Elevational Diversity Profiles of *Aves* and *Lepidoptera* (*Sphingidae*) – A Comparative Analysis in the Eastern Himalayas

A thesis
Submitted in partial fulfilment of the requirements
Of the degree of
Doctor of Philosophy

by

Mansi Mungee

Indian Institute of Science Education and Research, Pune

2018

To Mummy & Baba.

I love you.

CERTIFICATE

Certified that the work incorporated in the thesis entitled **“Elevation Diversity Profiles of *Aves* and L*epidoptera* (*Sphingidae*) – A Comparative Analysis in the Eastern Himalayas”** submitted by **Mansi Mungee** was carried out by the candidate, under my supervision. The work presented here or any part of it has not been included in any other thesis submitted previously for the award of any degree or diploma from any other University or institution.

Ramana Athreya

Ramana Athreya
(Supervisor)

Date: 3rd October 2018

Declaration

I declare that this written submission represents my ideas in my own words and where others' ideas have been included, I have adequately cited and referenced the original sources. I also declare that I have adhered to all principles of academic honesty and integrity and have not misrepresented or fabricated or falsified any idea/data/fact/source in my submission. I understand that violation of the above will be cause for disciplinary action by the Institute and can also evoke penal action from the sources which have thus not been properly cited or from whom proper permission has not been taken when needed.

Mansi Mungee
Roll No. 20113118

Date: 3rd October 2018

Acknowledgements

My experience during this PhD has been nothing short of amazing. The journey was as much about character building, as about science. Not many people can boast of travelling to the remotest and breathtaking tropical forests of eastern Himalayas as part of their PhD work. There are many people I want to thank – some for knowing when to stick around, and others for knowing when to leave!

Ramana, my advisor, mentor and friend. It has been an absolute pleasure. And a privilege. You made it possible! You made it fun! You made it a journey worth cherishing for life. Every single skill I have today, is because of your encouragement (and of course a fair bit of pushing). I am grateful for so much, and some more, but most importantly for all the time, energy and effort that you invested into this project. Working with you, I learnt how to run a lab and how to write a code. You insisted I learnt programming, in-spite of the strong resistance I threw your way, a skill that I never dreamt of possibly acquiring. You taught me the importance of high quality data and you never lowered your expectations when it came to the quality of research – I am a better scientist because of you. You helped me understand and exploit my strengths, and acknowledge my limitations. During the more stressful thesis writing phase, you somehow managed to turn all my fits of raging fury into bursts of laughter – I am a better person because of you. And finally, this seems as good a platform as any to thank you for the near infinite cups of coffee that you paid for during the last few months!!

I want to thank my friends in Arunachal Pradesh – the people behind the scenes. Mr. Indi Glow and Neema for managing the camp. Raju, Vicky, Phurpha, Gore, Bayung, Shyam mama, Chotu, Abu, Gambu, Kami and many others who made living in the forests trump 5-star luxury. Raju ensured a timely supply of my smokes from the nearby city to keep my sanity in check and for that alone, he deserves a special mention. I thank the Forest Department of Arunachal Pradesh, especially Mr. Pekyom Ringu, Mr. Milo Tassar and Dr. Bharat Bhatt for their support with permits and logistics.

The credit for the entire bird data goes to Rohan Pandit. He conducted exhaustive transect surveys and generated an excellent data set that I have used in this thesis.

Priya, Shruti, Srishti, Piyush, Monica, Raunaq, Chintan & Aamod – one can never underestimate the role that friends play in keeping a graduate student spirited. Priya, Shruti and Srishti have lifted my spirits on the most gloomy days and I thank them for all the silliness, the late-night coffee, our chocolate binge-eating phase, our yearly retreats, and other countless (unspeakable) adventures. Raunaq deserves a dedicated sentence for all the laughters and goofiness. Debjyoti, Alakananda and Srikrishna – the work family. Thank you Srikrishna for the Python Script that greatly improved my data and analysis. Thank you Alaka for taking the seat next to me in the common room – it had been empty for far too long.

Good work seldom comes cheap. I thank IISER-Pune, Department of Science and Technology (DST; Government of India) and Nadathur Trust for the financial (and by extension, moral) support. Prof. Shashidhara has contributed in myriad ways to better the lab at many different levels.

Nikhil Phadke and his team (especially Shatakshi) helped extensively with molecular work that never made it to this thesis but was one of the most rewarding experiences of my PhD.

Discussions with Deepak (Barua) have greatly benefited this work, and me. Dr. Sutirth Dey's comments and feedbacks have been very useful throughout the development of this project. I thank Dr. Sanjay Sane (NCBS, Bangalore) for his feedbacks. I thank Thomas for lending an ear whenever I needed to vent out.

And finally, I thank my parents for making sure that questions such as "When will she finish?" and "When will she marry?" never reach me. I must thank my siblings and cousins, for ensuring they do!!

Gattu, Coco and Bahubali – the cats, for making sure I left the lab timely to come home and feed them.

Table of Contents

List of Figures

Chapter 2.

Chapter 3.

Chapter 4.

Chapter 5.

Chapter 6.

Chapter 7.

List of Tables

Chapter 2.

Chapter 4.

Chapter 5.

Chapter 7.

List of Abbreviations

SAD	Species Abundance Distribution
WWF	World Wildlife Fund
EWS	Eaglenest Wildlife Sanctuary
CMDS	Classical Multi Dimensional Scaling
AIC	Akaike Information Criterion
UV	Ultra-violet
AC	Alternating current
DC	Direct current
nm	nanometer
cm	centimeter
W	Watt
V	Voltage
m	meter
ml	millilitre
EXIF	Exchangeable Image file Format
OTU	Operational Taxonomic Unit
MOT	Moths of Thailand
MOB	Moths of Borneo
STI	Sphingidae Taxonomic Inventory
SOTEP	Sphingidae of the Eastern Palearctic
HBW	Handbook of the birds of the world
BR	Bergmann’s Rule
BR-CWM	Bergmann’s Rule – Community Weighted Mean
BR-CIM	Bergmann’s Rule – Community Individual Mean
BR-S	Bergmann’s Rule – Species
BR-P	Bergmann’s Rule – Populations
NMDS	Non-metric Multi Dimensional Scaling
kg ha $^{-1}$ m $^{-1}$	Kilogram per hectare per metre
MDE	Mid-Domain Effect
MTE	Metabolic Theory of Energy
ECM	Elevational Climate Model

Synopsis

Elevational Diversity Profiles of *Aves* and Lepidoptera (*Sphingidae*) – A Comparative Study in the Eastern Himalayas

In this dissertation we present a comparative study of the diversity patterns of two disparate organismal groups – Lepidoptera: *Sphingidae* (hawkmoths) and *Aves* (birds) – along an elevational gradient spanning 200-2800 m in the eastern Himalayas of Arunachal Pradesh, India. The concurrent sampling of the two taxa along the same elevational transect should reduce the number of confounding factors due to the identical parameters associated with climate, vegetation and biogeography. We have investigated two important facets of diversity, viz. species and (functional) traits using multiple measures available for each (e.g. alpha diversity, beta diversity, evenness, etc.). It is hoped that this study would contribute to the growing field of identifying the taxon-specific and taxon-independent factors impacting diversity. To the best of our knowledge this is the first such simultaneous elevational diversity pattern study of two animal taxa in the eastern Himalayas of India.

We recorded 4731 hawkmoth individuals from 13 elevations between 200-2800 m, spanning 80 morpho-species and 30 genera. We reliably measured body and wing sizes for 3297 individuals using field images, after correcting for image distortions, one of the largest and systematic compilation of insect trait data from a single locality, and achieved without having to collect specimens (and the consequent allocation of large amount of resources for their preparation and maintenance). For birds, line transects at 48 elevations yielded 15,867 individual records spanning 235 species, 150 genera and 48 families. We obtained species mean body mass and wing span data from literature. We also carried out a similar sampling of birds during winter but is not presented in this thesis.

1. Species abundance distributions (SAD): We have shown that evenness of species abundances within a community decreases with elevation for both hawkmoth and birds. The decline in evenness was consistent across multiple measures including parameters from models (e.g. standard deviation of a Log-normal fit), as well as model-independent metrics such as the width of the octave binned species abundance distributions, slope of rank-abundance curves and Pielou's evenness index. High evenness has been previously observed in stable, more productive ecosystems with high species richness and more resource/niche partitioning (like at low elevations and latitudes), whereas low evenness is linked to unstable, variable and less productive environments where few species dominate (like at high elevations and latitudes). We also found that the Log-series and Neutral models fit the individual elevational communities of hawkmoths the best, while bird communities are more mixed with Log-normal dominating the fits. However, for the regional pool as a whole the Log-normal was by far the best fit for both taxa.

2. Alpha and beta diversity profiles: Birds and hawkmoths, both exhibited a mid-elevation peak in alpha diversity, although, the peak was lower and broader in hawkmoths than in birds. However, interestingly, when each species was represented only by the mean elevation of its distribution, the bird profile turned out to be essentially independent of elevation, while hawkmoths continued to show a mid-elevation peak. Analysis of beta diversity revealed a similar reduction of dissimilarity with elevation for both birds and hawkmoths, with species turn-over dominating nestedness. Despite this similarity, there is some indication from NMDS analyses that elevational communities in moths are clustered into 5 groups while those in birds showed a smoother transition in community composition across the gradient.

3. Bergmann's Rule: Previous investigations, in the hundreds, present a very confusing picture of the validity of Bergmann's rule, raising issues of its nature (pattern or process), of its applicability (ectotherms or endotherms or both), and the scale of investigation (intraspecific, interspecific and assemblage). In this study both hawkmoths and birds showed a strong but contrasting trend at the assemblage level, with the mean body mass increasing for hawkmoths (an ectotherm!) and decreasing for birds (endotherm!). We also found that the same data shows a considerably reduced signal when plotted as species mean values (as has been done by most previous studies) and a very weak signal at the intraspecific level. One way of reconciling the contradiction is to ascribe the effect to species turnover. The converse-Bergmann pattern in birds has previously been attributed to reduced food availability during winters at high elevations. As facultative endotherms, thermal explanations for Bergmann's rule that are normally applied to endothermic vertebrates could potentially operate in hawkmoths, especially as they are most active during the hours of the (cold) night. Our work shows that the result changes with the taxonomic level of investigation. Given the strong contrast in patterns for hawkmoths and birds at the same location, and the fact that the relationship is contrary to the original expectations for ectotherms and endotherms, we support the notion that Bergmann's Rule should be treated as a pattern and the underlying process has to be investigated separately depending on the taxon and the context.

4. Wing allometry and Flight: We found that the allometry of wing area is remarkably similar across more than 4 orders of magnitude of body mass spanning hawkmoths and birds. This suggests that very similar, biophysical, factors are operating across these two taxa in deciding flight dynamics. Notwithstanding which, somewhat curiously, the allometric indices for all genera (but one) of hawkmoths lie below the assemblage average. This suggests that while basic biophysical principles of flight dominates across the range of body mass, the small-scale allometry is decided by factors like inter- and intra-specific competition, local climatic variables (air density, perhaps wind) and perhaps historical contingency. We also found that the assemblage-mean wing loading decreased with elevation for both hawkmoths and birds suggesting better flight capacities at higher elevations. In common with the result from Bergmann's Rule we found that the strength of this correlation with elevation changes with the taxonomic level at which it is investigated: strongest at the assemblage level and weak or undetected at the interspecific and intraspecific levels.

5. Functional trait space in hawkmoths: Given the large data set of (functional) trait values for 3297 individual hawkmoths we investigated several issues related to functional diversity, occupancy in trait space and their implication for community assembly. We observed a decrease in trait overlap across communities with increasing elevational distance using the primary traits of body length, thorax width, wing length and wing breadth, as well as derived traits of body volume, wing area and aspect ratio. We also showed that hawkmoth subfamilies, and even the most abundant genera neatly segregate with almost no overlap in trait space involving just the 4 primary traits listed above. We also showed the presence of strong internal filters at all elevations using T-statistics, with individuals within species significantly more similar than individuals across species in each elevational community.

To sum up, using a large set of systematically collected diversity data on hawkmoths and birds along 2600 m of an elevational gradient we have been able to show several patterns with a high degree of statistical significance. We recognise that these are patterns and we need to progress towards processes. Yet, we believe that generating secure patterns is the first step towards understanding the underlying processes. Previous studies have highlighted the large “diversity” of patterns across different taxa and in different locations across the globe; and the quest for identifying the key processes has often floundered on the diversity of contexts of the different studies. We determined the patterns for two very different organismal groups, hawkmoths and birds, at the same place and during the same period. Our study fills an important geographical void in the multi-taxon investigations along elevational gradients. The comparison along multiple facets of diversity – alpha, beta, functional – is expected to complement the available meta-analyses of disparate data sets.

We are in the process of adding more taxa and genetic diversity to this mix at our study site. We hope that it will be a small step towards a better understanding of the process by which communities are assembled.

Chapter One

Introduction

> ***“There are more species of intertidal invertebrates on the coast of Washington than on the coast of New England, more species of birds breeding, and also more wintering, in forests than in fields [......] there is an even more dramatic difference in the number of species in the tropics than in the temperate [….] Will the explanation of these facts degenerate into tedious set of case histories, or is there some common pattern running through them all?”***
>
> ——— Robert H. MacArthur,
> Geographical Ecology: Patterns in the Distribution of Species (1972)

Since the beginning of 19th century, naturalists have been documenting that different regions on Earth differ markedly in the number of species that inhabit them. They also observed and recorded that the species shared between these regions differ dramatically in their abundances. Understanding this non-randomness in species segregation and aggregation still continues to be one of the central goals in ecology (McCain 2009, Kraft et al. 2011; Liu et al. 2017) and documenting biodiversity patterns across spatial and temporal gradients has become the cornerstone to understanding this heterogeneity. Environmental variables (e.g temperature; Allen 2002, precipitation; McCain 2009, edaphic factors; Tuomisto et al. 1994), landscape structure (e.g. connectivity; Liu et al. 2017), area (MacArthur and Wilson 1957), geometry (Colwell 1994), interspecific interactions; e.g. competition (Hutchinson 1959), mutualism and predation (Boucher 1982) and dispersal related stochasticity (Hubbell 2005) have been found to be some of the most important factors influencing species distribution. Some of the widely recognized spatial diversity patterns include latitudinal gradients (Stevens 1989; Gaston 2000, 2007; Lamanna 2014), elevational gradients (Able & Noon 1976; Rahbeck 1995; Brehm et al. 2003; Kromer et al.

2005; Wu et al. 2014; Beck et al. 2017), species-area relationships (Connor & McCoy 1979; Angermeier & Schlosser 1989; Lomolino 2000; Peay et al. 2007; Fattorini et al. 2016; Storch 2016), successional gradients (Pielou 1966; Bazzaz 1975; Clay & Holah 1999; Derroire et al. 2016; Huang et al. 2017), environmental gradients (e.g. pollution, soil types) (Borowitzka 1972; Rygg 1985; Rosenberg et al. 2004; He et al. 2017; Wehn et al. 2017) and many more.

