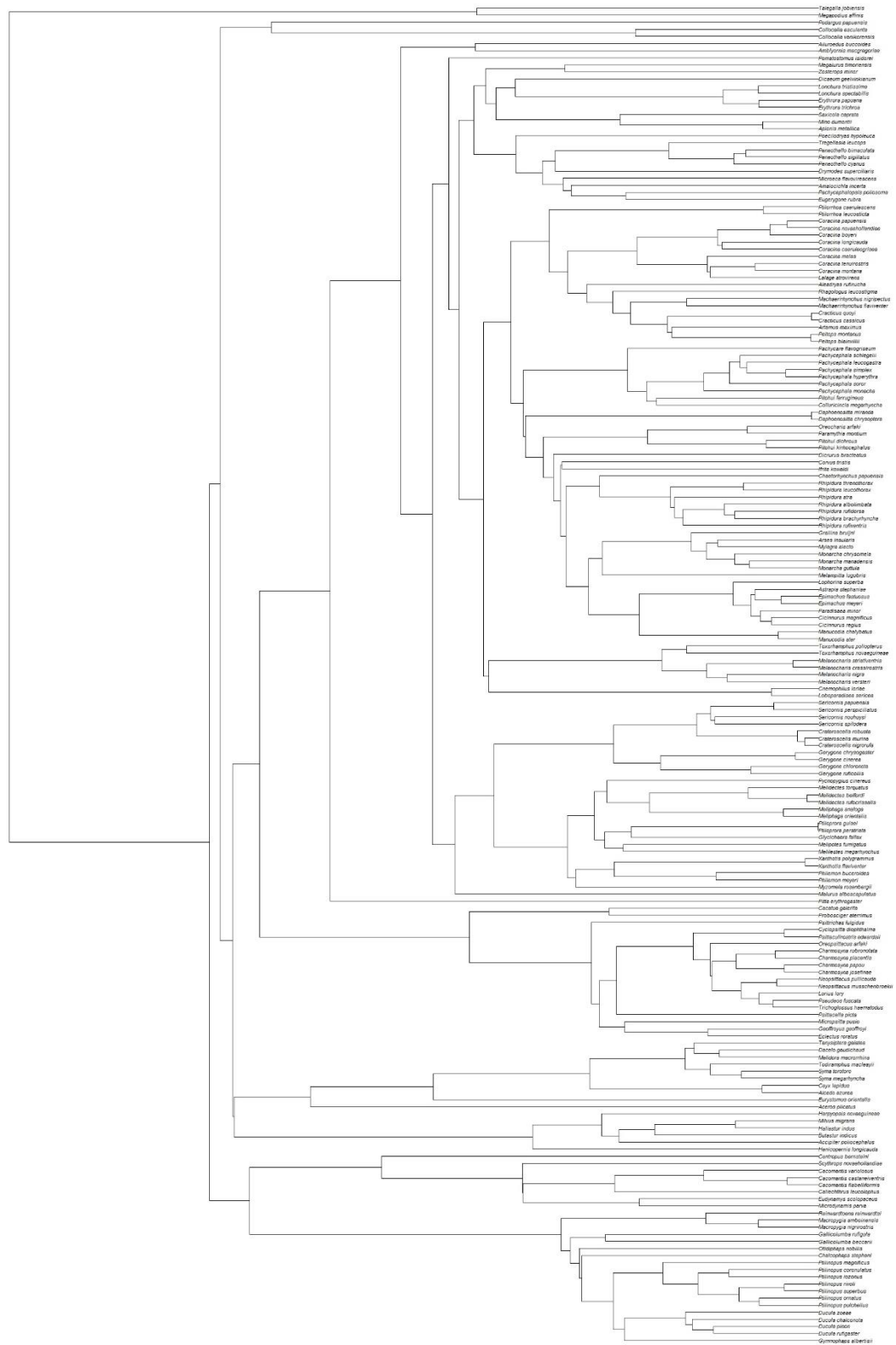


Figure A3.2. Maximum Clade Credibility (MCC) phylogenetic tree for all birds recorded at the Mt Wilhelm study sites. Phylogeny is based on the BirdTree global avian phylogeny of Jetz et al. (2012), using the Hackett et al. (2008) backbone. See Methods for more details.

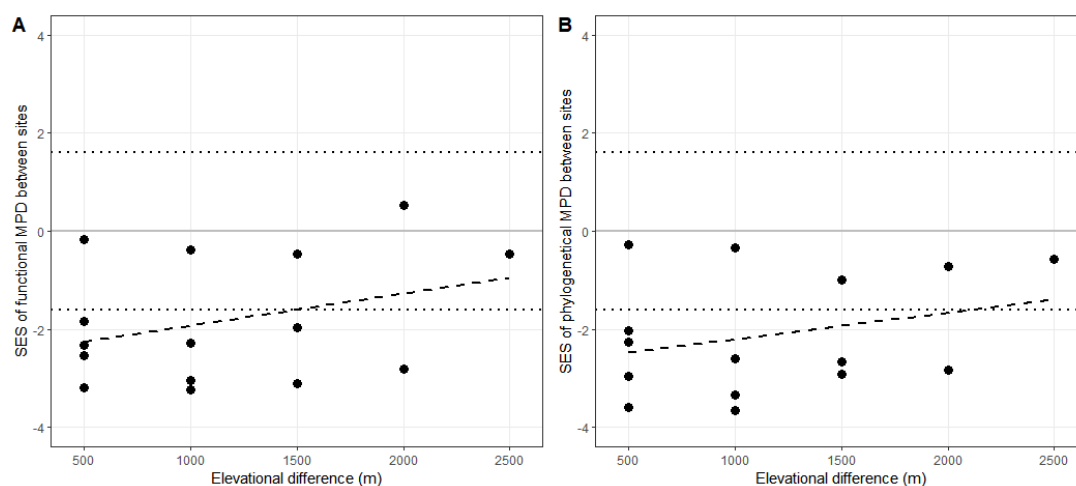


Figure A3.3. Standardised Effect Size (SES) of functional (a) and phylogenetic (b) between-site Mean Pairwise Distance (MPD), analogous to dissimilarity, for birds recorded along the Mt Wilhelm gradient. Each black circle represents a single pairwise comparison between elevations. Functional and phylogenetic dissimilarity between elevations is broadly lower than expected given species dissimilarity, signified by 10 out of 15 pairwise comparisons falling below the lower dotted horizontal line in both cases. Neither type of diversity shows evidence of increasing dissimilarity with increasing elevational distance between plots. SES values for each individual elevational pairwise comparison are displayed in Table S3.

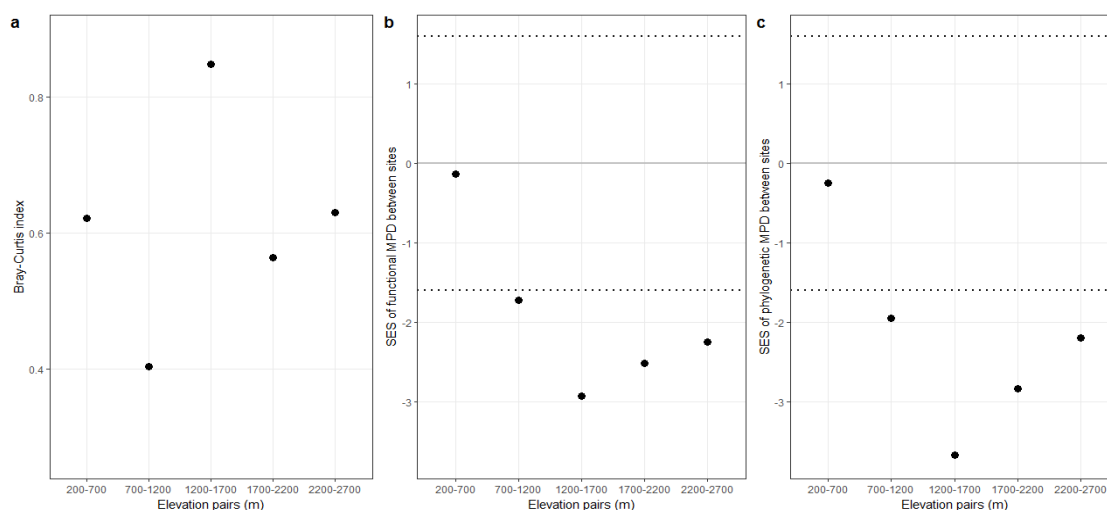


Figure A3.4. Taxonomic, functional and phylogenetic beta-diversity between neighbouring elevations. Taxonomic beta-diversity (a) is represented by Bray-Curtis dissimilarity, and shows a peak between 1,200 and 1,700 m. Functional (b) and phylogenetic beta-diversity (c) are represented by the Standardised Effect Size (SES) of between-site Mean Pairwise Distance (MPD), which reflects functional and phylogenetic dissimilarity after accounting for species dissimilarity between sites. Both show broadly lower dissimilarity than expected, with all comparisons other than 200 – 700 m falling below the lower dotted line. Functional and phylogenetic dissimilarity (after accounting for species dissimilarity) are lowest between 1,200 and 1,700 m.

Table A3.1. List of bird species recorded by point counts at Mt Wilhelm, together with information on their primary food source(s) (from Sam et al. 2017) and the total abundance recorded of each species at each elevation. Latin and common English species names are given. Food sources are categorised as either Vertebrates (Ve), Invertebrates (In), Fruit (Fr), Grains/Seeds (Gr) or Nectar (Ne). Species for which we lacked trait data ($n = 5$) and phylogenetic data ($n = 2$), and were thus excluded from functional and phylogenetic analyses, are marked in red and blue text respectively.

Latin Species Name	English Species Name	Food Source		Elevation (m)					
		1	2	200	700	1200	1700	2200	2700
<i>Accipiter poliocephalus</i>	Grey-headed Goshawk	Ve	In					2	
<i>Aceros plicatus</i>	Papuan Hornbill	Fr		51	8	2			
<i>Ailuroedus buccoides</i>	White-eared Catbird	Fr	In	4	5				
<i>Alcedo azurea</i>	Azure Kingfisher	In	Ve	11					
<i>Aleadryas rufinucha</i>	Rufous-naped Whistler	In					25	12	
<i>Amalocichla incerta</i>	Lesser Ground-robin	In				8			
<i>Amblyornis macgregoriae</i>	Macgregor's Bowerbird	Fr							1
<i>Aplonis metallica</i>	Metallic Starling	Fr	In	8					
<i>Arses insularis</i>	Rufous-collared Monarch	In		24	16				
<i>Artamus maximus</i>	Great Woodswallow	In							6
<i>Astrapia stephaniae</i>	Stephanie's Astrapia	Fr							6
<i>Butastur indicus</i>	Grey-faced Buzzard	Ve						4	
<i>Cacatua galerita</i>	Sulphur-crested Cockatoo	Fr		66	20	4			
<i>Cacomantis castaneiventris</i>	Chestnut-breasted Cuckoo	In				6			
<i>Cacomantis flabelliformis</i>	Fan-tailed Cuckoo	In					16	4	7
<i>Cacomantis variolosus</i>	Brush Cuckoo	In		10	7	1			
<i>Caliechthrus leucolophus</i>	White-crowned Koel	In		6					
<i>Centropus bernsteini</i>	Lesser Black Coucal			12					
<i>Ceyx lepidus</i>	Variable Kingfisher	In			7				
<i>Chaetorhynchus papuensis</i>	Pygmy Drongo	In			4	15			
<i>Chalcophaps stephani</i>	Stephan's Dove	Fr			6	6			
<i>Charmosyna josefinae</i>	Josephine's Lorikeet	Ne						6	
<i>Charmosyna papou</i>	Papuan Lorikeet	Fr	Ne				14	3	27
<i>Charmosyna placentis</i>	Red-flanked Lorikeet	Ne	Fr			19			
<i>Charmosyna rubronotata</i>	Red-fronted Lorikeet	Ne	Fr	6		4			
<i>Cicinnurus magnificus</i>	Magnificent Bird-of-paradise	Fr			17	15			
<i>Cicinnurus regius</i>	King Bird-of-paradise	Fr	In	16	20	2			
<i>Cnemophilus loriae</i>	Loria's Bird-of-paradise	Fr					1		
<i>Collocalia esculenta</i>	Glossy Swiftlet	In					1	58	11
<i>Collocalia vanikorensis</i>	Uniform Swiftlet	In		4			3		
<i>Colluricincla megarhyncha</i>	Little Shrike-thrush	In		17	18	7			
<i>Coracina boyeri</i>	Boyer's Cuckooshrike	Fr	In	8	3	4			
<i>Coracina caeruleogrisea</i>	Stout-billed Cuckooshrike	In				29	4		
<i>Coracina longicauda</i>	Hooded Cuckooshrike	In							3
<i>Coracina melas</i>	New Guinea Cuckooshrike	In			2				
<i>Coracina montana</i>	Black-bellied Cuckooshrike	Fr	In						1
<i>Coracina novaehollandiae</i>	Black-faced Cuckooshrike	Fr	In		1		16	1	