Tropical ecosystems shelter a much greater proportion of extant species than other terrestrial ecosystems (Barlow 1989; Myers 1992; Kraft et al. 2011). von Humboldt, Darwin, Wallace and Dobzhansky amongst others, were the first to systematically document the changes in species distribution across latitudes (Lomolino 2001; McCain & Grytnes 2010) and demonstrate the high diversity of the tropics. The ecological basis for this striking, widely studied correlation of considerable antiquity is still a matter of debate.

The obvious correspondence between latitudinal and altitudinal gradients led to the latter being investigated by naturalists and biogeographers from an early date but quantitative analyses of elevational profiles of species diversity came only much later (Grinell & Storer 1924; Able & Noon 1976; Terborgh 1977). Since then, studies of biodiversity along mountain slopes have gained much popularity (Rahbeck 1995; Brehm et al. 2003; Kromer et al. 2005; McCain 2009; Wu et al. 2014; Beck et al. 2017) as these gradients have the potential for separating the contribution of different factors influencing diversity:

1. Compression of climatic zones over a short distance makes the study of biodiversity across these gradients manageable (McCain & Grytnes 2010)
2. Historical contingency, and geological and evolutionary histories are more uniform across a montane diversity gradient than across latitudinal gradients.
3. High topographic diversity (slope, aspect, etc) in association with different regimes of substrates, nutrients and water leads to a multitude of micro-climatic situations which, create a great variety of micro-habitats supporting a much higher diversity than an equivalent area of a uniform elevation landmass (Brehm & Fiedler 2004)
4. Multiple mountains across the globe provide replicate systems with varying climatic, spatial, historical and biotic settings, and the differences in the response of

ecological communities to these factors forms the basis for assessing the relative importance of different causative mechanisms

The first step in understanding and unravelling the factors responsible for any pattern, is in fact documenting the pattern itself repeatedly and accurately! There has been a proliferation of studies of diversity along elevational gradients in the recent past but they are still mostly limited to the more conspicuous taxa such as plants, birds and mammals (Rahbeck 1995; Able & Noon 1976; G. Vazquez 1998; Sanchez-Cordero 2001; Heaney 2001; Sanders 2002; Vetaas & Grytnes 2002; Li et al. 2003; Bachman et al. 2004; Brehm & Fielder 2004; Kattan et al. 2004; Grytnes 2006; McCain 2007a, 2007b, 2009; Jankowski et al. 2009; Dehling et al. 2014). The few studies that exist on invertebrates and other taxa (Haber et al. 1989; Fiedler & Schulze 2004; Fu et al. 2007; Brehm et al. 2016; Beck et al. 2017), are still much fewer in number to draw secure generalizations from. While almost all latitudinal gradients of diversity follow a pattern of monotonic decrease (Willig & Presley 2018), elevational gradients, in addition, also show a pattern of unimodal decline in many cases (McCain & Grytnes 2010; Beck et al. 2017). There is as yet no consensus on the identity of the mechanisms generating these patterns, and there still remains large gaps in knowledge of the reasons behind the variability observed across different taxa and in different mountain systems.

The explanations proposed can be broadly grouped into four categories of climate, geometry, evolutionary history and (other) biotic processes (McCain & Grytnes 2010). Temperature, precipitation, productivity, elevational area, geometric constraints, and phylogenetic histories and biotic interactions are among the more common correlates investigated for developing theoretical frameworks and model mechanisms to understand diversity patterns (McCain 2009; Sanders & Rahbeck 2012). Direct tests for many of the hypothesized mechanisms are still lacking (correlation does not imply causation), and a comprehensive analysis requires extensive data on all the aforementioned variables at each study site. Additionally, these factors may well affect different organismal groups differently (for example, amphibians and ferns might be more responsive to gradients in humidity than other taxa).

There have been several investigations of multi-taxon patterns to identify taxon-specific and taxon-independent drivers of diversity (e.g. Grau et al. 2007, Bryant et al. 2008, Colwell & Rangel 2010, Mori et al. 2013, Turtureanu et al. 2013, Colwell et al. 2016, Duan et al. 2016, etc). A comparison of birds and mammals (bats and mice) along a Peruvian elevational gradient revealed a monotonic decline for birds and bats, whereas mice did not show any relationship with elevation (Patterson et al. 1998). Plants and soil bacteria showed contrasting patterns of mid-elevation peak and a monotonic decline respectively along a 1000 m elevational gradient in the Colorado Rocky Mountains (Bryant et al. 2008). On the other hand, the patterns were similar for geometrid moths, ants, epiphytes and Rubiaceae plants on the Barva Transect, Costa Rica with a unimodal profile, although the diversity peak changed with taxon (Colwell & Rangel 2010).

Moving away from alpha diversity patterns, cross-taxon congruence for species turnover patterns, or beta diversity, along an elevational gradient was investigated by Duan et al. (2016) in northern China using vascular plants, geometrid and arctiinid moths and carabid beetles, where they observed strong similarity for plants and beetles. Contrasting patterns for beta-diversity were obtained for plants and oribatids in Hokkaido, Japan (Mori et al. 2013). These results indicate that there is yet no universal rule shaping diversity distribution across multiple taxa, even when sampled along the same elevational transect, indicating the necessity to incorporate taxon-specific prescriptions for a unifying general theory of elevational diversity patterns.

The study of natural variation is continually evolving. There have been many shifts in paradigms with the recognition of biodiversity’s multi-faceted nature. A more recent conceptual development has been in the understanding of variation in species’ traits, which is now known to occur at all spatial, temporal and taxonomic or organizational scales (Messier et al. 2010). This growing field of trait-based ecology emerges from a simple underlying assumption that individuals interact with, and respond to, their biotic and abiotic environment via their (functional) traits (McGill et al. 2006). Quantifying traits can thus be considered a close approximation to quantifying a species’ niche, which has been the cornerstone for several community assembly theories.

Much of the progress in functional ecology is limited to plant communities, where not only the traits, but also their correlation to the individuals' fitness are easily quantifiable. For majority of invertebrate and other higher taxa, it is still not always clear which traits qualify as "*functional*" and how many functional traits should be measured to adequately describe community assembly patterns.

We contribute to this growing field by conducting a comparative study of diversity patterns of two contrasting organismal groups – Lepidoptera: *Sphingidae* (hawkmoths) and *Aves* (birds) – along a 2600 m altitudinal gradient in the eastern Himalayas of Arunachal Pradesh, northeast India. We are aware of no previous work from the study region that addresses diversity patterns of these two different faunal taxa in a multi-faceted approach. We hope that this comparative study will contribute to a deeper understanding of the community assembly rules, filling a major geographical void in a high diversity region.

We have investigated multiple facets of diversity – viz. species, traits and phylogeny – using the multiple measures available for each (e.g. alpha-diversity, beta-diversity, relative abundance distributions, etc) using the large primary data set that we obtained from field sampling of both birds and hawkmoths.

We have focused on the similarities and differences in patterns between hawkmoths and birds and attempted to link them to our knowledge of their life histories. An investigation of the causative mechanisms underlying the observed elevational diversity patterns is the next step planned in this programme.

Chapter Two in the current dissertation describes the study area and sampling sites in detail. It then discusses the choice of taxa, sampling methodology and a description of the data used for all subsequent analysis. It includes the measurements of morpho-traits (body and wing) for hawkmoths from size-referenced digital images.

Chapter Three deals with an under-appreciated aspect of ecological communities – evenness and species abundance distributions. Patterns in evenness were investigated in multiple ways, with and without the use of models.

Chapter Four focuses on patterns of alpha and beta diversity. In common with previous studies we investigated the relationship between diversity and some commonly hypothesized correlates like temperature, precipitation, area and Mid Domain Effect.

Chapter Five shifts the focus from taxonomic aspect of diversity to the recently emerging field of trait-based ecology. We investigate validity of the Bergmann's rule for endothermic birds and ectothermic hawkmoths.

Chapter Six continues the exploration into directional variation of traits, using wing area, wing shapes (aspect ratio) and wing loading.

Chapter Seven focuses on the intraspecific variation in body and wing measurements of hawkmoths using the recently proposed suite of T-statistic metrics (Violle et al. 2012) to analyze the relative strength of internal and external filters in shaping hawkmoth communities along the altitudinal gradient.

Each chapter between 3 and 7 deals with a specific result and includes a self-contained introduction, analysis, result and discussion on that topic. Finally, we summarise the entire work and conclude with future prospects arising from this work.

Chapter Two

Study Area, Study Taxa and The Data

2.1 Study area and sampling sites

Studies of geographic patterns in species diversity have helped to identify regions which are very rich in either overall diversity or have a high number of endemic/range restricted species (Myers 1992, Orme et al. 2005). These “biodiversity hot-spots” have served to focus conservation and/or research efforts. Two such hot-spots are located in India: The Western Ghats, which is rich in endemic species, and north-east India comprising the eastern Himalayas, which rates very high in species diversity as well as in the density of endemic/range-restricted species (Myers 1992; Orme et al. 2005). The Western Ghats have received much greater attention from ecologists over the last three decades (Ramesh & Pascal 1991; Nair 1991; Daniels 1992; Chandrashekara & Ramakrishnan 1994; Manoharan et al. 1997; Ghate, Joshi & Gadgil 1998; Menon & Bawa 1998; Prasad et al. 1998; Ayyappan 1999; Parthasarthy 1999, 2001; Jha et al. 2000; Gadagkar 2000; Aravind et al. 2001; Shanker 2001; Raman & Sukumar 2002; Devy & Davidar 2003; Ganesan & Davidar 2003; Dahanukar et al. 2004; Rai 2004; Vasudevan et al. 2006; Ganesh & Devy 2006; Krishnawamy et al. 2006; Priyadarsanan Dharma Rajan 2008; Tissot et al. 2010; Ravikanth G. et al. 2010; Badiger 2011; Krishnamurthy 2011; Ishtiyaq et al. 2012; Joshi & Karanth 2012; Vinayaka et al. 2013; Osuri, Kumar & Sankaran 2014; Robin et al. 2014; Marathe & Priyadarsanan 2016; Kunte 2016; Vanak et al. 2017; Zambre & Thaker 2017). North-east India, on the contrary, has remained largely under studied.

2.1.1 Eastern Himalayas

The eastern Himalayas in northeast India span a complex and rugged landscape with extreme topographic relief (Zomer et al. 2000) and cover a total area of 524,190 km^2 between 82.70°E and 100.31°E longitude and 21.95°N and 29.45°N latitude. They run through eastern Nepal, Sikkim (India), Bhutan, Arunachal Pradesh (India), northwest Yunnan (China), southeast Tibet and northern Myanmar. The eastern Himalayas are bounded by the Brahmaputra river valley to the south. The two, together with the mountain systems south of the river, constitute the north-east Indian biodiversity hotspot.

This region lies at the interface of the Indo-Malayan and Palaearctic biogeographic realms (Wallace, 1876). The recent revision in biogeography, based on phylogenetic relationships of 21,037 species of amphibians, birds and mammals, puts the region at the confluence of the Oriental (continental India and the Indo-Australian tropics) and the Sino-Japanese biogeographic regions (Holt et al. 2013). A WWF-India report in 2009 states that the eastern Himalayas are one of the least explored global hotspots with 211 new species discoveries

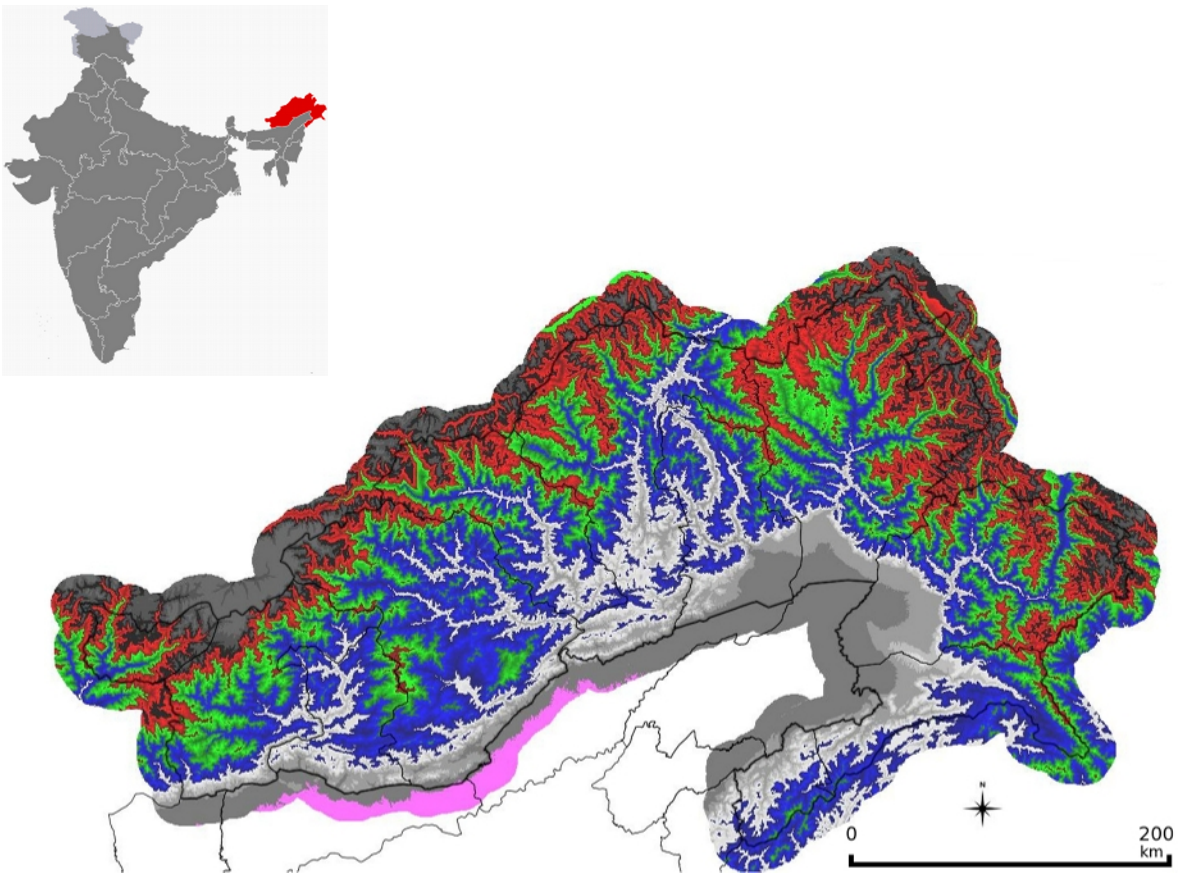


Figure 2.1 *Elevation map of the state of Arunachal Pradesh. Note the stratified landscape with elevations ranging from sea-level to 7000 m in a short stretch of ~1°. Dark grey: above 4000 m; Red: 3000 - 4000 m; Green: 2000 - 3000 m; Blue: 1000 - 2000 m; Remaining – less than 1000 m.*

between 2009 and 2014. The region is currently facing a wide range of threats including climate change, population growth, deforestation, overgrazing, poaching and hydro power development. Large-scale biodiversity investigations and conservation efforts are urgently needed to avoid the impending deforestation-driven biodiversity losses.