<i>Coracina papuensis</i>	White-bellied Cuckooshrike	In	3						
<i>Coracina tenuirostris</i>	Slender-billed Cicadabird	In		4	2				
<i>Corvus tristis</i>	Grey Crow	Fr	1	20	7			2	
<i>Cracticus cassicus</i>	Hooded Butcherbird	In Ve	83	2					
<i>Cracticus quoyi</i>	Black Butcherbird	In	3						
<i>Crateroscelis murina</i>	Rusty Mouse-warbler	In	1	35	48				
<i>Crateroscelis nigrorufa</i>	Bicoloured Mouse-warbler	In		1		7			
<i>Crateroscelis robusta</i>	Mountain Mouse-warbler	In				4	20	30	
<i>Cyclopsitta diophthalma</i>	Double-eyed Fig-parrot	Fr Ne		6					
<i>Dacelo gaudichaud</i>	Rufous-bellied Kookaburra	In Ve	51	8					
<i>Daphoenositta chrysoptera</i>	Varied Sittella	In							1
<i>Daphoenositta miranda</i>	Black Sittella	In							5
<i>Dicaeum geelvinkianum</i>	Red-capped Flowerpecker	Fr Ne	4	34	30	47	2		
<i>Dicrurus bracteatus</i>	Spangled Drongo	In	39	18					
<i>Drymodes superciliosus</i>	Northern Scrub-robin	In		6					
<i>Ducula chalconota</i>	Shining Imperial-pigeon	Fr				3			
<i>Ducula pinon</i>	Pinon Imperial-pigeon	Fr	30	2					
<i>Ducula rufigaster</i>	Purple-tailed Imperial-pigeon	Fr	1						
<i>Ducula zoeae</i>	Banded Imperial-pigeon	Fr	17	15	31				
<i>Eclectus roratus</i>	Eclectus Parrot	Fr In	22	3					
<i>Epimachus fastuosus</i>	Black Sicklebill	Fr						1	
<i>Epimachus meyeri</i>	Brown Sicklebill	Fr							26
<i>Erythrura papuana</i>	Papuan Parrotfinch	Fr			1				
<i>Erythrura trichroa</i>	Blue-faced Parrotfinch	Fr		4	2	11	16	1	
<i>Eudynamis scolopacea</i>	Asian Koel	In		1	3				
<i>Eugeryone rubra</i>	Garnet Robin	In					4		
<i>Eurystomus orientalis</i>	Asian Dollarbird	In	2						
<i>Gallicolumba beccarii</i>	Bronze Ground-dove	Fr		1					
<i>Gallicolumba rufigula</i>	Cinnamon Ground-dove	Gr			7				
<i>Geoffroyus geoffroyi</i>	Red-cheeked Parrot	Fr Ne	31						
<i>Gerygone chloronota</i>	Green-backed Gerygone	In		17	7				
<i>Gerygone chrysogaster</i>	Yellow-bellied Gerygone	In	8	6	5				
<i>Gerygone cinerea</i>	Mountain Gerygone	In				2		2	
<i>Gerygone ruficollis</i>	Brown-breasted Gerygone	In				8	4	11	
<i>Glycichaera fallax</i>	Green-backed Honeyeater	In	11	1	2				
<i>Grallina bruijnii</i>	Torrent-lark	In			2	1			
<i>Gymnophaps albertisii</i>	Papuan Mountain-pigeon	Fr							23
<i>Haliastur indus</i>	Brahminy Kite	Ve In				2	1		
<i>Harpyopsis novaeguineae</i>	New Guinea Eagle	Ve			1	7			
<i>Henicopernis longicauda</i>	Long-tailed Honey-buzzard	Ve In			1				
<i>Ifrita kowaldi</i>	Ifrit	In						3	10
<i>Lalage atrovirens</i>	Black-browed Triller	Fr In	44	5	4				
<i>Loboparadisea sericea</i>	Yellow-breasted Satinbird	Fr				2	2		
<i>Lonchura spectabilis</i>	Hooded Munia	Gr					12		
<i>Lonchura tristissima</i>	Streak-headed Munia	Gr	4						
<i>Lophorina superba</i>	Superb Bird-of-paradise	Fr				52			

Lorius lory	Black-capped Lory	Fr	Ne	31	17	10	16		
Machaerirhynchus flaviventer	Yellow-breasted Boatbill	In		1		3			
Machaerirhynchus nigripectus	Black-breasted Boatbill	In			10		18	6	10
Macropygia amboinensis	Brown Cuckoo-dove	Fr		3	6	3		1	2
Macropygia nigrirostris	Black-billed Cuckoo-dove	Fr			1	2			
Malurus alboscapulatus	White-shouldered Fairywren	In					5		
Manucodia ater	Glossy-mantled Manucode	Fr				4			
Manucodia chalybatus	Crinkle-collared Manucode	Fr					7		
Megalurus timoriensis	Tawny Grassbird	In	Gr	2			6	12	
Megapodius affinis	New Guinea Megapode	Fr		2			1		
Melampitta lugubris	Lesser Melampitta	In					5		12
Melanocharis crassirostris	Spotted Berrypecker	Fr	In				12		
Melanocharis nigra	Black Berrypecker	Fr	In	3	58	44			
Melanocharis striativentris	Streaked Berrypecker	Fr					11	1	
Melanocharis versteri	Fan-tailed Berrypecker	Fr	In				8	17	3
Melidectes belfordi	Belford's Melidectes	In	Fr				7	16	80
Melidectes rufocrissalis	Yellow-browed Melidectes	In	Ne				83	3	10
Melidectes torquatus	Ornate Melidectes	In	Ne				4		
Melidora macrorrhina	Hook-billed Kingfisher	In	Ve	7					
Melilestes mearnsi	Long-billed Honeyeater	In	Ne	12	41	43	14	1	
Meliphaga analoga	Mimic Honeyeater	In	Fr	80	40	14			
Meliphaga orientalis	Hill-forest Honeyeater	In	Ne						2
Melipotes fumigatus	Smoky Honeyeater	In					25	4	29
Microdynamis parva	Dwarf Koel	Fr		2		1			
Microeca flavovirescens	Olive Flyrobin	In		1	24	9	16	9	23
Micropsitta pusio	Buff-faced Pygmy Parrot	Fr	Ne	7	19	2			
Milvus migrans	Black Kite	Ve		2					
Mino dumontii	Yellow-faced Myna	Fr	In	46	4				
Monarcha chrysomela	Golden Monarch	In		19					
Monarcha guttula	Spot-winged Monarch	In		2	14				
Monarcha manadensis	Hooded Monarch	In		3	2				
Myiagra alecto	Shining Flycatcher	In	Fr	12					
Myzomela rosenbergii	Red-collared Myzomela	Ne	In				40	49	12
Nectarina aspasia	Black Sunbird	Ne	In	10					
Neopsittacus musschenbroekii	Yellow-billed Lorikeet	Fr	Ne					1	2
Neopsittacus pullicauda	Orange-billed Lorikeet	Ne	Fr				29	6	26
Oreocharis arfaki	Tit Berrypecker	Fr					19	3	
Oreopsittacus arfaki	Plum-faced Lorikeet	Ne	Fr					2	5
Otidiphaps nobilis	Pheasant Pigeon	Fr	In			2			
Pachycare flavogriseum	Goldenface	In			5				
Pachycephala hyperythra	Rusty Whistler	In			3	17			
Pachycephala leucogastra	White-bellied Whistler	In						13	
Pachycephala monacha	Black-headed Whistler	In					2		
Pachycephala schlegelii	Regent Whistler	In						13	42
Pachycephala simplex	Grey Whistler	In		6	15		1		14
Pachycephala soror	Sclater's Whistler	In					21		

Pachycephalopsis poliosoma	White-eyed Robin	In				22			
Paradisaea minor	Lesser Bird-of-paradise	Fr	In	52	59	55			
Paramythia montium	Crested Berrypecker	Fr							6
Peltops blainvillii	Lowland Peltops	In		4		6			
Peltops montanus	Mountain Peltops	In			3		5		3
Peneothello bimaculata	White-rumped Robin	In			5	27			
Peneothello cyanus	Blue-grey Robin	In					56	32	4
Peneothello sigillata	White-winged Robin	In	Fr					1	24
Philemon buceroides	Helmeted Friarbird	Ne	Fr	62	4		1		
Philemon meyeri	Meyer's Friarbird	Fr	Ne	1	9	12			
Pitohui dichrous	Hooded Pitohui	Fr	In		36	44	4		
Pitohui ferrugineus	Rusty Pitohui	In	Fr	29	1				
Pitohui kirhocephalus	Variable Pitohui	In	Fr		26	15	1		
<i>Pitta erythrogaster</i>	<i>Red-bellied Pitta</i>	In			3				
Podargus papuensis	Papuan Frogmouth	In	Ve			3			
Poecilodryas hypoleuca	Black-sided Robin	In		8	20				
Pomatostomus isidorei	New Guinea Babbler	In		3	4				
Probosciger aterrimus	Palm Cockatoo	Fr		13	9				
Pseudeos fuscata	Dusky Lory	Fr						31	
Psittacella picta	Painted Tiger-parrot	Fr							4
Psittaculirostris edwardsii	Edwards's Fig-parrot	Fr	Ne	20	16	1			
Psitttrichas fulgidus	Pesquet's Parrot	Fr				2			
<i>Ptilinopus coronulatus</i>	<i>Coroneted Fruit-dove</i>	Fr		2					
Ptilinopus iozonus	Orange-bellied Fruit-dove	Fr		17	15	11			
Ptilinopus magnificus	Wompoo Fruit-dove	Fr		5	4	1			
<i>Ptilinopus ornatus</i>	<i>Ornate Fruit-dove</i>	Fr			5				
Ptilinopus pulchellus	Beautiful Fruit-dove	Fr		39					
Ptilinopus rivoli	White-bibbed Fruit-dove	Fr					4	3	15
Ptilinopus superbus	Superb Fruit-dove	Fr		32	5	1			
Ptiloprora guisei	Rufous-backed Honeyeater	Fr					20	4	42
Ptiloprora perstriata	Black-backed Honeyeater	In	Fr				2	13	39
Ptilorhoa caerulescens	Blue Jewel-babbler	In		4	8	19			
Ptilorhoa leucosticta	Spotted Jewel-babbler	In			5				3
Pycnopygius cinereus	Marbled Honeyeater	Ne	In				16		
Reinwardtoena reinwardtii	Great Cuckoo-dove	Fr		1					
Rhagologus leucostigma	Mottled Whistler	Fr					7	1	
Rhipidura albolimbata	Friendly Fantail	In					32	31	24
Rhipidura atra	Black Fantail	In					9	10	
Rhipidura brachyrhyncha	Dimorphic Fantail	In					16	16	10
Rhipidura leucothorax	White-bellied Thicket-fantail	In		1					
<i>Rhipidura maculipectus</i>	<i>Black Thicket-fantail</i>	In			5	10			
Rhipidura rufidorsa	Rufous-backed Fantail	In		8					
Rhipidura rufiventris	Northern Fantail	In		15	2				
Rhipidura threnothorax	Sooty Thicket-fantail	In		11					
Saxicola caprata	Pied Bushchat	In					2	7	
Scythrops novaehollandiae	Channel-billed Cuckoo	Fr		2					

Sericornis nouhuysi	Large Scrubwren	In					31	18	25
Sericornis papuensis	Papuan Scrubwren	In					41		
Sericornis perspicillatus	Buff-faced Scrubwren	In					42	43	29
Sericornis spilodera	Pale-billed Scrubwren	In			2				
Syma megarhyncha	Mountain Kingfisher	In	Ve				2	1	
Syma torotoro	Yellow-billed Kingfisher	In		2	5	1	16	2	
Talegalla jobiensis	Brown-collared Brush-turkey	Fr	In	3		1			
Tanysiptera galatea	Common Paradise-kingfisher	In			2				
Todiramphus macleayii	Forest Kingfisher	In			1				
Toxorhamphus novaeguineae	Green-crowned Longbill	In	Ne	47	5				
Toxorhamphus poliopterus	Grey-winged Longbill	In	Ne		37	70	41	23	
Tregellasia leucops	White-faced Robin	In	Fr		10	11			
Trichoglossus haematodus	Rainbow Lorikeet	Ne	Fr	67	35	22			
Xanthotis flaviventer	Tawny-breasted Honeyeater	In	Ne	37	10	9			
Xanthotis polygrammus	Spotted Honeyeater	In	Ne						14
Zosterops minor	Black-fronted White-eye	In	Fr		8	13	23	2	1

Table A3.2. Summary tables of all GLM models. Each model was built following the same guidelines (see Methods) and significance was tested using deviance against a null model (~1). “DF” and “Res. DF” refer to degrees of freedom and residual degrees of freedom respectively. Deviance, F- and p-values are also displayed. Significant relationships are shown in bold.

Dependent variable	Data type	Independent variable	Error distribution	Deviance	DF	Residual Deviance	Res. DF	F	p-value
Species diversity	-	Elevation	poisson	12.62	1	0.95	4	-	<0.01
Functional MPD	abundance	Poly(Elevation,2)	gaussian	<0.01	2	<0.01	3	-	<0.01
Phylogenetic MPD	abundance	Poly(Elevation,2)	gaussian	<0.01	2	<0.01	3	-	<0.01
SES of functional MPD	abundance	Poly(Elevation,2)	gaussian	6.71	2	1.45	3	-	<0.01
SES of functional MPD	presence-absence	Elevation	gaussian	11	1	5.17	4	-	<0.01
SES of phylogenetic MPD	abundance	Poly(Elevation,2)	gaussian	6.18	2	2.01	2	-	<0.01
SES of phylogenetic MPD	presence-absence	Elevation	gaussian	12.6	1	8.14	4	-	0.01
Bray-Curtis total	-	Elevation difference	quasibinomial	2.3	1	0.86	13	35.46	<0.01
Bray-Curtis turnover	-	Elevation difference	quasibinomial	2.78	1	1.14	13	32.78	<0.01
Bray-Curtis nestedness	-	Elevation difference	quasibinomial	0.3	1	0.33	13	12.64	<0.01
functional MPD between sites	abundance	Elevation difference	gaussian	<0.01	1	<0.01	13	-	0.07

phylogenetic MPD between sites	abundance	Elevation difference	gaussian	<0.01	1	<0.01	13	-	0.06
SES of functional MPD between sites	abundance	Elevation difference	gaussian	2.49	1	20.49	13	-	0.21
SES of phylogenetic MPD between sites	abundance	Elevation difference	gaussian	1.7	1	18.86	13	-	0.28
SES of phylogenetic MPD	abundance	SES of functional MPD	gaussian	7.67	1	0.52	4	-	<0.01
SES of phylogenetic MPD between sites	abundance	SES of functional MPD between sites	gaussian	18.75	1	1.82	13	-	<0.01

Dependent variable	Independent variable	Error distribution	Deviance	DF	Residual Deviance	Res. DF	F	p-value
Mass	Poly(Elevation,2)	gaussian	0.34	2	0.01	3	-	<0.01
Kipp's Distance	Poly(Elevation,2)	gaussian	0.17	2	0.03	3	-	<0.01
Bill Width	Poly(Elevation,2)	gaussian	0.08	2	0.01	3	-	<0.01
Food Source - Fruit	Elevation	quasibinomial	0.08	1	0.01	4	2.96	0.16
Food Source - Nectar	Elevation	quasibinomial	0.02	1	0.04	4	1.68	0.26
Food Source - Seeds	Elevation	quasibinomial	0.01	1	0.07	4	0.57	0.49
Food Source - Invertebrates	Elevation	quasibinomial	0.16	1	0.05	4	12.28	0.02
Food Source - Vertebrates	Elevation	quasibinomial	0.08	1	0.05	4	6.86	0.06
Foraging Substrate - Water	Elevation	quasibinomial	0.01	1	<0.01	4	74.54	<0.01
Foraging Substrate - Ground	Elevation	quasibinomial	0.02	1	0.02	4	1.75	0.31
Foraging Substrate - Vegetation	Elevation	quasibinomial	0.04	1	0.04	4	4.4	0.1
Foraging Substrate - Air	Elevation	quasibinomial	0.02	1	0.11	4	0.91	0.39

Table A3.3. Results of null model analysis for functional (top table) and phylogenetic (bottom table) dissimilarity between pairs of elevations, measured using Mean Pairwise Distance (MPD). Observed MPD values are displayed for each pairwise comparison, together with the mean and standard deviation (SD) of MPD values obtained by randomising the tips of the trait dendrogram or phylogeny 999 times. The Standardised Effect Size (SES) is obtained by comparing observed values to those gained under null expectations. Negative SES values < -1.6 are indicative of functional and phylogenetic dissimilarity being significantly lower than expected compared to null values.

Elevation Pair (m)	Distance (m)	Observed MPD	Simulated MPD Mean	Simulated MPD SD	SES	Significant
200-700	500	0.154	0.157	0.014	-0.16	FALSE
200-1200	1000	0.152	0.158	0.014	-0.381	FALSE
200-1700	1500	0.153	0.159	0.012	-0.475	FALSE
200-2200	2000	0.165	0.158	0.014	0.519	FALSE
200-2700	2500	0.152	0.159	0.013	-0.468	FALSE
700-1200	500	0.123	0.155	0.017	-1.839	TRUE
700-1700	1000	0.119	0.158	0.013	-3.044	TRUE
700-2200	1500	0.131	0.158	0.013	-1.974	TRUE
700-2700	2000	0.120	0.158	0.014	-2.808	TRUE
1200-1700	500	0.112	0.157	0.014	-3.196	TRUE
1200-2200	1000	0.124	0.158	0.015	-2.275	TRUE
1200-2700	1500	0.113	0.158	0.015	-3.107	TRUE
1700-2200	500	0.111	0.155	0.017	-2.547	TRUE
1700-2700	1000	0.103	0.156	0.016	-3.239	TRUE
2200-2700	500	0.112	0.154	0.018	-2.32	TRUE

Elevation Pair (m)	Distance (m)	Observed MPD	Simulated MPD Mean	Simulated MPD SD	SES	Significant
200-700	500	0.138	0.142	0.012	-0.275	FALSE
200-1200	1000	0.138	0.142	0.012	-0.347	FALSE
200-1700	1500	0.133	0.144	0.01	-1.002	FALSE
200-2200	2000	0.136	0.144	0.011	-0.713	FALSE
200-2700	2500	0.138	0.144	0.011	-0.581	FALSE
700-1200	500	0.112	0.14	0.013	-2.038	TRUE
700-1700	1000	0.104	0.143	0.011	-3.665	TRUE
700-2200	1500	0.113	0.143	0.011	-2.674	TRUE
700-2700	2000	0.113	0.144	0.011	-2.826	TRUE
1200-1700	500	0.099	0.142	0.012	-3.591	TRUE
1200-2200	1000	0.11	0.143	0.013	-2.603	TRUE
1200-2700	1500	0.11	0.144	0.012	-2.908	TRUE
1700-2200	500	0.099	0.141	0.014	-2.956	TRUE
1700-2700	1000	0.096	0.142	0.014	-3.336	TRUE
2200-2700	500	0.107	0.141	0.015	-2.257	TRUE

Appendix: Chapter 4

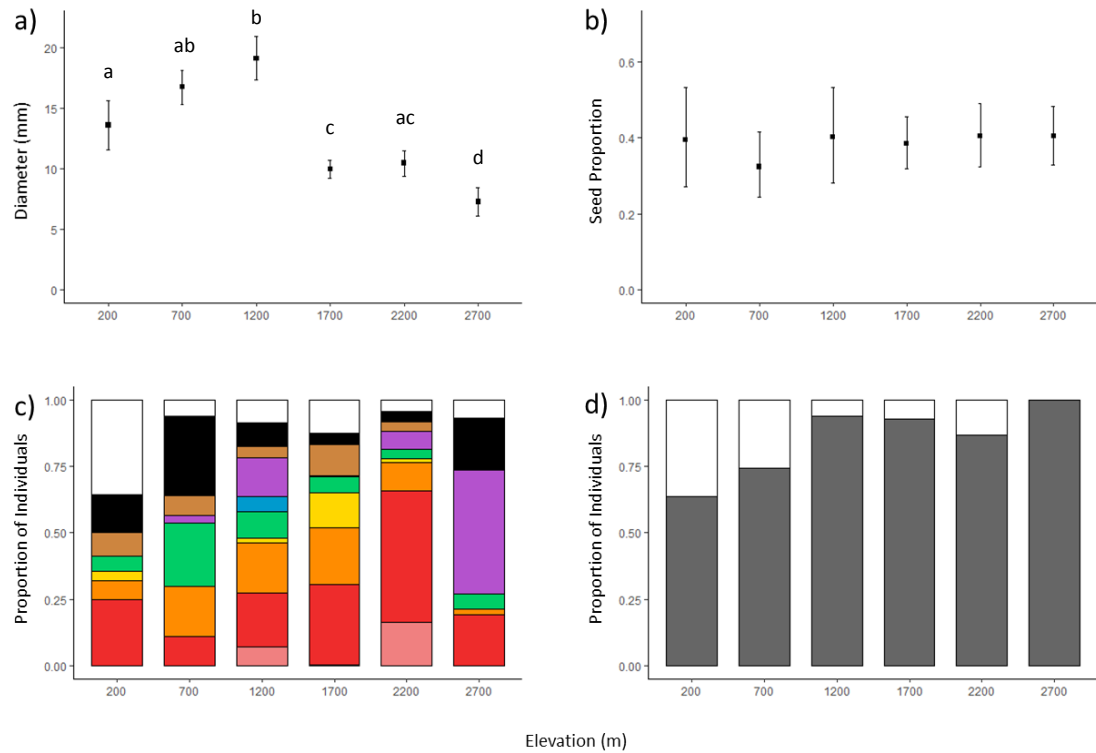


Figure A4.1. Effect of elevation on four fruit traits related to dispersal by frugivores, here weighted by plant individual. a) Mean fruit diameter per fruiting plant is represented by squares, with error bars displaying 95% confidence intervals. Letters above points denote significant differences after adjusting for multiple comparisons using Tukey pairwise tests. b) Squares here represent the mean proportion of fruit weight attributable to seed weight for fruiting plants at each elevation, with 95% confidence intervals. c) Proportion of individual fruiting plants displaying fruits of each colour (top to bottom: white, black, brown, purple, blue, green, yellow, orange, red and pink) at each elevation. d) Proportion of fruiting plants bearing cauliflorous fruits (white bars) and ramiflorous fruits (dark grey bars) at each elevation.