2.1.2 Arunachal Pradesh

The high diversity of the eastern Himalayas is also reflected within the Indian sector which contains about 5800 plant species with 36% endemicity (Myers 1988). Arunachal Pradesh, the largest state in north-east India, ranks 6th on Myers et al. (2000) list of "*hottest of hotspots*". 12% of its total area of 83,743 km^2 (*26.28°N-29.30°N* latitude and *91.20°E-97.30°E* longitude) lies within 13 Protected Areas. 70% of its area is mountainous and 82% is under forest cover (Paul 2005).

The area has a steep elevational gradient ranging from 100 m on the southern border with

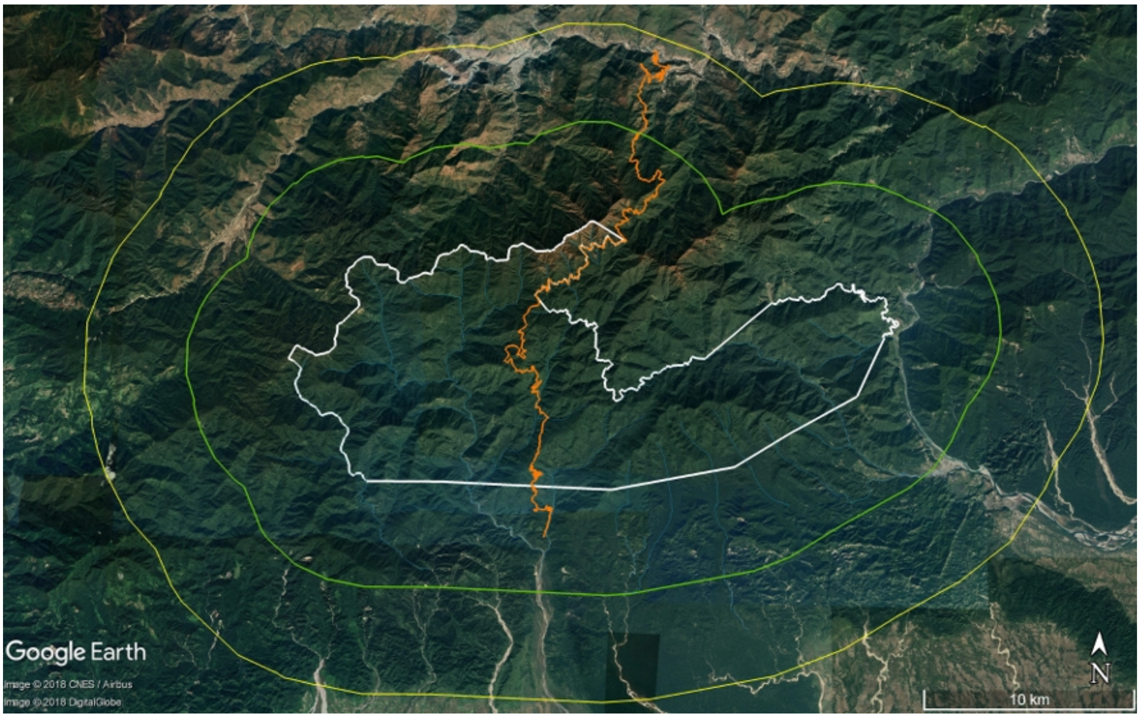


Figure 2.2 *A GoogleEarth image of Eaglenest Wildlife Sanctuary (white border). The 5- and 10-km buffer zones are marked in green around the sanctuary. The orange line is the dirt track that traverses through the sanctuary allowing easy access to some of the highest elevations*

Assam to about 7000 m along the northern border. The rainfall varies from about 3500 mm along the southern slopes to less than 1000 mm on the Tibetan border (Choudhary 2003). The mountain range is riven by several deep river gorges adding complexity to the landscape (Figure 2.1). These factors and its location at the boundary of two bio-geographic regions have served to make it a globally important biodiversity hotspot.

The paucity of biodiversity studies in Arunachal Pradesh is evidenced by the continuing discovery of species either completely new to science, or hitherto unknown from India, and that too in taxa as conspicuous as birds and mammals. Some recent discoveries from the state include *Muntiacus putaoensis* (Dutta et al. 2003), *Lophophorus sclateri arunachalensis* (Kumar & Singh 2004), *Macaca munzala* (Sinha et al. 2005), *Liocichla bugunorum* (Athreya 2006b) and *Leptobrachium bompuensis* (Sondhi & Ohler 2011), etc. Price (2012) comments that Arunachal Pradesh, on the scale of around 1000 km^2, may contain the second-highest biodiversity in the world, after the northern Andes.

The last two decades have seen some researchers attempting to inventory a wide variety of taxa such as plants, birds, mammals, reptiles, amphibians and invertebrates (Kanjilal et al. 1982; Datta 1998; Pawar & Birand 2001; Choudhury 2003; Birand & Pawar 2004; Nath & Arunachalam et al. 2005; Athreya 2006a; Mishra et al. 2006; Datta & Rawat 2008; Agarwal et al. 2010; Mukherjee et al. 2010; Srinivasan et al. 2010; Velho & Laurance 2013;Sondhi & Ohler 2011; Sondhi & Kunte 2014; Sondhi & Kunte 2016; Dahal et al. 2017). Much of this work has been descriptive or compilation of inventories apart from a few quantitative studies (Acharya et al. 2011; Price et al. 2014; Agarwal & Karant, 2015).

2.1.3 Eaglenest Wildlife Sanctuary

The current study was conducted in Eaglenest Wildlife Sanctuary (hereafter EWS; Figure 2.2) in the eastern Himalayas of West Kameng district in extreme western Arunachal Pradesh. It is a small Protected Area (PA) of 218 km^2 located between 27º 02´– 09´N and 92º 18 – 35´E. EWS hosts pristine forests across 100-3250 m of elevation. Uniquely, it provides vehicular access to such forest across most of this elevational range (Athreya 2006a).

The Eaglenest road, built by the Indian Army in the late 1950s, was soon abandoned with the construction of the wider highway connecting Bhalukpong and Bomdila, and remains a single-lane dirt track for the most part. The primary forest occurs in close proximity to the roadside scrubs and all transect counts for birds and light screen sampling for moths in the current study were conducted along this road (Figure 2.2)

Climatic conditions, within EWS, vary considerably across this wide elevational gradient. Elevations below 500 m can get very warm during the months of May-June (>25°C). Regions from 500-1900 m have average temperatures in the range 10°-18° C. February is the coldest month of the year. Occasional snowfall occurs during January and February above 2000 m. The primary rainy season lasts from June to October, although rainfall may occur at any time of the year. Annual rainfall varies from <1,500 mm on the northern slopes to >3,000 mm on the southern slopes. While not quantified it has been observed that fog condensation contributes substantially to the precipitation especially in the cloud forest zone between 1500 m and 2500 m. December is mostly dry and cloud-free.

The large altitudinal range coupled with extensive rainfall has resulted in diverse habitat types ranging from tropical wet evergreen (below 900 m) to coniferous temperate forests (>2800 m). Tropical semi evergreen (dominated by *Amoora wallichii, Pterospermum acerifolium, Stereospermum chelonoides, Altingia excelsa)* and tropical evergreen forests (*Kayea assamica, Mesua ferrea, Dysoxylum procerum, Echnocarpus sp.*) occur below 600 m. From 600 to 900 m is tropical wet evergreen forests with preponderance of species like *Phoeba paniculata, Actinodaphne obovata, Alnus nepalansis, Phoebe attenuata.* 900 to 1900 m is sub tropical broad leaved forests with abundance of *Bombax ceiba,* Lagerstroemia parviflora, Terminalia bellirica, Sterculia villosa. Wet temperate *(Quercus lamellosa, Quercus sp. Castanopsis indica, Acer hookeri)* and mixed coniferous forests *(Abies sp. Tsuga dumosa)* are found at elevations between 1800-2750 m and 2300-3350 m respectively (Champion & Seth 1968; Choudhury 2003).

While there was little information on the biodiversity of Eaglenest before 2003 (Choudhury 2003) there has been a concerted effort at documenting flora and fauna of the region following the advent of the Eaglenest Biodiversity Project (Athreya 2006a) by Athreya and collaborators (Athreya 2006b; Mistry et al 2007; Agarwal et al. 2010; Sondhi & Ohler 2011) and others (Srinivasan et al. 2010; Velho & Krishnadas 2011; Sondhi & Kunte 2014; Price et al 2014; Sondhi & Kunte 2016;)**.** Currently, the inventory stands at about 425 bird species, over 1500 (and counting) Lepidoptera, about 75 herpetofauna and more than 40 mammals. Despite being the most intensely studied area in Arunachal Pradesh the efforts in Eaglenest over the last decade have merely begun to scratch the tip of the diversity iceberg. The vast majority of arthropods which usually dominate rain-forest diversity and dynamics as detrivores, herbivores, predators and parasitoids (Erwin 1982; Basset 2003; Basset et al. 2012) have yet to be documented at any taxonomic level.

2.2 Study taxa – Birds and Sphingid Moths

Moths, which are known to be phototropic, were chosen as one of the two study taxa due to the relative ease of their sampling at ultraviolet light screens. As one of the principal herbivores of an ecosystem (De Vos et al. 2006), and with species-specific food plant, the changes in their population may be expected to reflect those in the plant community. This would make them excellent faunal targets for population monitoring programs under climate change studies. As important pollinators and agricultural pests, they have served as model organisms from the viewpoint of economics as well (Haber & Frankie 1989; Moulds 1981, 1984; Kitching & Cadiou 2000 and references therein).

Hawkmoths are easy to distinguish from species of other moth families even on a screen thereby reducing sampling effort in the field. The ability to identify the family at a glance meant that none of the other thousand moths on the screen had to be examined or processed, and we had an immediate count of the sampling success for each day. *Sphingids* have been the targets of considerable taxonomic studies and we have a better knowledge of their geographical distributions, compared to other families, largely through the on-going efforts of Ian Kitching and his team of collaborators (Kitching 2017).

Ironically, the lower species richness of hawkmoths compared to most other macrolepidopteran families – 1500 extant hawkmoth species, *contra* ~23,000 *Geometridae* (Scoble and Hausmann 2007) or ~35,000 *Noctuidae* (Quimbayo et al. 2010) – is an advantage in diversity studies. The rate limiting step in studies of tropical insect diversity is specimen identification (Brehm et al. 2003; Brehm et al. 2016), which may not even be possible at the level of species without DNA-based identifications for many groups and may lead to erroneous measures of diversity (Brehm et al. 2016).

Next to plants, birds have been the most popular target taxa for elevational diversity studies (Terborgh 1977; Kattan 2004; Navarro 1992; Peris 1997; Raman 2005; Sekersioglu 2008; McCain 2009; Wu et. Al 2014 – to list just a few of the hundreds of publications). This, together with the detailed inventory of birds in Eaglenest, made birds a practical choice for comparison with moths.

Our study is part of a much larger biodiversity project in EWS to investigate patterns in distribution of many other taxa (ongoing projects on other moth families, frogs and ants).

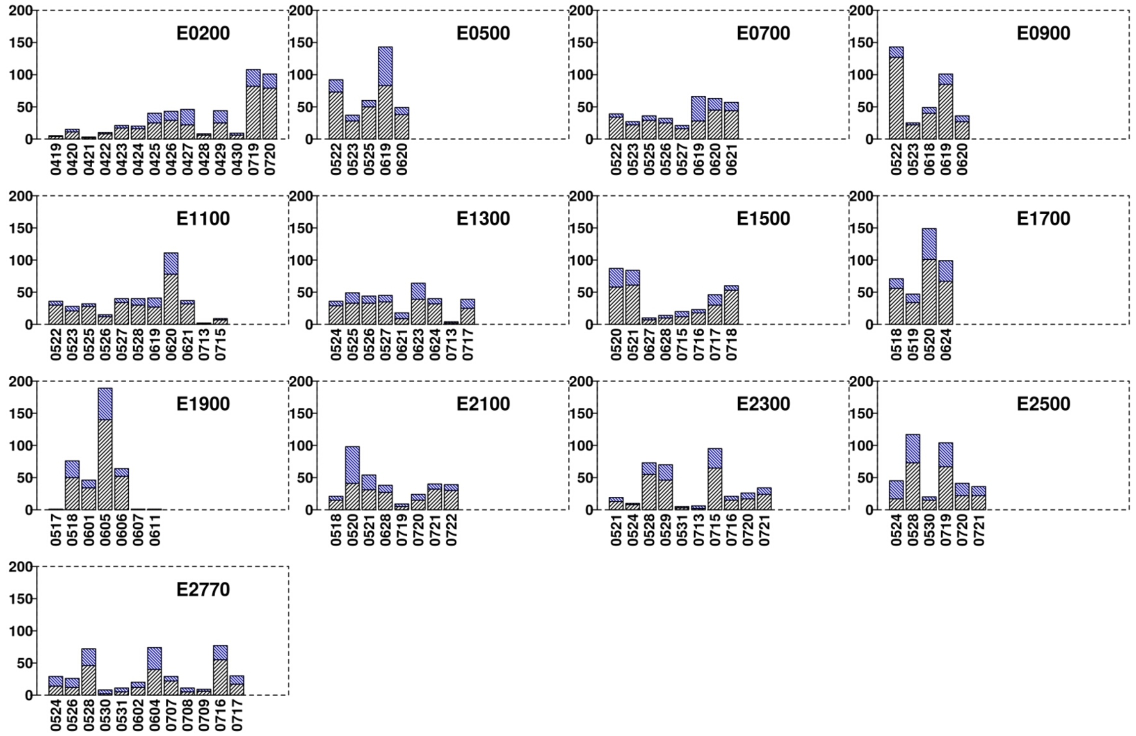


Figure 2.3 Daily fluctutations in hawkmoth abundance (and diversity; not shown) at our moth screens at different elevations.

2.3 Field Sampling – Hawkmoths

2.3.1 Methodology – Hawkmoths

Nocturnal phototropic *Sphingidae* were sampled at light screens at 13 elevations between 200 m and 2800 m. Holloway (2001), Brehm et al. (2003) and Schulze & Fiedler (2002) have discussed the advantages and disadvantages of light-trapping and factors that might influence the results of this technique. The most commonly cited issue is the possible, but unknown, systematic bias in the response of different moth species to a light trap. There is also disagreement on the radius within which moths flock to a light source. Some studies have reported ranges of 25-40 m but it can vary with weather, moon cycle and vegetation (e.g. See Figure 2.3; Brehm et al. 2003, Beck 2005). Another disadvantage is the large fluctuations in abundance (even up to 2 orders of magnitude) which makes population

Figure 2.4 *Portable moth-screen, consisting of a light-weight hollow aluminium pipes connected via screws and bolts into a frame. 2-UV (8W each) and 1 white light (8W) actinic tubes were used to attract moths. Moths typically settled on the gridded cloth screen (160 cm X 110 cm).*

estimation difficult.