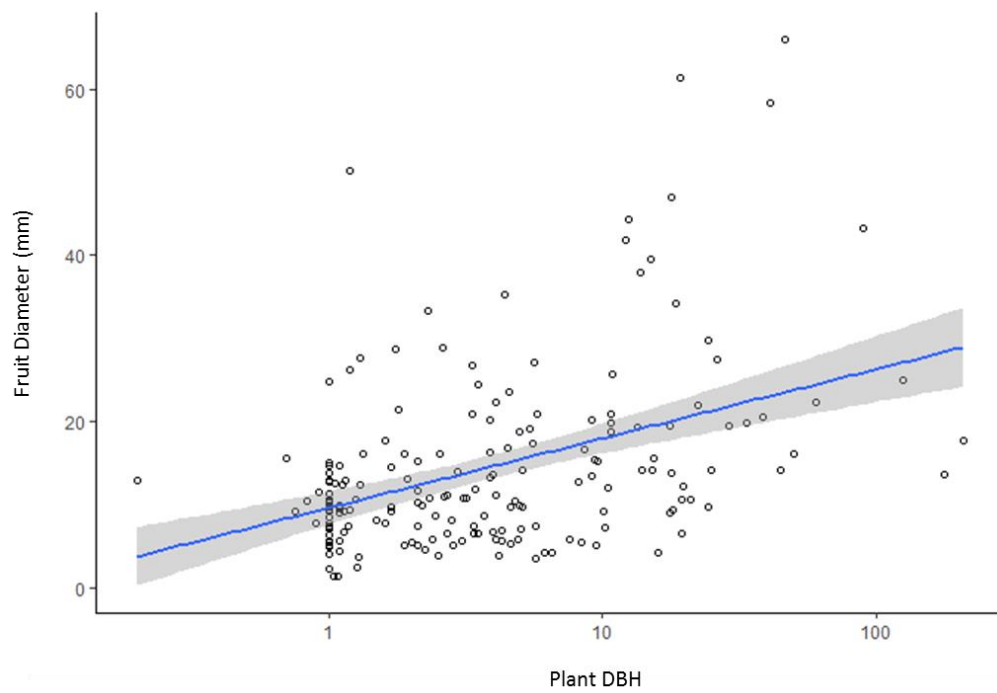


Figure A4.2. Relationship between plant diameter at breast height (DBH) and fruit diameter for all plant species recorded along the elevational gradient. Each circle represents mean DBH and fruit diameter values for a single species. The x-axis is log-transformed for display purposes. The blue line represents a line of best fit, with grey bars representing 95% confidence intervals. R^2 is 0.064.

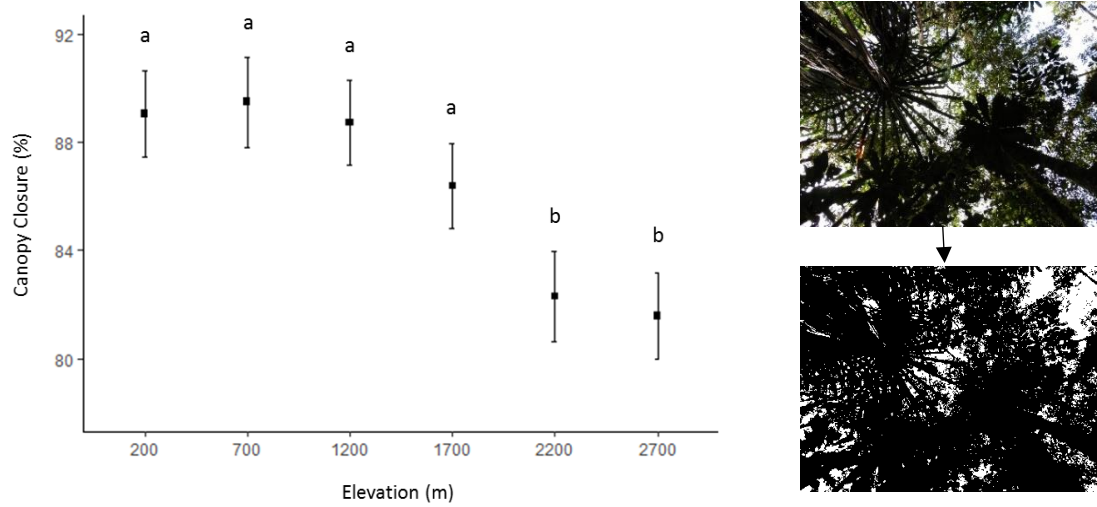


Figure A4.3. Relationship between elevation and canopy closure at each site along the elevational gradient. Black squares represent mean canopy closure, determined using 60 canopy photos taken at each elevation. Original photos (example top right) were converted into black and white images (bottom right) using the Image Processing Toolbox from Matlab version 2019a (Mathworks 2019), with code developed by Korhonen & Heikkinen (2009). Canopy closure is defined as the percentage of black pixels in the subsequent image. Vertical lines represent 95% confidence intervals. Letters denote significant differences between elevations.

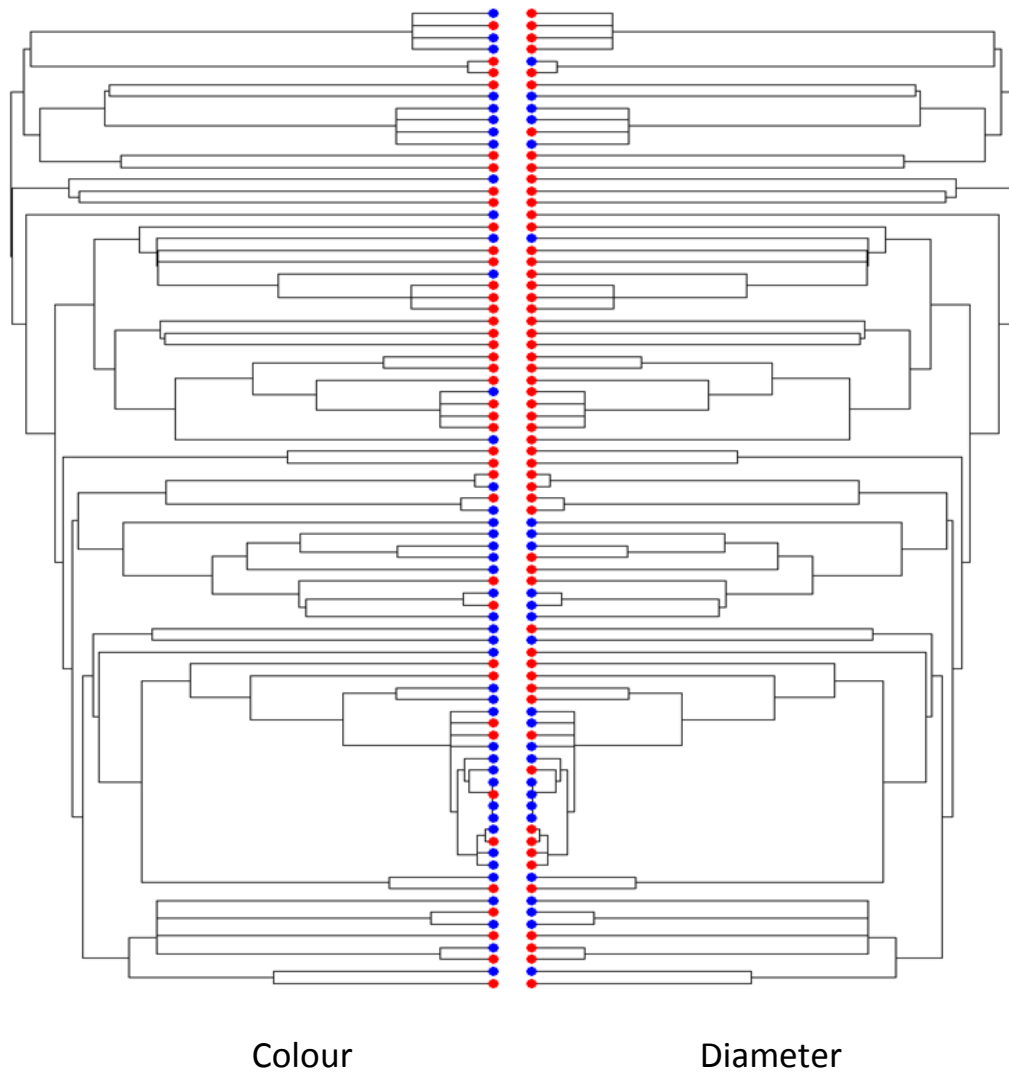


Figure A4.4. Visualisation of data used in Pagel's likelihood ratio test between the fruit traits of colour (left phylogeny) and size (right phylogeny). Each trait is represented by two binary states: species are divided by colour into those displaying "Type A" (green, yellow, orange and brown) fruits (blue circles) and "Type B" (red, pink, purple, blue, black and white) fruits (red circles). Species are divided by mean diameter into "large-fruited" species (blue circles) and "small-fruited" species (red circles).

Table A4.1. List of fruiting plant species and morpho-species recorded at each elevation, together with information on fruit traits. Species means are displayed for fruit diameter and for the proportion of fruit weight attributable to seeds. NA values are given where seeds could not easily be separately weighed (e.g. compound fruits). Presentation types include cauliflorous (C), ramiflorous (R) and “C+R” (species with individuals displaying either presentation type). NA values are given for species for which individuals displayed both types of presentation simultaneously. The mode fruit colour is also listed for each species.

Elevation	species	Fruit Diameter	Seed Proportion	Presentation	Colour
200 m	Aglaia sp. 1	21.4	0.453	NA	orange
200 m	Allophylus cobbe	6.47	0.398	C	red
200 m	ANNONACEAE sp. 1	13.98	0.537	C	black
200 m	Artocarpus lakoocha	7.23	NA	C	yellow
200 m	Casearia clutiifolia	16.05	0.405	NA	orange
200 m	Erythrospermum candidum	9	0.269	NA	green
200 m	Ficus congesta	38	0.325	C	brown
200 m	Ficus sp. 5	20.16	0.209	C	green
200 m	Ganadium sp. 1	22.07	0.431	R	black
200 m	Harpullia ramiflora	22.33	0.078	C	red
200 m	Leea indica	11.17	0.191	C+R	black
200 m	Litsea collina	14.26	0.494	NA	red
200 m	Micromelum minutum	5.9	0.361	NA	orange
200 m	Myristica sp. 3	20.5	0.14	NA	yellow
200 m	Myristica sp. 4	19.5	0.452	NA	brown
200 m	Pittosporum sinuatum	11.5	NA	R	red
200 m	Psychotria leptothyrsa	11.94	0.25	R	red
200 m	Psychotria sp. 1	5.53	0.459	R	white
200 m	Psychotria sp. 2	12.92	0.176	R	white
200 m	SAPINDACEAE sp. 1	25.63	0.594	C+R	red
200 m	Wenzelia dolichophylla	35.23	0.14	NA	orange
700 m	Aglaia sp. 2	13.83	0.593	R	red
700 m	ANNONACEAE sp. 2	9.43	0.442	R	red
700 m	Archidendron aruense	19.3	0.115	C	orange
700 m	Archidendron sp. 1	27.1	0.071	C	red
700 m	Ardisia imperialis	6.5	0.455	R	purple
700 m	Ardisia sp. 2	11.06	0.494	R	green
700 m	Ardisia sp. 1	10.88	0.3	R	green
700 m	Clerodendrum sp. 1	9.8	0.574	R	black
700 m	Cryptocarya sp. 1	11.27	0.513	R	green
700 m	Cupaniopsis acuticarpa	20.98	0.376	R	orange
700 m	Cupaniopsis sp. 1	13.7	0.155	R	green
700 m	Ficus badiopurpurea	5.1	0.235	R	green
700 m	Ficus bernaysii	18.8	0.31	C	green
700 m	Ficus hahliana	15.4	0.217	C	green
700 m	Ficus morobensis	39.55	0.129	C	brown
700 m	Ficus pungens	6.56	0.367	C	brown
700 m	Ficus saccata	18.3	0.125	NA	orange

700 m	<i>Ficus sangumae</i>	13.8	0.218	C	red
700 m	<i>Ficus</i> sp. 3	29.83	NA	R	brown
700 m	<i>Ficus</i> sp. 4	47.05	0.259	C	green
700 m	<i>Ficus wassa</i>	14.7	0.318	C	red
700 m	<i>Glochidion angulatum</i>	5.8	0.211	R	green
700 m	<i>Gymnacranthera paniculata</i>	20.85	0.095	R	orange
700 m	<i>Harpullia longipetala</i>	23.63	0.216	C+R	orange
700 m	<i>Harpullia</i> sp. 1	24.5	0.068	R	green
700 m	<i>Harpullia</i> sp. 2	20.16	0.03	C	green
700 m	<i>Homalanthus novoguineensis</i>	5.9	0.125	R	red
700 m	<i>Kibara</i> sp. 2	9.7	0.482	R	black
700 m	LAMIACEAE sp. 1	8.2	0.286	R	red
700 m	<i>Leucosyke australis</i>	14.7	0.255	R	white
700 m	<i>Leucosyke</i> sp. 1	10.57	NA	R	white
700 m	<i>Magnolia tsiampacca</i>	13.7	0.691	R	orange
700 m	<i>Medinilla crassinervia</i>	17.76	0.415	C+R	purple
700 m	<i>Melastoma</i> sp. 1	9.3	NA	R	red
700 m	<i>Myristica subululata</i>	5.47	0.467	R	orange
700 m	<i>Pandanus kaernbachii</i>	7.85	0.152	R	orange
700 m	<i>Pittosporum sinuatum</i>	9.2	NA	R	red
700 m	<i>Planchonella</i> sp. 1	61.32	0.562	R	black
700 m	<i>Popowia pisocarpa</i>	13.51	0.235	C+R	black
700 m	<i>Psychotria micrococca</i>	6.78	0.339	R	white
700 m	<i>Sterculia schumanniana</i>	26.73	0.174	R	green
700 m	<i>Syzygium gonathantum</i>	50.1	0.246	R	red
700 m	<i>Syzygium</i> sp. 1	27.6	0.239	R	red
1200 m	<i>Aglaia tomentosa</i>	12.37	0.276	R	green
1200 m	<i>Annesijoa novoguineensis</i>	19.58	0.085	R	yellow
1200 m	ANNONACEAE sp. 3	11.77	0.153	R	purple
1200 m	<i>Ardisia imperialis</i>	6.89	0.68	R	black
1200 m	<i>Ardisia lanceolata</i>	14.5	0.293	R	pink
1200 m	<i>Ardisia</i> sp. 2	10.76	0.43	R	red
1200 m	<i>Ardisia</i> sp. 1	9.85	0.684	R	red
1200 m	<i>Areca</i> sp. 1	10.51	0.733	R	red
1200 m	<i>Caryota rumphiana</i>	14.23	NA	C	black
1200 m	<i>Cyclophyllum brevipes</i>	7.3	0.417	R	blue
1200 m	<i>Cyrtandra erectiloba</i>	12.45	0.561	R	white
1200 m	FAGACEAE sp. 1	17.81	NA	R	black
1200 m	<i>Garcinia maluensis</i>	28.8	0.533	R	orange
1200 m	<i>Harpullia longipetala</i>	18.73	0.563	NA	red
1200 m	<i>Harpullia</i> sp. 3	13.22	0.582	C	red
1200 m	<i>Kibara</i> sp. 1	9.06	0.478	R	black
1200 m	<i>Magnolia tsiampacca</i>	24.93	NA	R	green
1200 m	<i>Medinilla crassinervia</i>	15.1	NA	C	green
1200 m	<i>Melastoma</i> sp. 1	16.15	0.32	R	pink
1200 m	<i>Myristica fatua</i>	58.4	0.028	R	orange

1200 m	<i>Myristica filipes</i>	65.9	0.225	R	brown
1200 m	<i>Myristica</i> sp. 1	16.38	0.519	R	orange
1200 m	<i>Myristica</i> sp. 2	19.8	0.319	R	brown
1200 m	<i>Myristica subalulata</i>	27.5	NA	R	brown
1200 m	<i>Planchonella macropoda</i>	43.2	0.318	R	black
1200 m	<i>Prunus dolichobotrys</i>	24.9	NA	R	orange
1200 m	<i>Rapanea involucrata</i>	10.3	0.469	R	red
1200 m	RUBIACEAE sp. 1	9.45	0.255	R	purple
1200 m	RUBIACEAE sp. 2	11.42	0.461	R	white
1200 m	RUBIACEAE sp. 3	9.84	0.088	R	purple
1200 m	RUBIACEAE sp. 3	10.48	0.271	R	blue
1200 m	RUBIACEAE sp. 3	10.57	0.27	R	purple
1200 m	SOLANACEAE sp. 1	29	0.524	NA	orange
1200 m	<i>Solanum</i> sp. 1	12.93	NA	R	orange
1200 m	<i>Solanum</i> sp. 2	15.3	0.647	R	red
1200 m	<i>Terminalia</i> sp. 1	31.1	0.688	R	green
1200 m	ULMACEAE sp. 1	5.03	NA	R	white
1200 m	<i>Ziziphus angustifolia</i>	12.71	0.568	R	purple
1700 m	<i>Ardisia</i> sp. 4	26.3	NA	R	pink
1700 m	<i>Canarium</i> sp. 1	9.8	0.224	R	black
1700 m	<i>Chisocheton</i> sp. 1	33.4	0.198	R	red
1700 m	<i>Ficus arfakensis</i>	16.85	0.413	R	brown
1700 m	<i>Ficus hahliana</i>	20.83	0.343	C+R	red
1700 m	<i>Ficus sangumae</i>	12.43	0.428	C	yellow
1700 m	<i>Ficus subulata</i>	4.4	0.147	R	yellow
1700 m	<i>Ficus trachypison</i>	14.15	0.324	R	orange
1700 m	<i>Ficus trichocerasa</i>	12.25	0.202	C+R	red
1700 m	<i>Ficus wassa</i>	9.8	0.24	C+R	red
1700 m	<i>Kibara coriacea</i>	10.23	0.421	R	purple
1700 m	<i>Lepidopetalum comesperma</i>	9.8	0.478	R	green
1700 m	<i>Melicope elleryana</i>	17.4	0.026	R	brown
1700 m	<i>Myristica filipes</i>	44.3	NA	R	brown
1700 m	<i>Osmoxylon</i> sp. 1	1.43	NA	R	orange
1700 m	<i>Osmoxylon</i> sp. 2	5.7	0.625	R	black
1700 m	<i>Piper interruptum</i>	7.47	NA	R	red
1700 m	<i>Piper macropiper</i>	2.40	NA	R	brown
1700 m	<i>Piper recessum</i>	6.78	NA	R	yellow
1700 m	<i>Piper</i> sp. 1	8.5	NA	R	red
1700 m	<i>Piper</i> sp. 2	9.2	NA	R	red
1700 m	<i>Piper</i> sp. 3	10.4	NA	R	orange
1700 m	<i>Pittosporum</i> sp. 1	10.54	0.62	R	orange
1700 m	<i>Psychotria micrococca</i>	9.85	0.548	R	white
1700 m	<i>Psychotria</i> sp. 3	4.6	0.5	R	white
1700 m	RHAMNACEAE sp. 1	10.2	0.507	R	black
1700 m	RUBIACEAE sp. 4	4.01	0.511	R	white
1700 m	<i>Saurauia conferta</i>	29.67	NA	R	green

1700 m	<i>Smilax nova-guineensis</i>	13	0.326	R	black
1700 m	<i>Sterculia schumanniana</i>	15.54	0.548	R	black
1700 m	<i>Tabernaemontana pandacaqui</i>	10.2	NA	R	red
1700 m	VITACEAE sp. 1	2.28	NA	R	purple
1700 m	<i>Xanthophyllum papuanum</i>	10.6	0.376	R	brown
2200 m	ANNONACEAE sp. 1	28.9	0.126	R	green
2200 m	<i>Ardisia</i> sp. 2	9	0.346	R	pink
2200 m	<i>Ardisia</i> sp. 1	7.42	0.234	R	black
2200 m	<i>Astronidium</i> sp. 1	12.8	0.173	R	white
2200 m	<i>Cayratia trifolia</i>	9.50	0.26	R	black
2200 m	<i>Cyrtandra erectiloba</i>	10.7	NA	R	green
2200 m	<i>Decaspermum alpinum</i>	5.05	0.588	R	orange
2200 m	<i>Decaspermum forbesii</i>	5.2	0.25	R	orange
2200 m	<i>Embelia cotinoides</i>	12.5	NA	R	pink
2200 m	<i>Ficus iodotricha</i>	41.84	NA	C	red
2200 m	<i>Ficus microdictya</i>	19.8	NA	NA	brown
2200 m	<i>Ficus sangumae</i>	15.55	0.292	C+R	pink
2200 m	<i>Ficus</i> sp. 1	16.05	0.139	R	green
2200 m	<i>Ficus</i> sp. 2	22.35	0.26	R	red
2200 m	<i>Ficus wassa</i>	7.48	0.4	C+R	pink
2200 m	<i>Hydriastele</i> sp. 1	14.22	0.493	C+R	red
2200 m	<i>Ichnocarpus frutescens</i>	9.4	0.267	R	black
2200 m	<i>Kibara coriacea</i>	10.73	0.653	R	black
2200 m	<i>Maesa haplobotrys</i>	3.97	0.333	R	brown
2200 m	<i>Medinilla crassinervia</i>	5.2	NA	C+R	white
2200 m	<i>Medinilla lorentziana</i>	5.5	0.25	R	brown
2200 m	<i>Melastoma</i> sp. 2	7.5	0.429	R	green
2200 m	<i>Melicope</i> sp. 1	16.58	0.018	R	yellow
2200 m	<i>Myrsine womersleyi</i>	5.35	0.366	R	purple
2200 m	<i>Osmoxylon</i> sp. 1	1.39	NA	R	orange
2200 m	<i>Pandanus</i> sp. 1	9.42	0.043	C+R	red
2200 m	<i>Piper celtidiforme</i>	12.8	NA	R	orange
2200 m	<i>Piper macropiper</i>	3.75	NA	R	red
2200 m	<i>Piper</i> sp. 5	7.1	NA	R	orange
2200 m	<i>Pittosporum</i> sp. 1	7.74	NA	R	red
2200 m	<i>Polyosma cunninghamii</i>	8.1	0.125	R	black
2200 m	<i>Psychotria murmurensis</i>	5.2	NA	R	orange
2200 m	<i>Scaevola oppositifolia</i>	5.65	0.5	R	black
2200 m	<i>Smilax nova-guineensis</i>	10.2	0.438	R	brown
2200 m	<i>Timonius</i> sp. 1	31.4	NA	R	red
2200 m	<i>Tinospora cordifolia</i>	5.6	0.364	R	yellow
2200 m	<i>Tripetalum cymosum</i>	34.25	0.222	R	red
2200 m	<i>Zehneria mucronata</i>	6.4	0.154	R	brown
2700 m	<i>Ardisia</i> sp. 1	5.78	0.224	R	black
2700 m	<i>Ardisia</i> sp. 3	5.63	0.348	R	black
2700 m	<i>Bhesa archboldiana</i>	3.6	0.6	R	red