Although the physiological and behavioral factors are not well understood, light traps are known to yield the least biased and the highest diversity of species compared to other methods such as bait and pheromone traps (Brehm et al. 2003, Bowden 1982). Moth traps were not used to avoid non-specific collections of non-sphingid moths.

A portable “moth-screen” (Figure 2.4) was designed and used throughout the study to maintain uniformity of sampling. The frame was made of light-weight aluminum pipes which could be conveniently dismantled during transport. Two UV actinic tubes (300-400 nm; to attract moths) and one white light bulb (for human eyes) were hung from the top of the frame. The lamps (8 W each) were powered by a car battery through inexpensive, off-the-shelf 12 V DC to 220 V AC converters. UV transparent acrylic covers were used to protect the light bulbs from rain. The screen, below the lamps, consisted of a stretched 160 cm X 110 cm fabric (shirt piece) with a printed uniform grid on a white background. The grid provided a size and shape standard for the moths photographed on the screen.

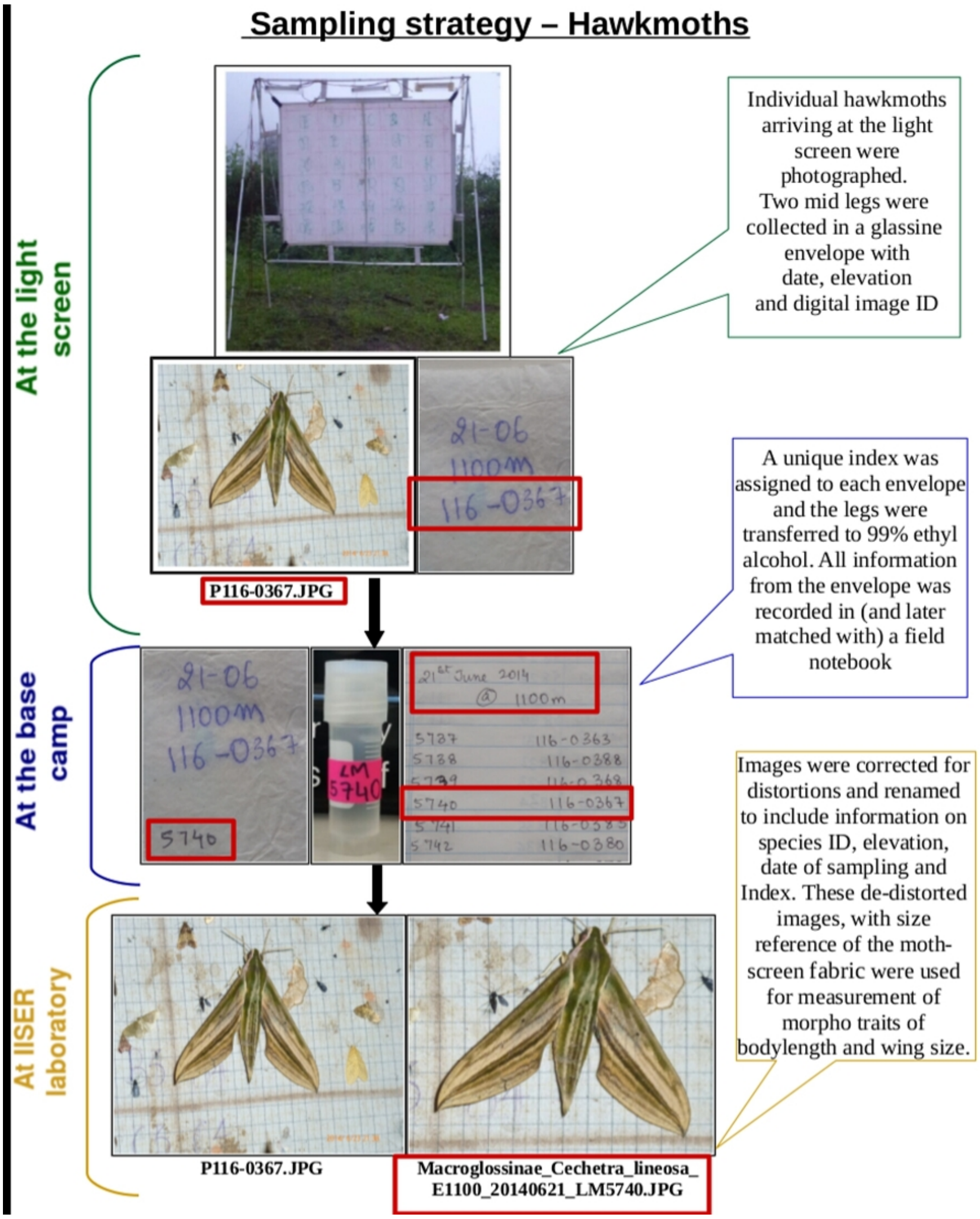
During 2013 we collected about a thousand voucher specimens between 500 and 2800 m (Table 2.1). Live moths picked off the screens were rendered unconscious in chloroform jars and packed into glassine envelopes marked with the elevation. These were transported to the base camp in boxes and on subsequent days killed in ethyl acetate jars and preserved in the usual manner. Three of the legs (all from one side) were stored for future DNA analysis. The quantum of work led to considerable delays in the processing of

Elevation (m)	Individuals sampled	Elevation (m)	Individuals sampled	Elevation (m)	Individuals sampled
500	95	1300	83	2100	86
700	85	1500	99	2300	91
900	91	1700	80	2500	74
1100	82	1900	95	2800	68

Table 2.1 *Sampling effort in 2013*

specimens. Despite the care taken while cataloging specimens in the field diary we suspect that the increasing backlog may have resulted in mixing of individuals between elevations in 5-10 % of the specimens.

Therefore, when about 20% of the envelopes were inadvertently destroyed when being dessicated over a wood fire in the humid climate we decided to not use the 2013 samples



Individual hawkmoths arriving at the light screen were photographed. Two mid legs were collected in a glassine envelope with date, elevation and digital image ID

A unique index was assigned to each envelope and the legs were transferred to 99% ethyl alcohol. All information from the envelope was recorded in (and later matched with) a field notebook

Images were corrected for distortions and renamed to include information on species ID, elevation, date of sampling and Index. These de-distorted images, with size reference of the moth-screen fabric were used for measurement of morpho traits of bodylength and wing size.

Figure 2.5 *Sampling procedure for hawkmoths - 2014* for formal analysis in the absence of demonstrable provenance of the specimens. However, while the elevational provenance was suspect in some cases, we do have photographic evidence of the specimen–tissue vial correspondence in all cases and the sample continues to be available for DNA work. For what it is worth, the elevational diversity profile of 2013 is very similar to that of 2014.

During 2014, we only photographed the individuals against the screen and collected the 2 middle legs for DNA. The moths were released after clipping the wing tips to avoid double counting of individuals. The legs were stored in paper envelopes on which were written the date, elevation and moth image file number (Figure 2.5).

We set up light screens at 2-5 elevations simultaneously to sample across elevations as uniformly as possible (with regard to climatic conditions), and also to accumulate a large number of records within the short period of dark nights during a month. The sampling team comprised up to a dozen members with diverse backgrounds and skills, split into 2-3 people at each screen. While the use of multiple screens and teams every night improved efficiency and uniformity of sampling it did introduce variability in the quality of the photographs in terms of image resolution, image distortion, and exposure level. The intensity of rain during screen time also contributed to variability in image quality.

We aimed to collect approximately equal number of individuals from all elevations, rather than equalising the number of sampling days. We had observed in 2013 that the day-to-day variation in moth visitation was large even within the 10 day period around the new-moon. Daily changes in moth captures are thought to be more due of changes in flight activity than in species abundance (Muirhead-Thomson 1991) which may be related to very local weather conditions of temperature, wind speed and rain. Occasional “flushes” of a single species are often encountered at light screens that vitiate true population size estimations (Yela & Holyoak 1997). Equalising the sampling effort at each elevation could have led to very different sample sizes at different sites, and so wasted effort.

After the initial collection of a thousand specimens from across the elevational range in 2013 we deemed that a good photograph would be sufficient for our purposes. Sphingids are visually sufficiently different from each other for the most part for morpho-specific delineation; securing identifications using genitalic dissections was neither feasible nor necessary on a scale of thousands of specimens. The lack of expertise in or resources for handling, processing and storing thousands of specimens was also an issue. We also discussed within the team the ethics of plucking 2 legs from a live insect. We noticed that the plucking of legs (i) did not lead to the oozing of any haemolymph and (ii) did not seem to impair their flight. Indeed, we found such moths strongly flying back to the screen after being released. On balance we felt that collecting 2 legs was also better from a conservation perspective than thousands of specimens.

The leg tissue and the images were assigned a collection index which was noted on the envelope as well as in the field notebook while the tissue was being transferred into a 1.5 ml vial of 99% ethyl alcohol. While the small volume occupied by the tissue did not really dilute the alcohol, we did change the alcohol after a few days to retain its optimum concentration in view of the planned long-term storage.

Many of the individuals sampled in 2014 rested on the fabric but about a fifth of them rested on the frame itself or on the surrounding vegetation. The moths were photographed where they rested to avoid (i) scaring them off and (ii) damaging the wings prior to the archival photograph. Only the ones on the grids have been used for trait measurement.

During data curation we excluded less than 1% of the records which showed a conflict between the information on the envelope, in the field plan notebook, tissue collection notebook and the EXIF data (primarily date, time and image sequence) in the image file. We also examined the color and label of the screen to resolve or confirm inconsistencies in the data. With this careful examination we are confident that our database accurately reflects the correct mapping between photo-specimen, tissue sample, elevation and date.

2.3.2 Species Identification – Hawkmoths

‘Species’ is the fundamental unit of data collected for most community ecology studies. However, recognizing, naming and identifying species, especially for hyper-diverse invertebrates, is not easy, requiring some degree of expertise and experience (Krell 2003). Due to a persistent decline of human resources in taxonomy (e.g. Hopkins & Freckleton 2002), 'morpho-species' sorting – i.e. taxa readily separable by morphological differences that are obvious to individuals without extensive taxonomic training – with minimum or no involvement of taxonomists has become a widely used strategy in conservation biology and species diversity-based ecology (Krell 2003; Brehm et al. 2003). To quote Oliver & Beattie (1993) *"Ninety percent agreement has been found between morpho-species classification by non-specialists and specialist taxonomists."* Oliver (1994) showed that morpho-species provided accurate estimates of species richness of ants, spiders and beetles. They suggest the use of morpho-species as surrogates for species when comparing richness of sites over time or space. More recently, Brehm et al. (2016) compared analyses using morpho-species and DNA-barcodes to confirm that incomplete

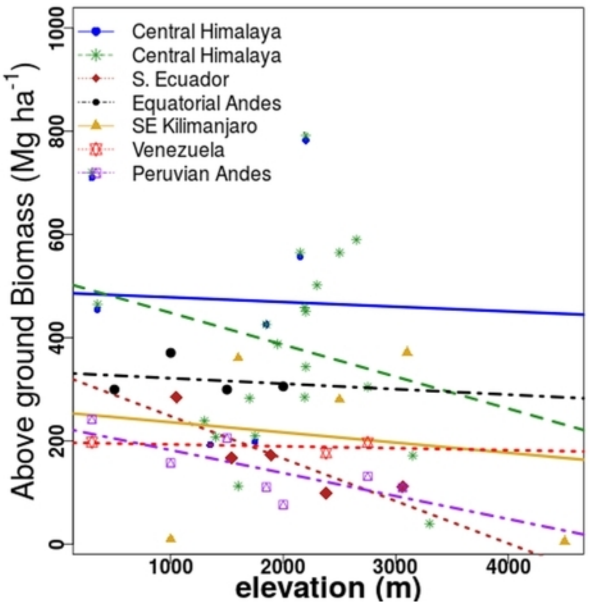


Figure 2.6 *Forest biomass with elevation from 7 published sources (Rana et al. 1989 – Central Himalaya (blue); Singh et al. 1994 – Central Himalaya (Green); Moser et al. 2011 (South Ecuador); Unger et al. 2012 (Equatorial Andes); Ensillin et al. 2015 (Kilimanjaro); Girardin et al. 2014 (Venezuela and Peruvian Andes)*

Data	Intercept	Slope	P value
Central Himalaya (Rana et al. 1989)	488 ± 205	-0.009 ± 0.13	0.95
Central Himalaya (Singh et al. 1994)	511 ± 123	-0.060 ± 0.06	0.30
South Ecuador (Moser et al. 2011)	331 ± 57	-0.080 ± 0.03	0.06
Equatorial Andes (Unger et al. 2012)	333 ± 51	-0.010 ± 0.04	0.80
Southeast Kilimanjaro (Ensillin et al. 2015)	256 ± 197	-0.020 ± 0.08	0.81
Venezuela (Girardin et al. 2014)	197 ± 17	-0.004 ± 0.01	0.73
Peruvian Andes (Girardin et al. 2014)	227 ± 37	-0.044 ± 0.02	0.06

species delineation does not necessarily conceal trends of biodiversity along a gradient, but it might underestimate the true magnitude of diversity (a case study on G*eometridae*).

We were able to assign individuals to taxonomic species in most cases because *Sphingidae* identification is relatively easy due to the large amount of available literature and type-specimen inventories. Where we were not confident of our identifications, we assigned individuals to morpho-species. Nevertheless, we only use the assigned taxonomic name as a label for an OTU; i.e. we only claim that individuals which share a name belong to the same (morpho-) species, but they may not be the one named, but a similar looking sister species. For instance, most of the individuals that we have listed as *Ambulyx tobii* are all very likely to belong to the same species, but that species may not be *A. tobii*. We relied chiefly on the following reference material for identification:

1. Moths of Thailand Vol. 2 Sphingidae, *H. Inoue, R.D. Kennett & I.J.Kitching (MOT)*
2. Moths of Borneo *J.D. Holloway (MOB)*
3. Sphingidae Taxonomic Inventory http://sphingidae.myspecies.info *(STI)*

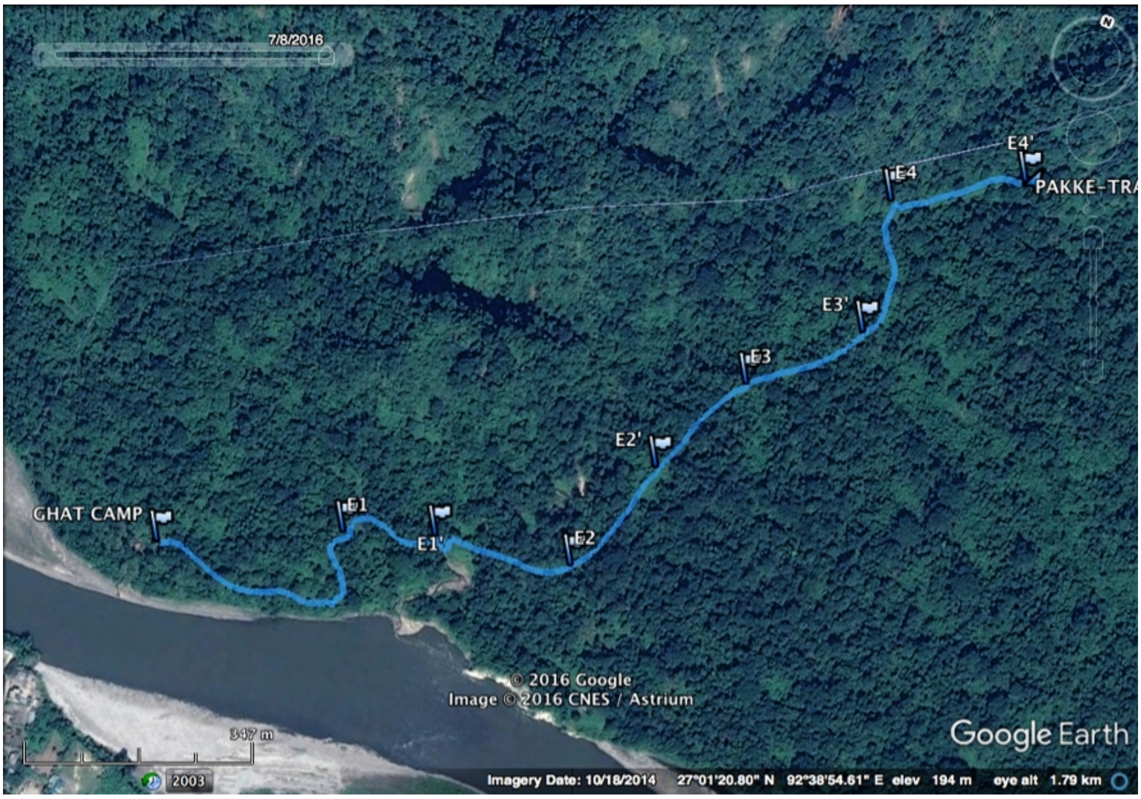


Figure 2.7 *Bird transect locations for the 200 m elevation (Pakke Tiger reserve)*

4. Sphingidae of the eastern Palaearctic http://tpittaway.tripod.com/china/ (*SOTEP)*
5. Sphingidae of Southeast- Asia https://www.sphin-sea.unibas.ch/ *(SSA)*

2.3.3 Elevational abundance profiles of hawkmoth species

Moth visitations at UV screens tend to vary a lot from day to day and so our sampling effort was designed to get approximately equal number of individuals at each elevation. In most of the analyses in this thesis diversity or assemblage metrics were calculated within each elevation and then compared across elevations. Therefore, the disconnect of individual moth species abundance across neighbouring elevations is in general not an issue. However, it would be an issue while, for example, calculating the elevational range (profile, mean value, etc.) of a hawkmoth species. We compensated for this lack by a multiplicative factor which equalised the elevational profile of moth abundance to the published forest biomass profiles (Figure 2.6). This is a reasonable approach as moths are among the principal herbivores in an ecosystem. In any case, we have compared such results using the extreme values of the slope of the elevational profiles of biomass (slope = zero, i.e. no change with elevation; and slope = – 80 kg ha^{-1} m^{-1}) to encompass the full range of uncertainty in the elevational range parameters.

2.4 Field Sampling – Birds

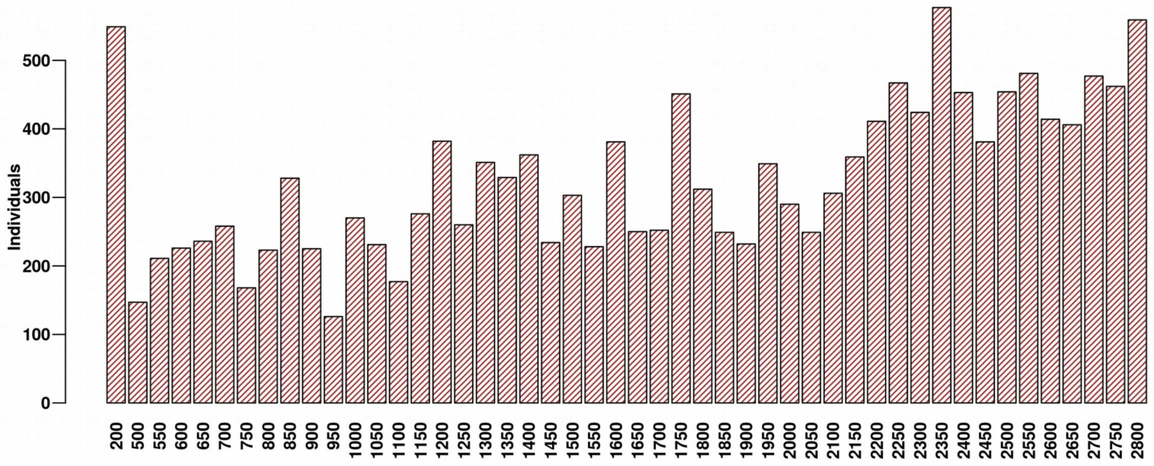


Figure 2.8. Bird transect counts were conducted at 50 m intervals between 500m and 2800m Individuals recorded at each elevation are shown above.

2.4.1 Methodology – Birds

Bibby and his colleagues (2000) have provided a fairly comprehensive description of the many bird census and monitoring techniques, along with their advantages and disadvantages. Some of the strategies include five-minute point counts (Spurr 1991, 1994, 2000; Miller & Anderson 1992; Empson & Miskelly 1999; Innes et al. 2004), territory mapping (Powlesland et al. 1998, 1999), radio-telemetry (Powlesland et al. 1998), color banding (Powlesland et al. 1998, 1999, 2000; Davidson & Armstrong 2002), distance sampling (Westbrooke et al. 2003), and fixed-width strip-transect counts (Westbrooke et al. 2003; Westbrooke & Powlesland 2005). The choice of method depends on the scale of study, resources available to the researcher and most importantly, on the study objectives.

We chose line transects for their several advantages. They sample a larger number of (independent) locations, record more birds, have a lower chance of double counting the same bird, are better for shy species which ‘flush’ easily, and less affected by errors in distance estimation than point counts (Bibby 1998). All bird sampling was conducted by a single person (*Rohan Pandit)* to minimize identification bias. Pandit, who has spent many years in Eaglenest, is one of the most knowledgeable birdwatchers of the area.

Forty-nine elevations between 500 m and 2800 m, in intervals of 50 m were surveyed along the Eaglenest road. Birds were recorded along a 200 m transect during a steady walk over 5 minutes. The same transect was sampled again while returning to the motor-cycle parked at the head of the transect. The two counts were recorded separately. It took a total of 30 min per transect, including travel from one to the next. Birds recorded, both visually and aurally, within a perpendicular distance of about 20 m from the road were dictated into a voice recorder. These audio clips were later transcribed into a spreadsheet and checked for errors by two different transcribers. The same transects were sampled on 12 different days (12 sets per elevation) in both summer (May and June, 2012-14) and winter (mostly in January and February, 2012-13; about 10% of the transects before mid-March, 2013). The sampling was done during 6.00-12.00 hr in summer and 7.00-13.00 hr in winter. A maximum of 12 elevations were covered during a day, though rain, especially during summer, often reduced the number.

We avoided any systematic bird activity difference across the 6-hr window, by subdividing it into three 2-hr slots – Early morning (E), Mid morning (M) and Late morning (L). The 12 transects at each elevation were equally distributed across these 3 slots. Further, we had planned to sample alternate elevations on a given day (e.g. 2800, 2700, 2600, ... , 1700 m) and the lower elevations on the next day (1600 – 500 m) to cover the entire elevational gradient within a short interval. The other, intervening, elevations (i.e. 2750, 2650, 2550 m, etc) were to be sampled on the next two days. However, summer rains wrecked the 4-days-per-set schedule. In fact, the loss of time to rain caused the summer effort to spill into a third year for completion. Of the 12 sets each from summer and winter we have archived the transect count audio clips of all except sets 1 and 2 of summer which was lost due to a system failure (post transcription).

Security issues precluded us from sampling elevations below 500 m in EWS. We attempted to fill in this lacuna between 150 m and 300 m by sampling the lowest elevations in Pakke Tiger Reserve, about 20 km from the last, 500 m elevation, transect in Eaglenest, but more importantly across the gorge of the Kameng river. Even here, the topography meant that we could not access higher elevations since the broad dirt track in Pakke essentially followed the 200 m contour (Figure 2.7). Therefore, we sampled 4 different transects all at 200 m resulting in the high number of individuals at that elevation (Figure 2.8)

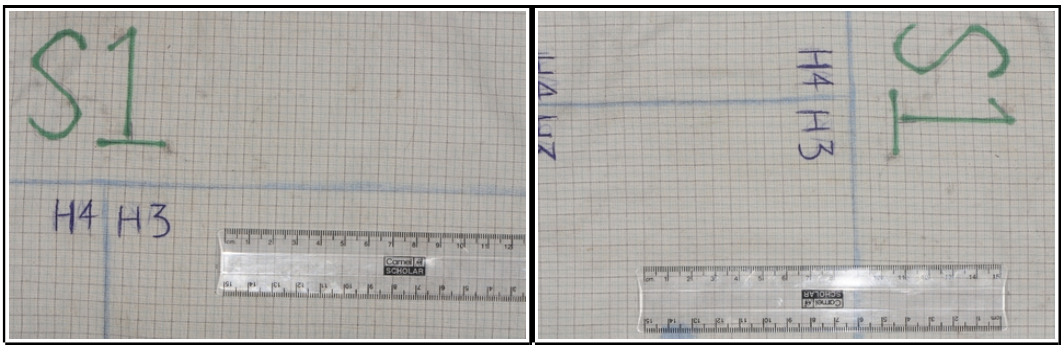


Figure 2.9 *Moth screen with a gridded pattern of known dimensions on a white background*

Figure 2.10 *Distortions in the images of hawkmoths, as evidenced by the distortion in grid shapes.*

2.4.2 Species Identification – Birds

Bird identifications and initially the taxonomy were linked to Rasmussen & Anderton (2005). The taxonomy was subsequently modified to the latest published Handbook of Birds of the World (HBW) and Birdlife International (http://www.birdlife.org/).

2.5 Trait measurements

2.5.1 Hawkmoths

The intimidating diversity and abundance of invertebrates demands immense resources for any reasonable amount of morphometric analyses. Typically, a large number of specimens are collected often by default in insect traps. They are then mounted and photographed either as-is or under a microscope to measure their morpho-traits. We greatly reduced this effort by directly photographing hawkmoths on a gridded screen (Figure 2.9 & 2.10) without the burden of having to process and preserve specimens. These were sufficient to measure the two obvious functional traits, viz. Body and wing sizes.

Figure 2.11 *Dedistortion of images for morpho-trait measurement using the background grids as reference. Each pair includes the raw image (left) and dedistorted image (right).*

Unless a moth is imaged from a sufficient distance and from directly above its mid body the resulting image is bound to suffer from multiple types of distortions, including rotation, perspective, and pin-cushion. Some of these distortions are shown in Figure 2.10. We corrected these distortions by photographing the moths against a fabric screen with a printed rectangular grid of known size. The distortions of the grids in the images were subsequently “undone” by using the ImageMagick suite of tools (Figure 2.11). The image scale (mm per pixels) was calibrated using the size of the grids to measure the trait values.

Nevertheless, the final images contained residual errors for several reasons:

1. Non-rectangularity of the grids because the fabric itself was distorted when stretched across the frame
2. The moth was not parallel to the screen

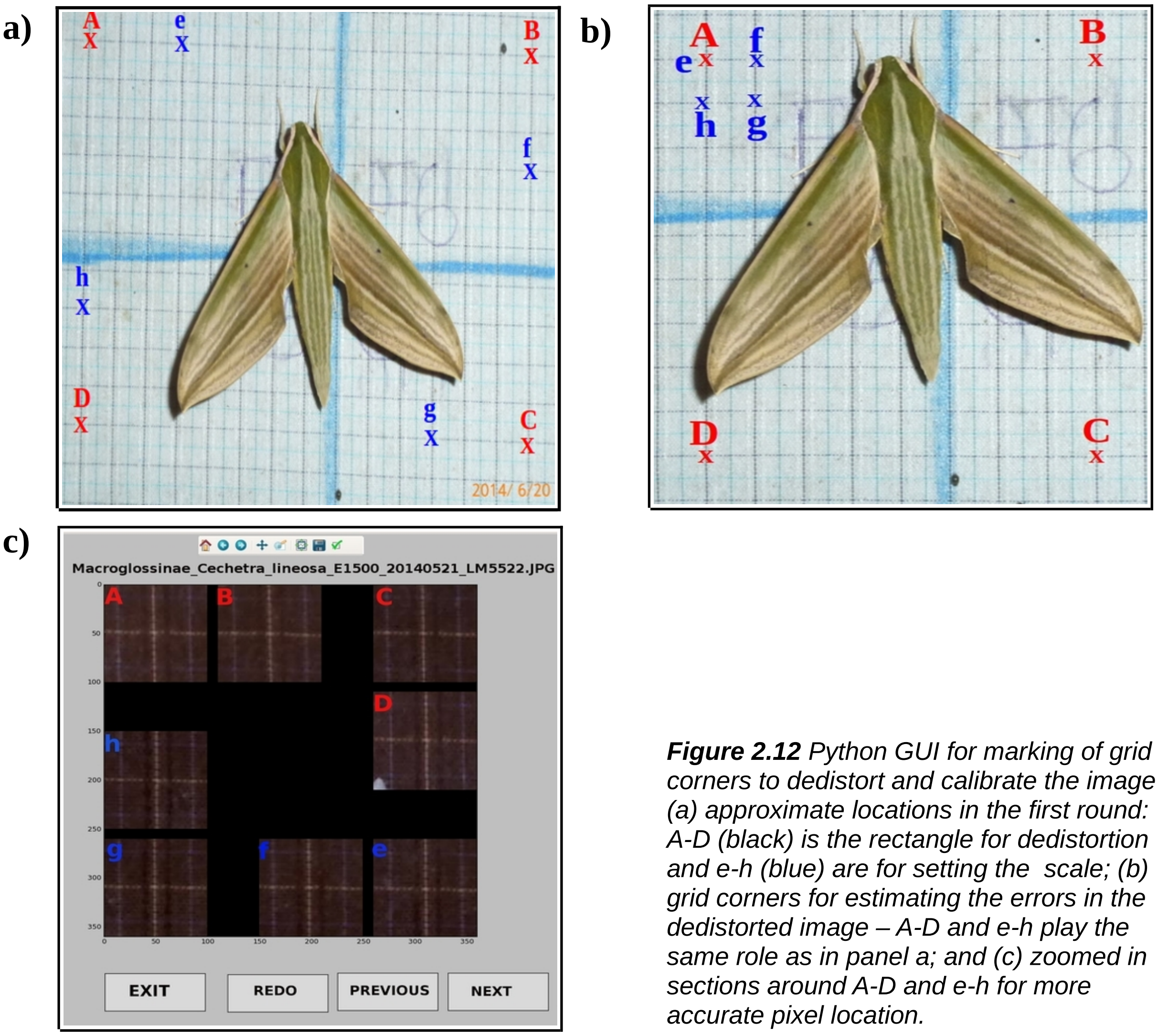


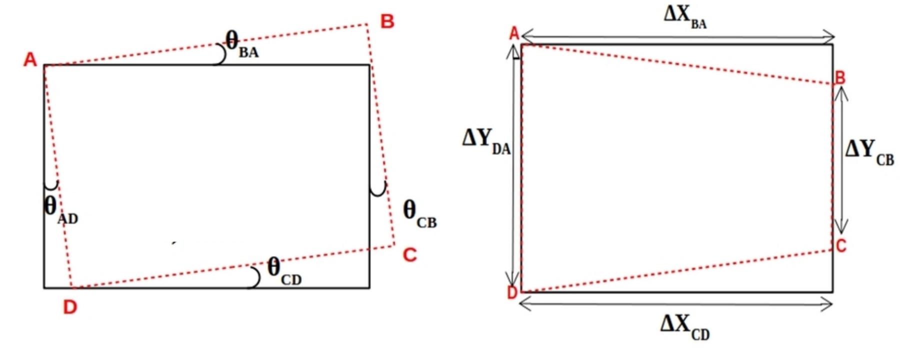
Figure 2.12 *Python GUI for marking of grid corners to dedistort and calibrate the image (a) approximate locations in the first round: A-D (black) is the rectangle for dedistortion and e-h (blue) are for setting the scale; (b) grid corners for estimating the errors in the dedistorted image – A-D and e-h play the same role as in panel a; and (c) zoomed in sections around A-D and e-h for more accurate pixel location.*