2700 m	Breynia cernua	6.6	0.435	R	black
2700 m	Decaspermum alpinum	9.3	NA	R	red
2700 m	Elaeocarpus nymanii	14.16	0.806	R	green
2700 m	Eurya tigang	9.2	NA	R	purple
2700 m	Glochidion sp. 2	4.3	0.375	R	red
2700 m	Glochidion sp. 1	4.22	0.397	R	red
2700 m	Kibara coriacea	11.12	0.516	R	black
2700 m	Kibara sp. 3	19.08	0.267	R	red
2700 m	Maesa edulis	4.17	0.4	R	red
2700 m	Myrsine involucrata	3.96	0.405	R	purple
2700 m	Myrsine womersleyi	7.01	0.429	R	purple
2700 m	Palmeria sp. 1	7.87	0.448	R	red
2700 m	Piper sp. 4	16.2	NA	R	orange
2700 m	Polyosma cunninghamii	8.63	0.42	R	purple
2700 m	Prunus oligantha	13.16	0.481	R	red
2700 m	Prunus sp. 1	14.7	0.453	R	black
2700 m	Psychotria multicostata	9.99	0.299	R	white
2700 m	RUBIACEAE sp. 1	7.8	NA	R	orange
2700 m	Saurauia sp. 1	12.01	0.291	R	green
2700 m	Solanum sp. 1	8.6	0.625	R	red
2700 m	Steganthera sp. 1	9.24	0.631	R	black
2700 m	Streblus glaber	5.6	0	R	green
2700 m	Streblus sp. 1	7.43	0.379	R	black
2700 m	Zygogynum haplopus	5.22	0.295	R	black
2700 m	Zygogynum oligostigma	15.25	NA	R	red

Table A4.2. Results of Tukey pairwise comparisons from generalised linear models testing the effect of elevation on different fruit traits (left column). Estimate and standard error values are displayed, together with z ratios and p values adjusted for multiple comparisons. Significant comparisons are displayed in bold.

Parameter	Elevation Pairs	Estimate	SE	z-ratio	p-value
Fruit Diameter	200 - 700	-0.885	2.76	-0.321	1
	200 - 1200	-1.672	2.81	-0.594	0.99
	200 - 1700	4.148	2.89	1.436	0.71
	200 - 2200	4.819	2.81	1.713	0.52
	200 - 2700	7.781	2.99	2.605	0.1
	700 - 1200	-0.787	2.3	-0.342	1
	700 - 1700	5.032	2.39	2.101	0.29
	700 - 2200	5.703	2.3	2.475	0.13
	700 - 2700	8.665	2.51	3.448	<0.01
	1200 - 1700	5.819	2.46	2.363	0.17
	1200 - 2200	6.49	2.37	2.734	0.07

	1200 - 2700	9.452	2.58	3.667	<0.01
	1700 - 2200	0.671	2.46	0.272	1
	1700 - 2700	3.633	2.66	1.366	0.75
	2200 - 2700	2.962	2.58	1.149	0.86
Seed Proportion	200 - 700	0.178	0.599	0.298	1
	200 - 1200	-0.342	0.611	-0.559	0.99
	200 - 1700	-0.202	0.662	-0.305	1
	200 - 2200	0.175	0.648	0.271	1
	200 - 2700	-0.34	0.645	-0.527	1
	700 - 1200	-0.52	0.51	-1.019	0.91
	700 - 1700	-0.381	0.57	-0.668	0.99
	700 - 2200	-0.003	0.554	-0.005	1
	700 - 2700	-0.518	0.55	-0.942	0.94
	1200 - 1700	0.139	0.582	0.239	1
	1200 - 2200	0.517	0.567	0.912	0.94
	1200 - 2700	0.002	0.563	0.004	1
	1700 - 2200	0.378	0.621	0.608	0.99
	1700 - 2700	-0.137	0.617	-0.223	1
	2200 - 2700	-0.515	0.603	-0.854	0.96
Colour Type: A	200 - 700	-0.883	0.452	-1.954	0.37
	200 - 1200	-0.231	0.486	-0.475	1
	200 - 1700	-0.671	0.428	-1.566	0.62
	200 - 2200	0.087	0.455	0.192	1
	200 - 2700	1.222	0.539	2.268	0.21
	700 - 1200	0.652	0.381	1.709	0.53
	700 - 1700	0.213	0.304	0.699	0.98
	700 - 2200	0.97	0.341	2.843	0.05
	700 - 2700	2.105	0.446	4.716	<0.01
	1200 - 1700	-0.439	0.353	-1.244	0.81
	1200 - 2200	0.319	0.386	0.826	0.96
	1200 - 2700	1.453	0.481	3.02	0.03
	1700 - 2200	0.758	0.309	2.451	0.14
	1700 - 2700	1.892	0.422	4.481	<0.01
	2200 - 2700	1.134	0.45	2.521	0.12
Colour Type: B	200 - 700	0.883	0.452	1.954	0.37
	200 - 1200	0.231	0.486	0.475	1
	200 - 1700	0.671	0.428	1.566	0.62
	200 - 2200	-0.087	0.455	-0.192	1
	200 - 2700	-1.222	0.539	-2.268	0.21
	700 - 1200	-0.652	0.381	-1.709	0.53
	700 - 1700	-0.213	0.304	-0.699	0.98
	700 - 2200	-0.97	0.341	-2.843	0.05
	700 - 2700	-2.105	0.446	-4.716	<0.01
	1200 - 1700	0.439	0.353	1.244	0.81
	1200 - 2200	-0.319	0.386	-0.826	0.96
	1200 - 2700	-1.453	0.481	-3.02	0.03

	1700 - 2200	-0.758	0.309	-2.451	0.14
	1700 - 2700	-1.892	0.422	-4.481	<0.01
	2200 - 2700	-1.134	0.45	-2.521	0.12
Colour: Red	200 - 700	0.995	0.491	2.026	0.33
	200 - 1200	0.737	0.517	1.426	0.71
	200 - 1700	0.029	0.425	0.068	1
	200 - 2200	0.172	0.447	0.386	1
	200 - 2700	0.362	0.467	0.776	0.97
	700 - 1200	-0.258	0.476	-0.541	0.99
	700 - 1700	-0.966	0.374	-2.585	0.1
	700 - 2200	-0.823	0.398	-2.064	0.31
	700 - 2700	-0.633	0.421	-1.504	0.66
	1200 - 1700	-0.708	0.407	-1.74	0.51
	1200 - 2200	-0.565	0.43	-1.314	0.78
	1200 - 2700	-0.375	0.451	-0.833	0.96
	1700 - 2200	0.143	0.313	0.458	1
	1700 - 2700	0.333	0.341	0.977	0.93
	2200 - 2700	0.19	0.368	0.516	1
Colour: Orange	200 - 700	-0.506	0.613	-0.824	0.96
	200 - 1200	-0.443	0.651	-0.681	0.98
	200 - 1700	-0.257	0.594	-0.432	1
	200 - 2200	-0.19	0.621	-0.306	1
	200 - 2700	1.54	0.896	1.719	0.52
	700 - 1200	0.062	0.475	0.131	1
	700 - 1700	0.249	0.394	0.632	0.99
	700 - 2200	0.316	0.433	0.73	0.98
	700 - 2700	2.046	0.778	2.631	0.09
	1200 - 1700	0.187	0.45	0.414	1
	1200 - 2200	0.253	0.485	0.523	1
	1200 - 2700	1.984	0.808	2.455	0.14
	1700 - 2200	0.067	0.406	0.165	1
	1700 - 2700	1.797	0.763	2.355	0.17
	2200 - 2700	1.73	0.784	2.208	0.23
Colour: Yellow	200 - 700	19.14	3926.92	0.005	1
	200 - 1200	1.176	1.247	0.943	0.94
	200 - 1700	-0.554	0.792	-0.699	0.98
	200 - 2200	0.977	1.023	0.954	0.93
	200 - 2700	19.048	3919.62	0.005	1
	700 - 1200	-17.964	3926.92	-0.005	1
	700 - 1700	-19.694	3926.92	-0.005	1
	700 - 2200	-18.163	3926.92	-0.005	1
	700 - 2700	-0.092	5548.34	0	1
	1200 - 1700	-1.73	1.056	-1.639	0.57
	1200 - 2200	-0.199	1.239	-0.161	1
	1200 - 2700	17.872	3919.62	0.005	1
	1700 - 2200	1.53	0.779	1.965	0.36

	1700 - 2700	19.602	3919.62	0.005	1
	2200 - 2700	18.071	3919.62	0.005	1
Colour: Green	200 - 700	-1.738	0.777	-2.236	0.22
	200 - 1200	-0.522	0.87	-0.6	0.99
	200 - 1700	0.034	0.829	0.041	1
	200 - 2200	0.021	0.865	0.024	1
	200 - 2700	-0.388	0.847	-0.458	1
	700 - 1200	1.216	0.541	2.246	0.22
	700 - 1700	1.772	0.471	3.761	<0.01
	700 - 2200	1.759	0.532	3.305	0.01
	700 - 2700	1.35	0.503	2.682	0.08
	1200 - 1700	0.556	0.613	0.908	0.94
	1200 - 2200	0.543	0.661	0.821	0.96
	1200 - 2700	0.134	0.638	0.21	1
	1700 - 2200	-0.013	0.605	-0.022	1
	1700 - 2700	-0.422	0.58	-0.728	0.98
	2200 - 2700	-0.409	0.63	-0.649	0.99
Colour: Blue	200 - 700	0.554	16245	0	1
	200 - 1200	-20.124	12246	-0.002	1
	200 - 1700	0.952	16048	0	1
	200 - 2200	0.628	16133	0	1
	200 - 2700	0.462	16232	0	1
	700 - 1200	-20.678	10674	-0.002	1
	700 - 1700	0.398	14883	0	1
	700 - 2200	0.074	14975	0	1
	700 - 2700	-0.092	15082	0	1
	1200 - 1700	21.077	10371	0.002	1
	1200 - 2200	20.753	10502	0.002	1
	1200 - 2700	20.586	10655	0.002	1
	1700 - 2200	-0.324	14760	0	1
	1700 - 2700	-0.49	14869	0	1
	2200 - 2700	-0.166	14961	0	1
Colour: Purple	200 - 700	-16.139	1657.35	-0.01	1
	200 - 1200	-17.314	1657.35	-0.01	1
	200 - 1700	-15.253	1657.35	-0.009	1
	200 - 2200	-16.329	1657.35	-0.01	1
	200 - 2700	-18.449	1657.35	-0.011	1
	700 - 1200	-1.175	0.734	-1.601	0.6
	700 - 1700	0.886	0.926	0.957	0.93
	700 - 2200	-0.19	0.782	-0.243	1
	700 - 2700	-2.31	0.648	-3.563	<0.01
	1200 - 1700	2.061	0.836	2.465	0.13
	1200 - 2200	0.985	0.674	1.463	0.69
	1200 - 2700	-1.135	0.512	-2.214	0.23
	1700 - 2200	-1.076	0.879	-1.224	0.83
	1700 - 2700	-3.196	0.762	-4.192	<0.01

	2200 - 2700	-2.12	0.579	-3.66	<0.01
Colour: Pink	200 - 700	0.554	9853.38	0	1
	200 - 1200	-19.552	7427.74	-0.003	1
	200 - 1700	-18.253	7427.74	-0.002	1
	200 - 2200	-20.725	7427.74	-0.003	1
	200 - 2700	0.462	9845.47	0	1
	700 - 1200	-20.106	6474.4	-0.003	1
	700 - 1700	-18.807	6474.4	-0.003	1
	700 - 2200	-21.279	6474.4	-0.003	1
	700 - 2700	-0.092	9147.67	0	1
	1200 - 1700	1.299	0.93	1.397	0.73
	1200 - 2200	-1.173	0.665	-1.763	0.49
	1200 - 2700	20.014	6462.36	0.003	1
	1700 - 2200	-2.472	0.772	-3.202	0.02
	1700 - 2700	18.715	6462.36	0.003	1
	2200 - 2700	21.187	6462.36	0.003	1
Colour: Brown	200 - 700	0.144	0.894	0.161	1
	200 - 1200	0.034	0.943	0.036	1
	200 - 1700	-0.954	0.777	-1.227	0.82
	200 - 2200	0.021	0.865	0.024	1
	200 - 2700	18.048	2377.37	0.008	1
	700 - 1200	-0.11	0.788	-0.14	1
	700 - 1700	-1.098	0.578	-1.899	0.4
	700 - 2200	-0.124	0.692	-0.179	1
	700 - 2700	17.904	2377.37	0.008	1
	1200 - 1700	-0.987	0.652	-1.515	0.65
	1200 - 2200	-0.013	0.754	-0.018	1
	1200 - 2700	18.014	2377.37	0.008	1
	1700 - 2200	0.974	0.532	1.831	0.45
	1700 - 2700	19.001	2377.37	0.008	1
	2200 - 2700	18.027	2377.37	0.008	1
Colour: Black	200 - 700	-0.11	0.54	-0.204	1
	200 - 1200	0.519	0.63	0.823	0.96
	200 - 1700	1.138	0.584	1.948	0.37
	200 - 2200	0.904	0.603	1.499	0.67
	200 - 2700	-0.308	0.538	-0.572	0.99
	700 - 1200	0.629	0.524	1.199	0.84
	700 - 1700	1.248	0.468	2.665	0.08
	700 - 2200	1.013	0.491	2.063	0.31
	700 - 2700	-0.198	0.409	-0.484	1
	1200 - 1700	0.619	0.57	1.086	0.89
	1200 - 2200	0.385	0.589	0.653	0.99
	1200 - 2700	-0.827	0.523	-1.581	0.61
	1700 - 2200	-0.234	0.54	-0.434	1
	1700 - 2700	-1.446	0.466	-3.1	0.02
	2200 - 2700	-1.212	0.49	-2.475	0.13

Colour: White	200 - 700	1.211	0.797	1.52	0.65
	200 - 1200	0.799	0.802	0.996	0.92
	200 - 1700	0.799	0.663	1.205	0.83
	200 - 2200	0.785	0.707	1.11	0.88
	200 - 2700	1.119	0.798	1.403	0.73
	700 - 1200	-0.413	0.839	-0.492	1
	700 - 1700	-0.413	0.707	-0.584	0.99
	700 - 2200	-0.426	0.749	-0.569	0.99
	700 - 2700	-0.092	0.835	-0.111	1
	1200 - 1700	0	0.713	0	1
	1200 - 2200	-0.013	0.754	-0.018	1
	1200 - 2700	0.321	0.84	0.382	1
	1700 - 2200	-0.013	0.605	-0.022	1
	1700 - 2700	0.321	0.708	0.452	1
	2200 - 2700	0.334	0.75	0.445	1
Presentation:	200 - 700	0.055	0.472	0.116	1
Cauliflorous	200 - 1200	1.77	0.714	2.478	0.13
	200 - 1700	0.999	0.475	2.1	0.29
	200 - 2200	1.09	0.517	2.106	0.28
	200 - 2700	19.817	2363.89	0.008	1
	700 - 1200	1.715	0.651	2.633	0.09
	700 - 1700	0.944	0.374	2.522	0.12
	700 - 2200	1.035	0.426	2.428	0.15
	700 - 2700	19.762	2363.89	0.008	1
	1200 - 1700	-0.771	0.653	-1.18	0.85
	1200 - 2200	-0.68	0.685	-0.993	0.92
	1200 - 2700	18.048	2363.89	0.008	1
	1700 - 2200	0.091	0.43	0.212	1
	1700 - 2700	18.819	2363.89	0.008	1
	2200 - 2700	18.728	2363.89	0.008	1
Presentation:	200 - 700	-2.133	0.498	-4.287	<0.01
Ramiflorous	200 - 1200	-3.041	0.592	-5.139	<0.01
	200 - 1700	-2.361	0.474	-4.982	<0.01
	200 - 2200	-2.341	0.494	-4.739	<0.01
	200 - 2700	-3.608	0.605	-5.967	<0.01
	700 - 1200	-0.908	0.482	-1.884	0.41
	700 - 1700	-0.228	0.326	-0.699	0.98
	700 - 2200	-0.208	0.355	-0.586	0.99
	700 - 2700	-1.475	0.497	-2.965	0.04
	1200 - 1700	0.68	0.457	1.486	0.67
	1200 - 2200	0.7	0.478	1.465	0.69
	1200 - 2700	-0.568	0.592	-0.96	0.93
	1700 - 2200	0.02	0.321	0.063	1
	1700 - 2700	-1.247	0.474	-2.632	0.09
	2200 - 2700	-1.268	0.494	-2.567	0.11

Table A4.3. Results of phylogenetic null model analysis on individual fruit colours (top) and presentation types (bottom). Standardised effect sizes (SES) were obtained for each colour and presentation type by comparing the observed mean phylogenetic distance (MPD) between species displaying the trait with a null value obtained by randomising the tips of the phylogeny 999 times. Negative SES values indicate phylogenetic clustering, while positive values indicate phylogenetic evenness. Significant results ($p < 0.05$) are displayed in bold.

Colour	Randomised					
	N	Observed MPD	MPD Mean	Randomised MPD SD	Standardised Effect Size	p-value
Red	16	241.5	239.73	9.28	0.19	0.54
Orange	17	243.05	239.46	8.97	0.40	0.62
Yellow	5	242.55	239.27	21.57	0.15	0.48
Green	9	232.21	240.18	13.85	-0.58	0.23
Blue	1	NA	NA	NA	NA	NA
Purple	5	210.87	239.26	20.84	-1.36	0.07
Pink	3	228.09	236.6	36.73	-0.23	0.25
Brown	12	213.91	239.16	11.43	-2.21	0.03
Black	11	259.85	238.72	13.1	1.61	1
White	4	209.53	240.1	24.33	-1.26	0.11

Presentation	Randomised					
	N	Observed MPD	MPD Mean	Randomised MPD SD	Standardised Effect Size	p-value
Cauliflorous	13	161.48	238.92	10.88	-7.12	<0.01
Ramiflorous	63	245.65	239.50	2.52	2.44	1

Appendix: Chapter 5

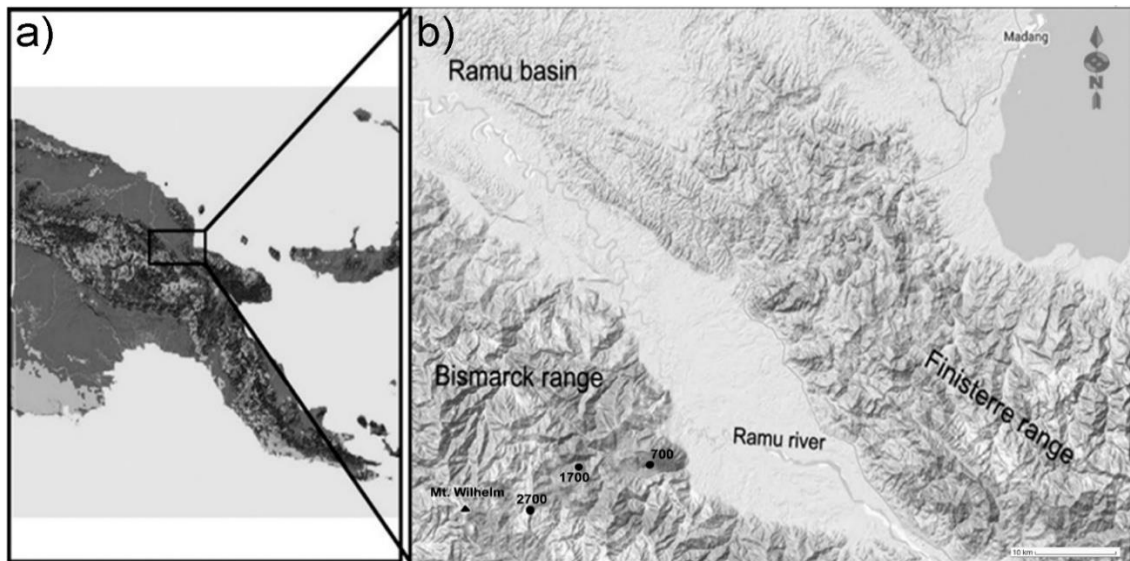


Figure A5.1. Location of the elevational gradient of Mt. Wilhelm in Papua New Guinea (a) and the study sites along the gradient (b).

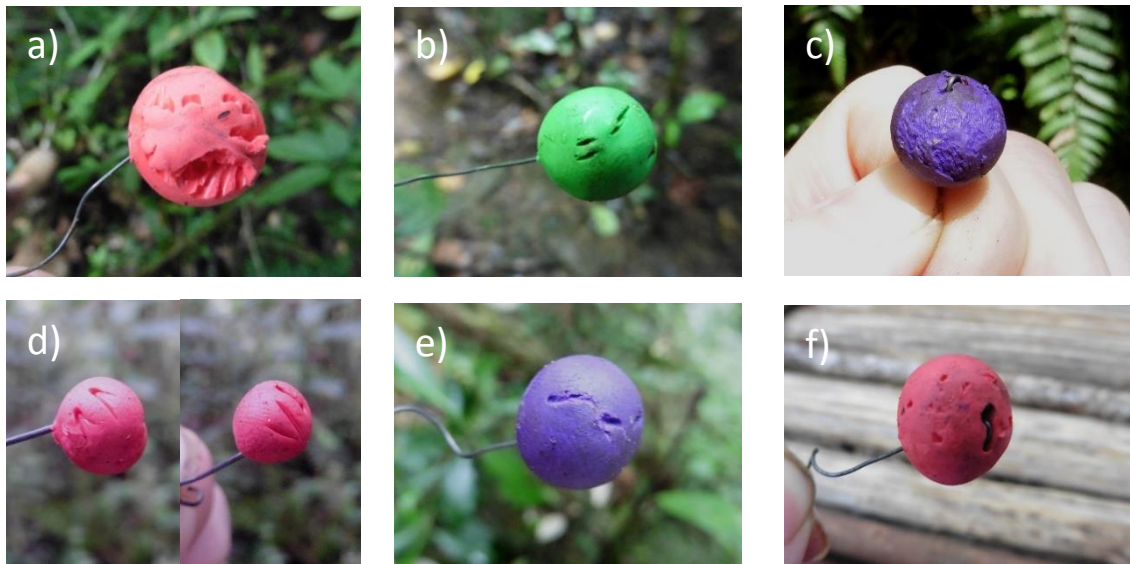


Figure A5.2. Photographs of artificial fruits showing evidence of attack by different taxa: arboreal mammals (a), bats (b), arthropods (c) and birds (d-f). Bird-attacked fruits are subdivided into: (d) “held” fruits that had been grasped on both sides (both sides shown here), (e) “intermediate attack” fruits showing imprints from a single feeding attempt whose maximum distance was less than the fruit’s diameter and (f) “pecked” fruits showing small individual holes characteristic of pecking.