3. The moth-screen distance was a substantial fraction of the camera-screen distance; i.e. the camera was held too close to the screen.
4. The angle between the camera axis and the screen was much less than 90°
5. Random (human) errors while locating the grids on the images

Therefore, we defined and estimated several error metrics to eliminate images in which the de-distortion had not worked. We developed Python[1] and R scripts to process over 3540 images in a semi-automated pipeline with a relatively short amount of manual effort

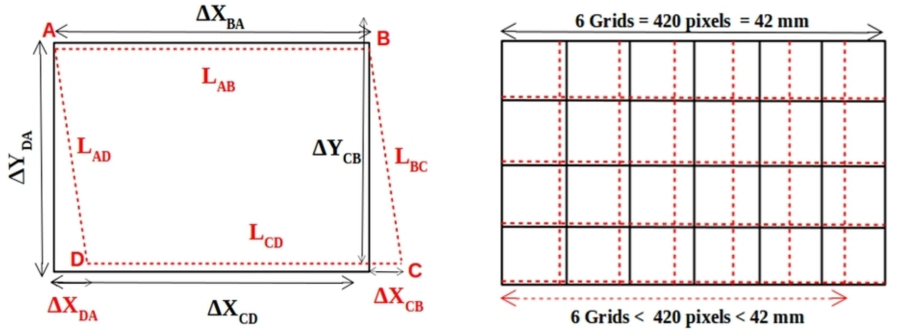
---

[1] Thank you – Srikrishna Sekhar



a). Rotation

b). Perspective



c). Shear

d). Scale

Figure 2.13 *Rotation (a); Perspective (b); Shear (c) and Scale errors (d). All errors are shown with red dotted lines and were calculated with respect to horizontal and vertical axis (black solid lines).*

(approximately 2 minute per image in total).

The steps were as follows:

A. Identify a rectangle for de-distortion – using a Python script (Figure 2.12 a)

1. Outline a rectangle by marking its 4 vertices (points **A**, **B**, **C** and **D**) using mouse-clicks at grid line intersections. The rectangle was usually chosen to include the moth. When this was not possible – e.g. when every such rectangle had at least one vertex covered by a moth – any nearby rectangle was chosen
2. The size of the rectangle, in grids, was provided to the script by marking 4 more points (**e**, **f**, **g**, and **h**) on its perimeter and at a fixed distance from **A-D**.
3. The pixels were located accurately by a 2-step process: the first set of mouse-clicks extracted 50 x 50 pixel postage stamps around the approximate locations of **A-D** and **e-h**. The next set of clicks accurately located the grid line intersections on the postage stamps which were displayed with high zoom and resolution.
4. The script can cycle through some or all the images in a directory and we

processed anywhere from 1 to 200 images at a sitting. The script output a CSV file with the image name and (X, Y) coordinates of the 8 points, **A-D** and **e-h**.

B. Create a batch file for image de-distortion – using an R script

1. The lengths, Ae, Bf, Cg and Dh in pixels, and the known grid size in mm were used to calculate the actual coordinates of the undistorted rectangle ABCD in millimeters.
2. These information was used to create an ImageMagick batch file for a Linux shell environment (using the command ***convert --distort Perspective***) which generated dedistorted images with a scale of 0.1 mm per pixel.
3. The script made allowance for sections near the edge of the image which would have resulted in the subject being pushed off the edge during dedistortion.

C. Estimate the error in dedistortion – using a Python + R script

1. Mark locations A-D and e-h (pattern in Figure 2.12 b) using the Python as in step A
2. The following error metrics were used to quantify the quality of dedistortion (see Figure 2.13)

   Notation: For any 2 pixels L and M

   $\Delta X_{LM} = X_L - X_M$ the difference between their X-coordinates

   $\Delta Y_{LM} = Y_L - Y_M$ the difference between their Y-coordinates

   i. Error in visually identifying the target pixel and clicking on it (measured in

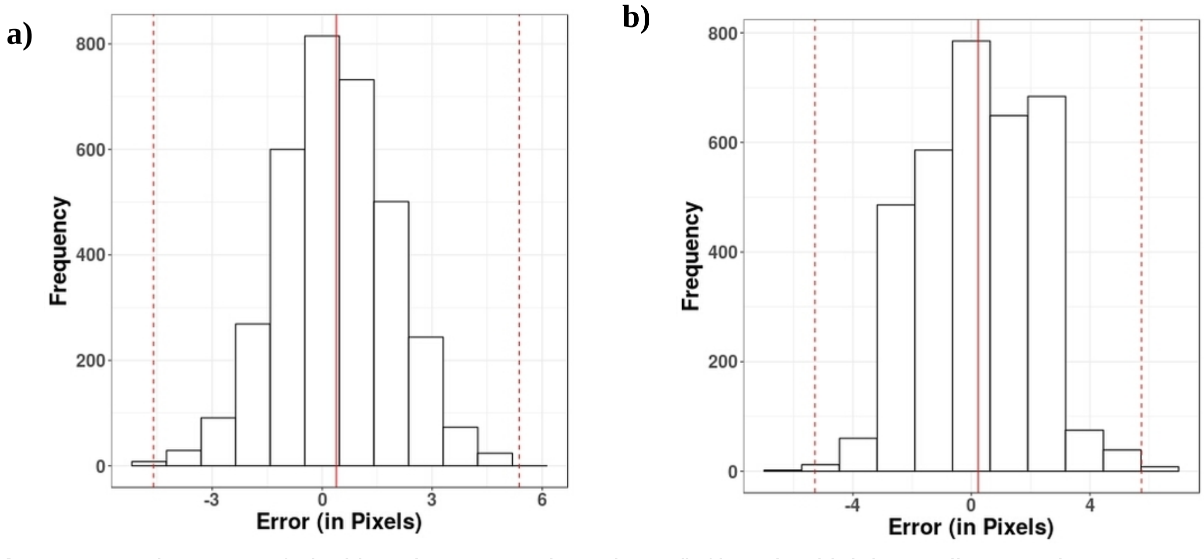


Figure 2.14 *Histogram of pixel locating errors along the X (left) and Y (right) coordinates. The mean and ±3 standard deviations are marked by solid and dashed red lines.*

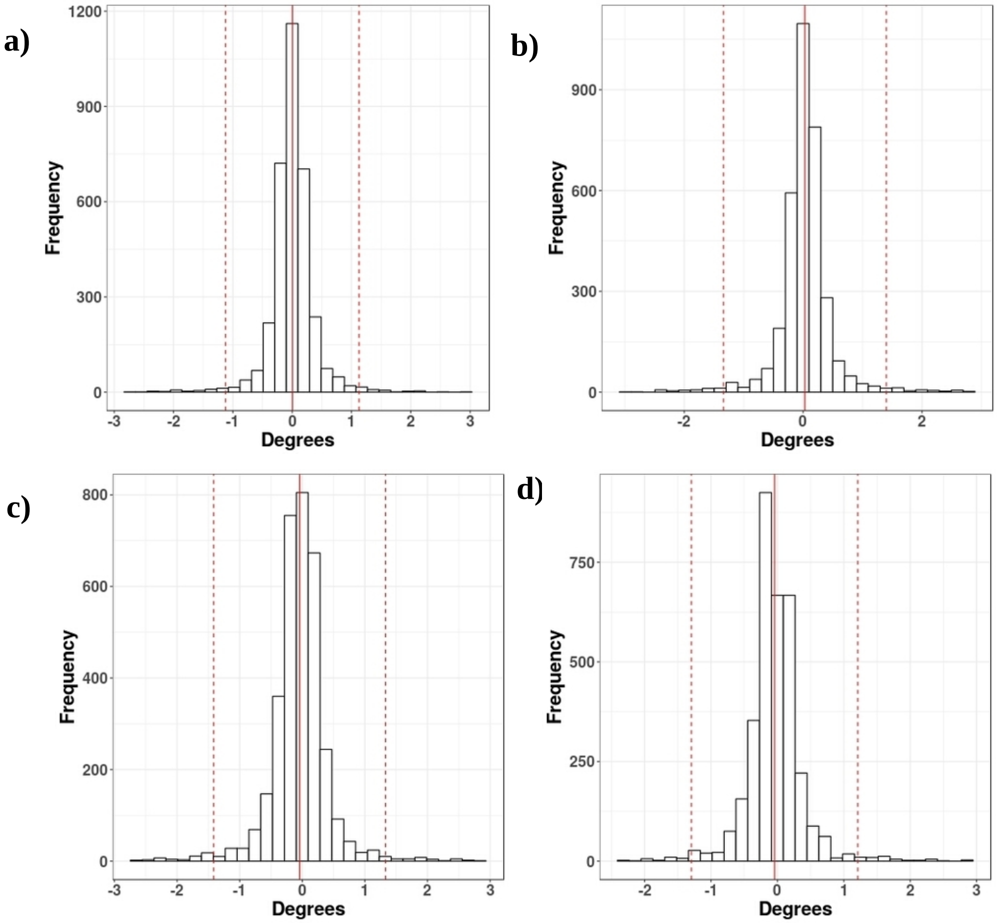


Figure 2.15 *Deviations from horizontality of the lines AB (a) & CD (b) and from verticality of the lines BC (c) and DA (d). The mean and ± 3 standard deviations are indicated by solid and dashed red lines.*

pixels). The points **A** and **e** are meant to be the same and their difference is a measure of the error in clicking on the desired pixel

$$C_X = \Delta X_{EA} \qquad\qquad C_Y = \Delta Y_{EA}$$

ii. Angle to the horizontal of the horizontal lines AB and CD, and to the vertical of the vertical lines BC and AD

$$\theta_{BA} = \frac{(\Delta Y_{BA})}{(\Delta X_{BA})} \quad \theta_{CD} = \frac{(\Delta Y_{CD})}{(\Delta X_{CD})} \quad \theta_{BC} = \frac{(\Delta X_{CB})}{(\Delta Y_{CB})} \quad \theta_{AD} = \frac{(\Delta X_{DA})}{(\Delta Y_{DA})}$$

iii. X- and Y-components of the residual perspective:

$$P_X = \frac{2*(\Delta X_{BA} - \Delta X_{CD})}{(\Delta Y_{CB} + \Delta Y_{DA})} \qquad P_Y = \frac{2*(\Delta Y_{CB} - \Delta Y_{DA})}{(\Delta X_{BA} + \Delta X_{CD})}$$

iv. X- and Y-scale error

Metric	Units	Mean	Std. Devn
C-X (mouse click error)	pixels	0.43	1.68
C-Y (mouse click error)	pixels	0.23	1.81
θ_{BA} , θ_{CD} (rotation of horizontal lines)	degree	0.02	0.42
θ_{BC} , θ_{AD} (rotation of vertical lines)	degree	-0.04	0.44
P_X (residual perspective – X component)	degree	0.02	0.79
P_Y (residual perspective – Y component)	degree	0.02	0.99
SH_X (residual shear – X component)	degree	–0.04	0.33
SH_Y (residual shear – Y component)	degree	0.02	0.32
SC_X (scale error – X component)	percentage	0.07	2.24
SC_Y (scale error – Y component)	percentage	0.22	2.82

Table 2.2 *Errors in dedistorted images as measured in various metrics*

$$SC_{X1}=100*1-\frac{\Delta X_{AB}}{(L_{AB}/L_{ef})/grid_X} \qquad SC_{X2}=100*1-\frac{\Delta X_{CD}}{(L_{CD}/L_{hg})/grid_X}$$

$$SC_{Y1}=100*1-\frac{\Delta Y_{BC}}{(L_{BC}/L_{fg})/grid_Y} \qquad SC_{Y1}=100*1-\frac{\Delta Y_{AD}}{(L_{AD}/L_{eh})/grid_Y}$$

$$SC_X=\frac{SC_{X1}+SC_{X2}}{2} \qquad SC_Y=\frac{SC_{Y1}+SC_{Y2}}{2}$$

The histogram of errors are shown for pixel location (Figure 2.14) and angles to the horizontal and vertical (Figure 2.15); the other error statistics are shown in Table

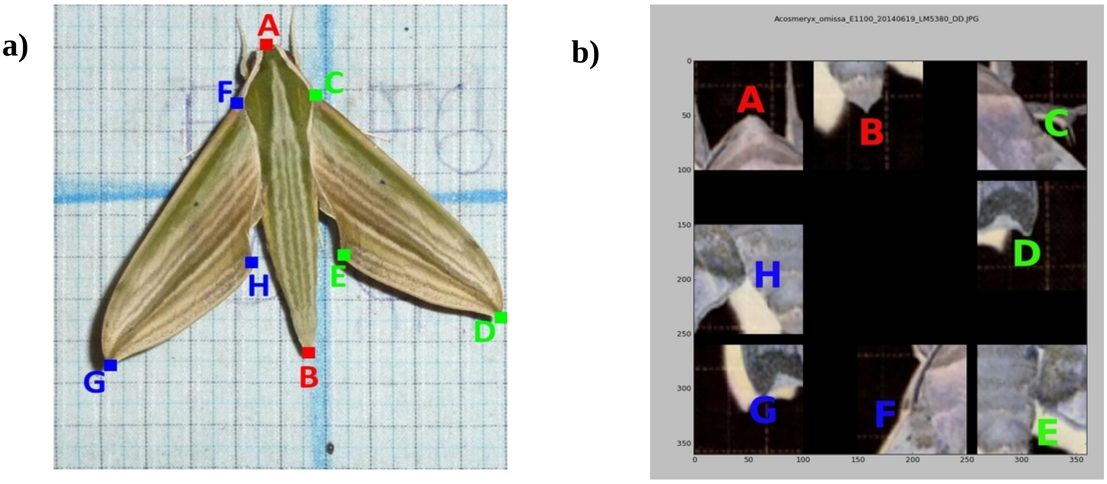


Figure 2.16 *a) Digitization of 8 landmarks for trait calculation on a dedistorted image of Cechetra lineosa; b) Full resolution snapshots of the 8 digitized points for accurate coordinate measurement.*