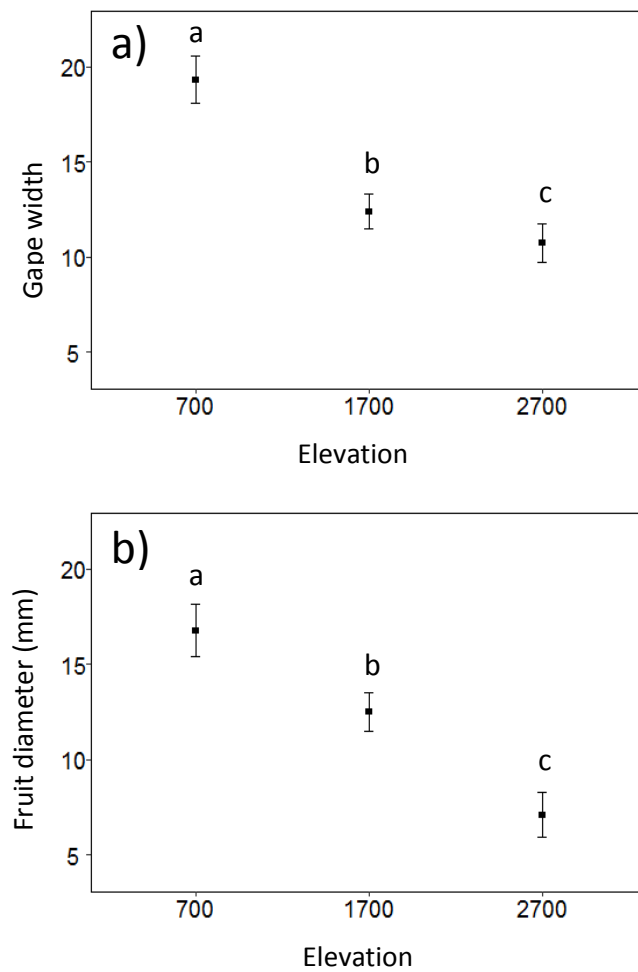


Figure A5.3. Community-weighted mean understory frugivore gape widths (a) and fruit diameter of fruiting plants (b) at each of the three elevations. Black squares denote mean values, weighted by species' relative abundances. Average values for each individual fruiting plant from which fruit was collected were used to calculate the mean across all individual plants. Error bars represent 95% confidence intervals. Letters above points denote statistically significant differences between elevations ($p < 0.05$).

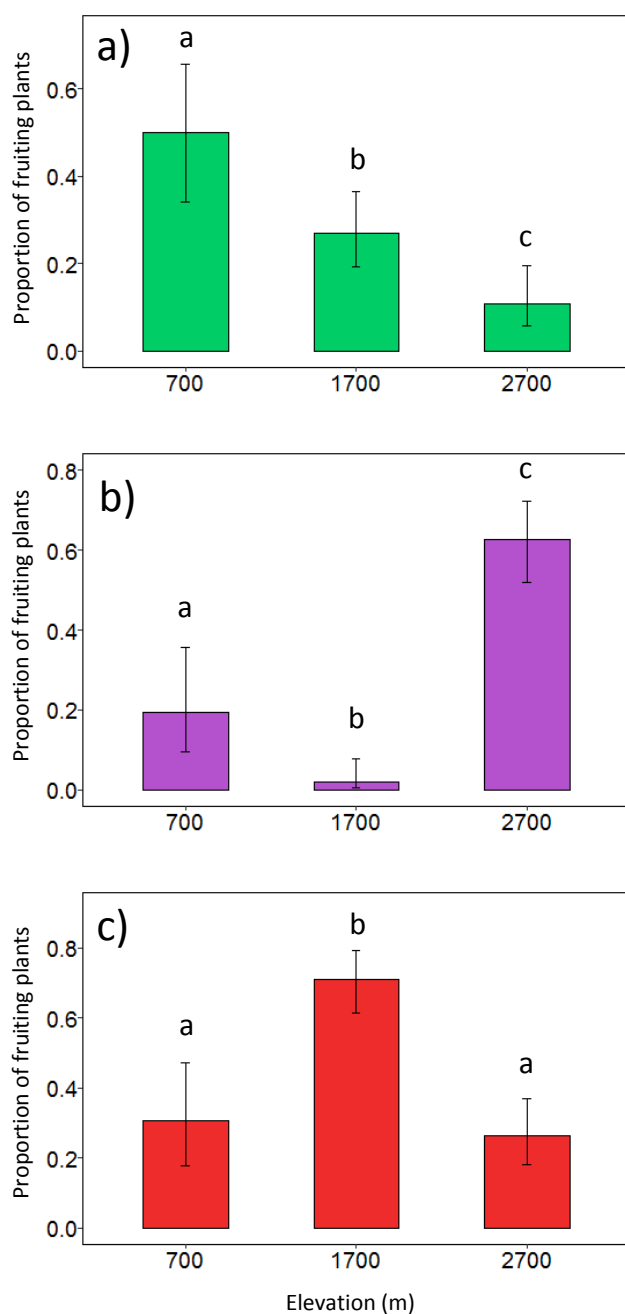


Figure A5.4. Relative abundance of real fruiting plants at each elevation for the fruit colours represented in this study, represented here as a proportion of the total number of plants bearing fruits of those three colours. Mean proportions are displayed for green (a), purple (b) and red (c) fruits. Error bars represent 95% confidence intervals. Letters above columns denote statistically significant differences between elevations ($p < 0.05$).

Table A5.1. Attack rates on artificial modelling clay fruits, divided by frugivore type and elevation. "Category" describes the fruit colour/size combination: L = large, M = medium, S = small; G = green, P = purple, R = red. Numbers in columns represent the number of artificial fruits showing evidence of a feeding attempt by members of the taxon in question, out of a total of 360 (180 * 2 exposures) for each elevation/colour/size combination. For example, at 700 m, 9 out of 360 exposed large green fruits showed evidence of attempted frugivory by birds.

	Category	Birds	Arboreal Mammals	Bats	Arthropods	All taxa
700 m	LG	9	15	3	7	34
	MG	5	2	7	9	23
	SG	5	0	1	4	10
	LP	17	0	3	3	23
	MP	10	5	7	14	36
	SP	12	2	2	10	26
	LR	18	1	3	6	28
	MR	12	2	1	8	23
	SR	16	2	0	9	27
	700 m Total	104	29	27	70	230
1700 m	LG	6	3	0	1	10
	MG	10	1	0	0	11
	SG	8	1	0	3	12
	LP	25	1	0	1	27
	MP	59	1	1	17	78
	SP	31	1	0	8	40
	LR	34	17	0	0	51
	MR	32	2	0	1	35
	SR	17	0	0	6	23
	1700 m Total	222	27	1	37	287
2700 m	LG	6	1	0	0	7
	MG	5	10	0	0	15
	SG	11	0	0	3	14
	LP	19	4	0	6	29
	MP	28	1	0	1	30
	SP	40	1	0	0	41
	LR	24	5	2	7	38
	MR	25	3	0	3	31
	SR	26	2	0	1	29
	2700 m Total	184	27	2	21	234
All Elevations Total		510	83	30	128	751

Table A5.2. Results of generalised linear model for the subset of bird attack rates in which artificial fruits were held in the beak, including fixed effects of fruit size, fruit colour and elevation and their interactions. We present deviance values for each fixed effect and each pairwise/triple interaction between effects. Estimate and standard error of multiple comparisons are displayed for fixed effects and interactions that were significant at $p \leq 0.05$. P-values for multiple comparisons are adjusted using Tukey pairwise comparisons. Significant results are displayed in bold.

Parameter	Deviance	P value	Multiple Comparisons	Estimate	SE	Adjusted p-value
Size	34.15	<0.01	L vs. M	-0.61	0.24	0.03
			L vs. S	-1.08	0.22	<0.01
			M vs. S	-0.47	0.19	0.03
Colour	91.07	<0.01	G vs. P	-1.98	0.25	<0.01
			G vs. R	-1.45	0.26	<0.01
			P vs. R	0.53	0.15	0.00
Elevation	54.04	<0.01	700 vs. 1700	-1.42	0.23	<0.01
			700 vs. 2700	-0.97	0.25	<0.01
			1700 vs. 2700	0.45	0.17	0.02
Size:Colour	9.25	0.06				
Size:Elevation	9.43	0.05	700:L vs. 700:M	-0.16	0.56	0.96
			700:L vs. 700:S	-0.93	0.49	0.14
			700:M vs. 700:S	-0.77	0.46	0.21
			1700:L vs. 1700:M	-0.82	0.27	<0.01
			1700:L vs. 1700:S	-0.72	0.27	0.02
			1700:M vs. 1700:S	0.1	0.22	0.90
			2700:L vs. 2700:M	-0.85	0.38	0.07
			2700:L vs. 2700:S	-1.6	0.35	<0.01
			2700:M vs. 2700:S	-0.75	0.26	0.01
Colour:Elevation	6.59	0.16				
Size:Colour:Elevation	14.23	0.08				

Table A5.3. Results of generalised linear models for obligate understory frugivore abundance and gape width, and for real fruit size and relative abundances of real green, purple and red fruits at the three study sites. Elevation was the single fixed effect included in each GLM, for which deviance values are displayed here. Estimate and standard error of multiple comparisons between elevations are displayed when the effect of elevation was significant at $p \leq 0.05$. P-values for multiple comparisons are adjusted using Tukey pairwise comparisons. Significant results are displayed in bold.

Parameter	Deviance	P value	Multiple Comparisons	Estimate	SE	Adjusted p-value
Frugivore Abundance	15.01	<0.01	700 vs. 1700	-0.58	0.15	<0.01
			700 vs. 2700	-0.37	0.16	0.05
			1700 vs. 2700	0.21	0.14	0.29
Frugivore Gape Width (species weighted)	98.63	0.27				
Frugivore Gape Width (abundance weighted)	3128.8	<0.01	700 vs. 1700	6.95	0.78	<0.01
			700 vs. 2700	8.6	0.81	<0.01
			1700 vs. 2700	1.66	0.7	0.05
Fruit Size (species weighted)	1741.4	<0.01	700 vs. 1700	5.35	2.55	0.09
			700 vs. 2700	9.95	2.58	<0.01
			1700 vs. 2700	4.61	2.87	0.24
Fruit Size (abundance weighted)	6530.1	<0.01	700 vs. 1700	4.29	0.88	<0.01
			700 vs. 2700	9.67	0.93	<0.01
			1700 vs. 2700	5.39	0.8	<0.01
Fruit Colour: Green	15.35	<0.01	700 vs. 1700	1.36	0.34	<0.01
			700 vs. 2700	1.32	0.34	<0.01
			1700 vs. 2700	-0.04	0.4	0.99
Fruit Colour: Purple	157.11	<0.01	700 vs. 1700	2.9	0.81	<0.01
			700 vs. 2700	-2.21	0.45	<0.01
			1700 vs. 2700	-5.11	0.74	<0.01
Fruit Colour: Red	1.32	0.52				