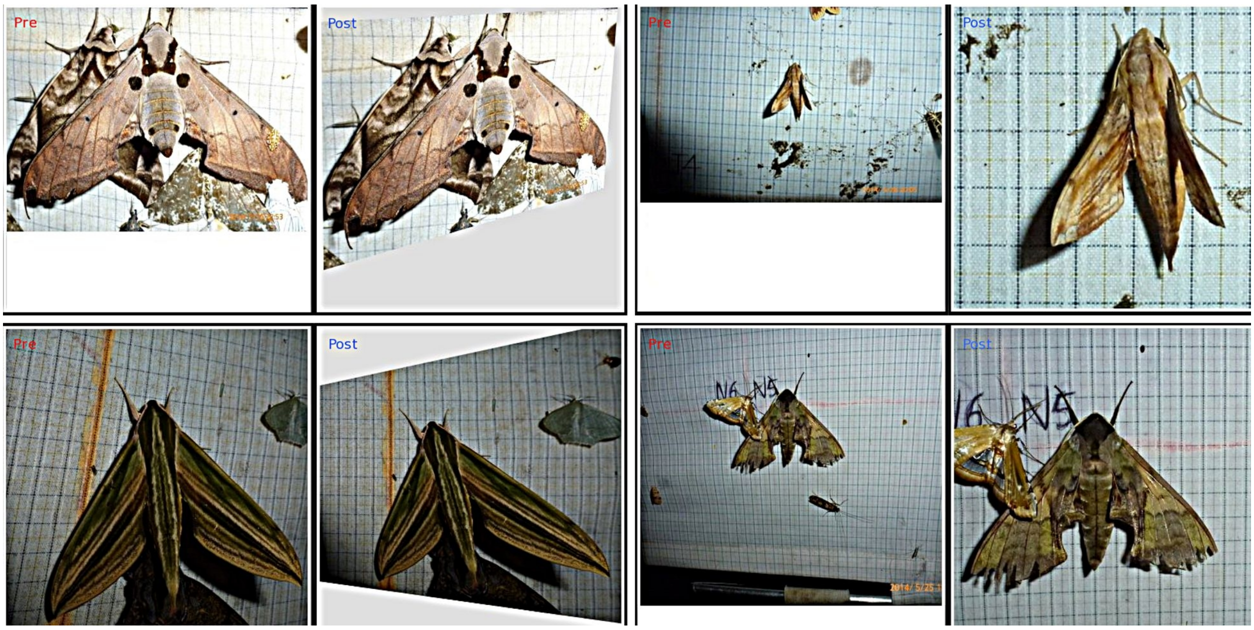


Figure 2.17 *Examples images for poor de-distortion presented for 4 individuals. Left panel contains the original (raw) image for each individual, where as the right panel shows the de-distorted image.*

2.2. The dispersion in mouse clicks is 1.68-1.81 pixels, corresponding to a measurement error of less than 0.2 mm. For a typical moth size of 50 mm this constitutes an error of 0.4%. The dispersions in the horizontal and vertical rotation angles were 0.42° and 0.44° corresponding to a length error of 0.01% along the line (and hence negligible) and 0.7% in the orthogonal direction. The perspective dispersion is less than 1°, which translates into a length error of 0.02% along the line and less than 1.75% in the orthogonal direction. The error was dominated by the scale factors with dispersions of 2.2 and 2.8%. These errors are not independent of each other but assuming that they were, and added in quadrature they yielded a combined error dispersion (standard deviation) of 3.7%. Even if the errors are fully correlated this corresponds to an error dispersion of about 6%.

D. Measure the traits on the calibrated images

1. Mark moth trait locations as follows (Figure 2.16):
    - i. Tip of the head – A
    - ii. Tip of the abdomen – B
    - iii. Base of the right forewing – C
    - iv. Apex of the right forewing – D

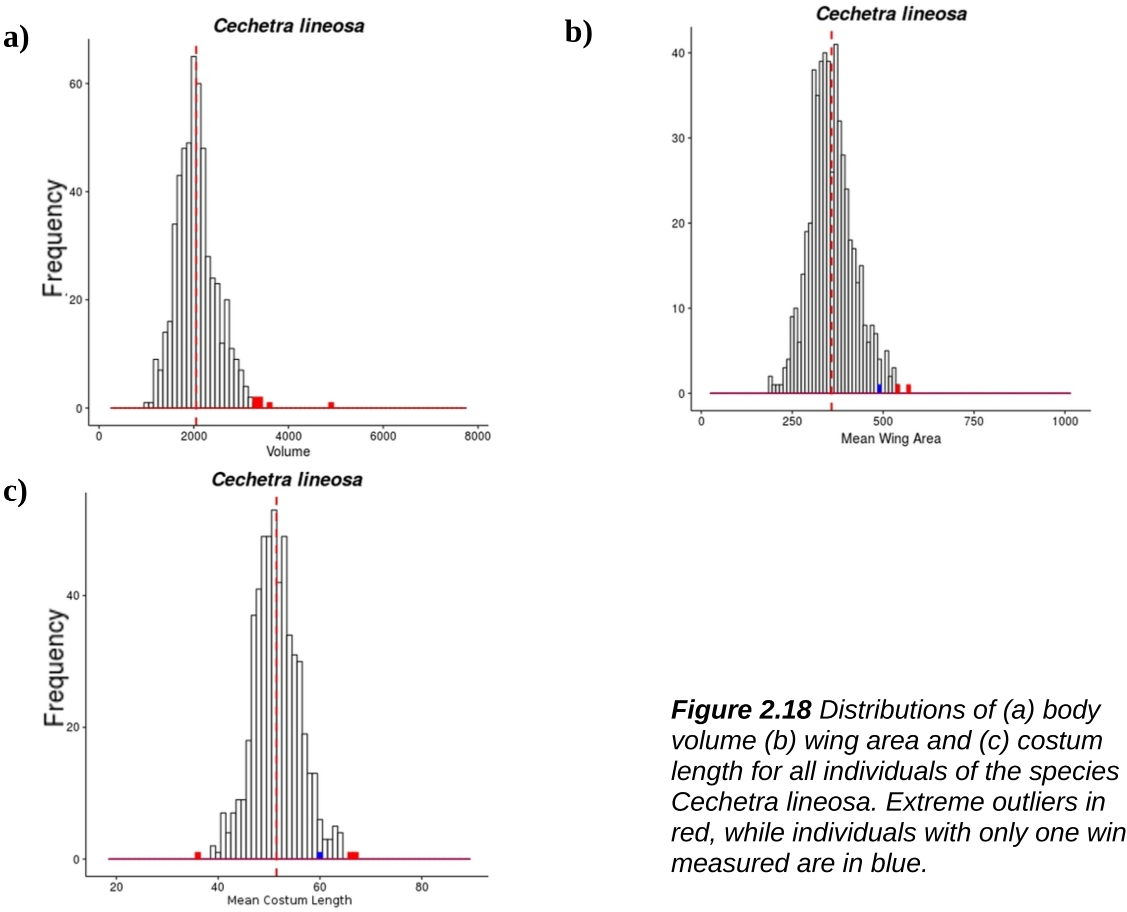


Figure 2.18 *Distributions of (a) body volume (b) wing area and (c) costum length for all individuals of the species Cechetra lineosa. Extreme outliers in red, while individuals with only one wing measured are in blue.*

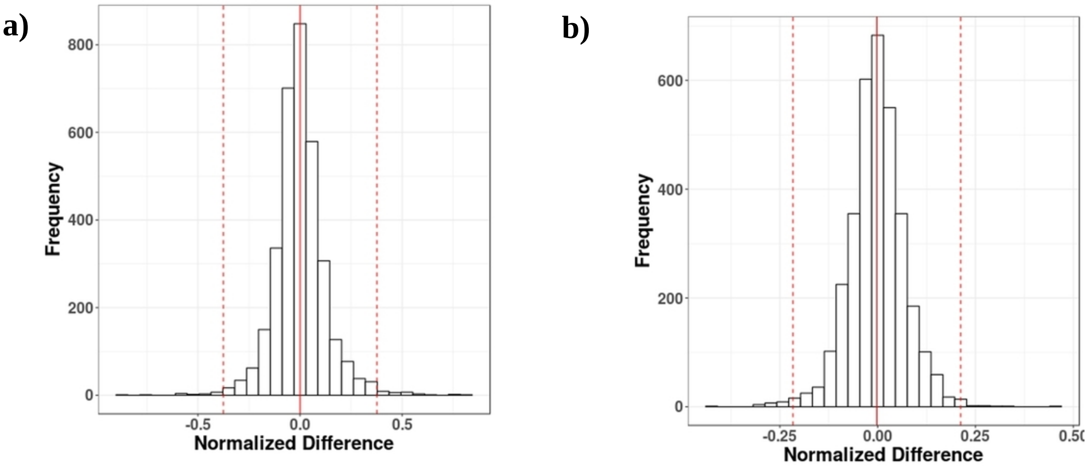


Figure 2.19 *Normalized difference between the left and right wing for all hawkmoth individuals (a) wing area, and (b) costum length.*

- v. Tornal tip of the right forewing – E
- vi. Base of the left forewing – F
- vii. Apex of the left forewing – G
- viii. Tornal tip of the left forewing – H

2. The distance between A & B (L_{AB}) was used as a measure of body length and similarly L_{CF} was used as the thorax width (diameter). The volume of the spindle-shaped body was calculated as two conjoined cones. The three sides of the right wing were calculated as the lengths L_{CD} ($Costum_R$), L_{DE} ($Termen_R$) and L_{EC} ($Dorsum_R$) and that of the left wing as L_{FG} ($Costum_L$), L_{GH} ($Termen_L$) and L_{HF} ($Dorsum_L$). Consequently, we were able to calculate the area of each wing as

$$Wing\,area=\sqrt{(s*(s-L_{Costum})*(s-L_{Termen})*(s-L_{Dorsum}))} \quad \text{, where} \quad s=\frac{L_{Costum}+L_{Termen}+L_{Dorsum}}{2}$$

We reprocessed images which were outliers on the error histograms, and in most cases were able to improve the de-distortion. Images which continued to be outliers on the error distributions were subsequently eliminated from further analyses (e.g. Figure 2.17). We examined the species-wise distribution functions for the body volume, wing area and costum length. Figure 2.18 shows an example. Outliers were assigned a temporary flag to

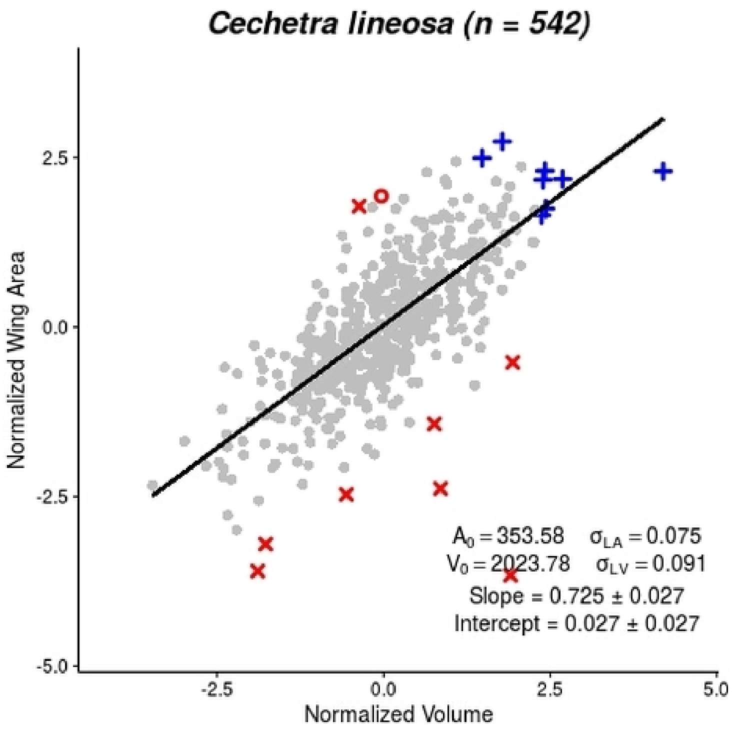


***Figure 2.20** Regression plots for normalzed wing area on normalized body volume for Cechetra lineosa. Regression outliers are in red and outliers of left-right difference are in blue. Legend contains the following values :*
A_0 = Species mean wing-area, σ_{LA} = log of standard deviation of species specific wing-area,
V_0 = Species mean body- volume, σ_{LV} = log of standard deviation of species specific body-volumes
Slope and intercept for the robust regression with associated standard errors.

identify them in case of any undue influence on the results. We observed that in some cases the wings of the resting hawkmoth was not in the plane of the moth-screen (Figure 2.17). In these cases, even though the moth-screen itself was properly de-distorted the trait for that individual would not be accurate. Such images would not only have the wing area deviating from other individuals of that species, but would also have a large difference between the two wings. So, we used the statistics of the normalized difference between the left and the right wing values to identify distortions. The distribution of the left-right difference is shown in Figure 2.19.

$$normalized_{diff} = \frac{(Trait_L - Trait_R)}{(Trait_L + Trait_R)/2}$$

In some moths only one wing could be measured either because the other was highly damaged, or it was hidden under another moth, or in a very few cases was located outside the image. Of course, the left-right comparison could not be made for such wings (11 individuals; < 1%). These left-right discrepants and single-wing specimens were assigned the temporary flags. Additionally, two images had to be removed because both wings were damaged and could not be measured (e.g. Figure 2.17d).

We also performed a robust regression of normalized wing-area on normalized body volume for all species with 10 or more individuals to identify outliers (see Figure 2.20 for an example). The data with temporary flags (blue) which fit into the regression scatter were used in subsequent analyses. Outliers on these regression plots (plotted in red) were eliminated from all subsequent analyses. Lepidoptera are known to exhibit sexual

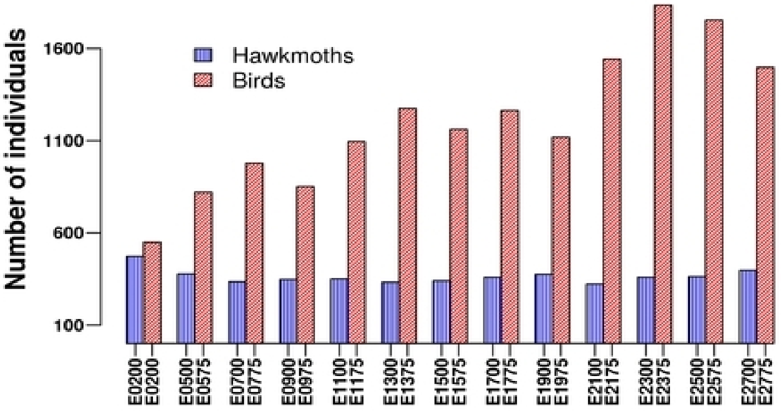


Figure 2.21 *Number of individuals sampled at different elevations for hawkmoths (blue) and birds (red; summer only). 4 adjacent elevations of the bird data has been to facilitate comparison with hawkmoth. (i.e. E575 = E0450 + E0500 + E0550 + E0600, E0775 = E0650 + E0700 + E0750 + E0800, etc; and E0200 = summed over 4 transects, all at 200 m).*

Elevation (meters)	No. of. Individuals Sampled	ID'd to genus level	ID'd to species level	No. of Species	No. of individuals with trait		Traits with Species ID	
					Count	Percentage	Count	Percentage
200	473	473	473	43	434	100%	434	100%
500	382	382	378	39	304	80%	304	80%
700	341	341	335	33	277	81%	274	80%
900	354	354	347	45	229	65%	228	64%
1100	391	391	350	48	255	65%	253	64%
1300	339	339	332	31	215	63%	211	64%
1500	344	344	340	40	178	52%	176	51%
1700	366	366	359	36	104	28%	103	27%
1900	376	376	376	40	303	81%	303	81%
2100	323	323	323	29	323	100%	211	65%
2300	359	359	359	27	359	100%	314	88%
2500	363	363	363	23	255	70%	255	70%
2770	396	396	396	32	304	77%	304	77%

Table 2.3 *Summary statistics for the hawkmoth dataset.*

dimorphism in body size. We did not see any such signal in our data, though we do not

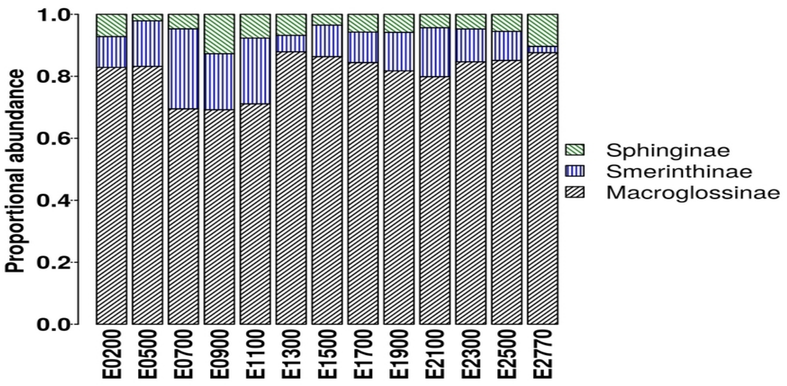


Figure 2.22 *Relative proportions of the three subfamilies at different elevations. Multinomial test showed that the elevational dependence abundance of all 3 subfamilies is consistent with being flat (Macroglossinae: p-value = 0.2; Smerinthinae: p-value = 0.99; Sphinginae: χ2 = 0.22, p-value = 0.99)*

have sex information for the specimen. Nevertheless, the lack of bimodality in the distribution for each species suggests that any such dimorphism was unlikely to affect any results significantly.

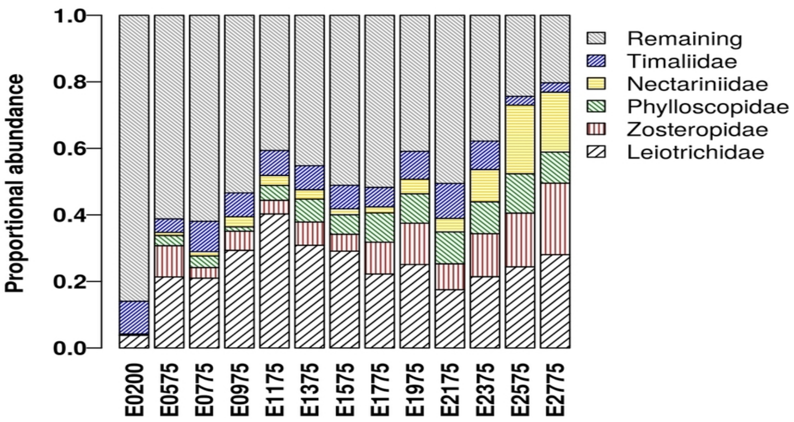


***Figure 2.23** Relative proportions of the 5 most abundant bird families across different elevations.*

2.5.2 Birds

The traits for birds (species means of body mass and wing length) were obtained from Price et al. (2014) (who source it from Dunning 2008; Price 1979;; unpublished field data from their own surveys; museum measurements).

2.6 Data – Summary Statistics

Figure 2.21 shows the elevational profile of the number of individuals of birds and hawkmoths recorded in this work. We have a final sample of 4731 individuals identified to species/OTU, and an additional 76 individuals identified to genus for use in taxon-diversity analyses, comprising 30 genera and 80 species/OTU for all subsequent diversity analysis (Table 2.3). Of these we have trait information for 3442 hawkmoth individuals across 26 genera and 57 species (2.9% had images but were eliminated from trait analysis because of poor images). Figure 2.22 shows the relative proportions of the 3 subfamilies across the elevational range. Appendix I lists all the species recorded with representative images and identification keys.

15,867 birds were recorded during summer, spanning 48 families, 150 genera and 235 species. Winter data included 19,280 individuals from 48 families, 114 genera and 213 species. Only summer (breeding) data has been used in this thesis. Elevational variation of bird numbers recorded for the 5 most abundant families in shown in Figure 2.23. The list of all the species recorded in this study is provided in Appendix II.

2.7 Summary

1. Of the two globally important biodiversity hot-spots in India, the Western Ghats and northeast India (including the eastern Himalayas), the latter is largely unexplored by ecologists due to complex terrain and difficult logistics. This study was conducted in Eaglenest Wildlife Sanctuary in the state of Arunachal Pradesh in northeast India.
2. The lepidopteran family *Sphingidae* and the birds of Eaglenest were sampled along an elevational transect between 200 m and 2800 m.
3. We recorded 4807 hawkmoths across 13 elevations, including 4731 individuals identified to 80 morphospecies and 30 genera. We measured body and wing dimensions of 3442 individuals by photographing against a gridded screen.
4. Birds were sampled along line transects at 50 m elevation intervals resolution in summer and winter, during 2012-2015. 15,867 birds, spanning 48 families, 150 genera and 235 species were recorded for the summer season. We have not included the winter data in this thesis. We obtained species mean body mass and wing length for 235 species from literature.

Chapter Three

Species Abundance Distributions

3.1 Introduction

Most investigations into elevational patterns in diversity focus only on species richness of communities, and in some cases species composition. Elevational patterns in species abundance distributions and community evenness are far less explored (but see Fauth et al. 1989; Wang et al. 2011, 2017). Recent studies have shown that the response of species richness and abundance distributions to environmental changes may be different (Walker et al. 2006; Langenheder et al. 2012; Godbold et al. 2011; Wohlgemuth et al. 2016). This chapter deals with the under-explored and under-appreciated species abundance distributions and community evenness of ecological communities.

The distribution of individuals across species, also known as Species Abundance Distribution (hereafter SAD), is a fundamental property of an ecological community, next only to species richness and diversity. Indeed, some indices of species diversity are based on the SAD (e.g. Fisher 1943). A SAD is the vector of abundances of all species present in the community and this distribution can be plotted in a variety of ways to facilitate visual comparisons amongst communities. In fact, the diversity of plotting forms used to depict SADs sometimes hinders comparative analysis across studies (Magurran 2004).

The commonest, and the most informative, depiction is the Rank-Abundance Curve (hereafter RAC; Whittaker 1965), also called a dominance-diversity plot (Magurran 2004), which plots the (relative) abundance of a species against its rank (from the most to the least abundant). RACs lend themselves easily to analysis of community evenness: a steeper slope is indicative of dominance by a few species, while a shallower slope reflects a more even community (Whittaker 1965). They have long been used as indicators of disturbance such as succession phases of a vegetation plot, anthropogenic disturbance gradients, environmental gradients, etc (Whittaker 1965; Magurran 2004; Izsak 2012). RACs display characteristic, and easily discernible, changes in shape along such gradients (Nee et al. 1992; Tokeshi 1993; Smith & Wilson 1996; Izsak 2012). Indeed, Magurran (2004) remarks that *“the first thing an investigator should do with species abundance data is to plot them as a rank abundance curve”*.

Despite their fundamental role in characterizing a community, RACs have not been popular topics of study because of our lack in understanding of the way in which species richness impact them. McGill et al. (2007) comment that *“changes in richness so strongly dominate in rank-abundance plots that no other changes are easily considered”*. Recently, Saeedghalati et al. (2017) have proposed a method of normalizing RACs to the same species richness, analogous to the use of rarefaction curves, which may give an impetus to the increased use of RACs in comparing communities.

Several mathematical models have been proposed to link the shape of RACs to ecological processes of community assembly and organization. These processes differ in the way the total niche space is partitioned amongst species (MacArthur 1957; Tokeshi 1993), or in terms of other factors like dispersal limitation (Hubbell 2001).

Mathematical modeling of SADs was quite popular during the middle of the 20th century (Motomura 1932; Fisher et al. 1943; Kendall 1948a; Preston 1948; MacArthur 1957) but their popularity and progress dipped subsequently (see reviews in Gray 1987; Marquet et al. 2003; McGill et al. 2007; Matthews et al. 2014). McGill et al. (2007) highlight six inferential issues ranging from employment of poor model comparison statistics, to the failure in successfully testing and rejecting older theories with newer ecological data. They comment that newer models proliferated in the mid-20th century and without the rejection of older theories, this lead to a *“collective scientific stagnation”*. The resurgence in SAD investigations in the last decade has been attributed to the increase in computer power, coupled with recent advances in statistical theory (Ugland et al. 2007; Saether et al. 2013; Chen et al. 2014; Huang et al. 2014; Hirao 2013; Matthews & Whittaker 2014; Chao et al. 2015; Chai et al. 2016; Shoemaker et al. 2016).

One of the simplest inferences from SADs, and one which has wide implications, pertains to the evenness of communities. A (hypothetical) perfectly even community will have equal number of individuals of each constituent species. Conversely, uneven communities will be characterized by a large range in abundance of the constituent species. Communities react to anthropogenic and environmental stressors not just by modifying species richness, but also their relative abundance and evenness (Stirling & Wilsey 2001; Wilsey et al. 2005; Wohlgemuth et al. 2016). Some studies have shown that evenness responds more rapidly to changing environments than species richness (Chapin et al. 2000; Hillbrand et al. 2008). Previous studies have yielded mixed results for the relationship between community evenness and species richness (Stirling & Wilsey 2001; Wilsey et al. 2005), although some theories predict a positive relationship due to increased synergistic inter-specific interactions leading to the accommodation of larger number of species and with more even abundance distribution (Hillbrand et al. 2008; Wohlgemuth et al. 2016).

The SAD of every single natural community that has been observed till date, without exception, is characterized by a few very abundant species and a relatively large number of rare species (McGill et al. 2007; Ulrich et al. 2010; Matthews & Whittaker 2014). Although this broad feature is universal, communities are known to differ in the exact shape of the curve. SAD models essentially focus on capturing this change in shape using as few parameters as possible, while being anchored to ecologically meaningful theoretical prescriptions (MacArthur 1947; Tokeshi 1993; Hubbell 2001; recent reviews in McGill et al. 2007 and Matthews & Whittaker 2014). Broadly, these can be categorized as either statistical (quantitatively descriptive!) or biological (mechanistic).

Biological models include the entire set of niche-apportionment models (MacArthur 1967; Tokeshi 1993) and are based on the implicit assumption that abundance of a species, at some level, reflects its ability to compete for limiting resources. It is expected that the nature of the ecosystem – simple-complex, variable-stable, successional-climax, diverse-depauperate, anthropogenic-environmental disturbance, etc – will impact the shape of the curve (Tokeshi 1993; Hurlbert 2004; Chase 2010; Brown 2014). The niche concept of Hutchinson (1957) has been very influential in the development of all biological, and many statistical, models of SAD (Magurran 2004).

Statistical models such as the Log-normal (Preston 1948), Log-series (Fisher 1943) and the more recent Gambin (Ugland et al. 2007) were proposed purely as a description of the data without any suggestion of an underlying biological process. Though, they have subsequently been identified with specific ecological processes (Magurran 2004). For example, more even communities or those in more productive environments are more likely to follow a Log-normal distribution; whereas, uneven communities or those in resource-limited environments are better approximated by the Log-series model. Ugland (2007) aimed to capture this transition in shape (along an environmental gradient) through the value of the Gambin alpha parameter: high values are characteristic of Log-normal shapes while low values correspond to Log-series profiles. The change in Gambin alpha has also been used to evaluate the relative importance of competition and environmental filtering in a community (Arellano et al. 2017).

Both biological and statistical models describe local communities as non-random subsets of species “sorted” or “filtered” from a regional pool, depending on their specific traits or niches (Hutchinson 1957; MacArthur 1957; Rominger et al. 2009). In contrast, the Neutral models emphasize the role of random dispersal in structuring local communities suggesting that species-specific traits, or niches, are not required for predicting community level processes (Caswell 1976; Hubbell 2001). Hubbell's Unified (Neutral) Theory of Biodiversity and Biogeography, which builds on the theory of Island Biogeography (MacArthur & Wilson 1967), has two basic assumptions: zero-sum dynamics, and a per capita ecological equivalence among all individuals of all species. Neutral models have been applied to a broad range of ecological and macroecological phenomena such as distance decay of similarity and species-area relationships, but have most often been used to study species abundance distributions (Matthews & Whittaker 2014). Hubbell’s proposition resulted in a heated debate (McGill 2003; Ricklefs 2003, 2006; Clark 2012; Matthews & Whittaker 2014) which was not surprising given that the per capita ecological equivalence challenged the Hutchinsonian niche concept that has been the cornerstone of traditional ecology for decades.

The subject has remained under-explored due to a variety of reasons. McGill et al. (2007) lists 27 different models for species abundance distributions (also, Matthews & Whittaker 2014). There are no clear prescriptions for *a-priori* choice of a specific model though the objectives of the study play a role in it. Obtaining large sets of abundance data is not easy, and many extant large data sets only provide presence-absence information. There is also a lack of consensus on the methodology of model fitting (least squares versus maximum likelihood), goodness of fit tests (asymptotic goodness-of-fit tests such as χ^2, linear regression using R^2, Monte-Carlo test and parametric boot-strapping) and the statistics employed for model comparisons (Akaike's information criterion (AIC), Bayesian methods and Deviance information criterion). The choice of statistical prescriptions can play a critical role, especially given the paucity of data, and can lead to erroneous and/or conflicting conclusions (Fisher et al. 1943; Gray 2005; Matthews & Whittaker 2014;

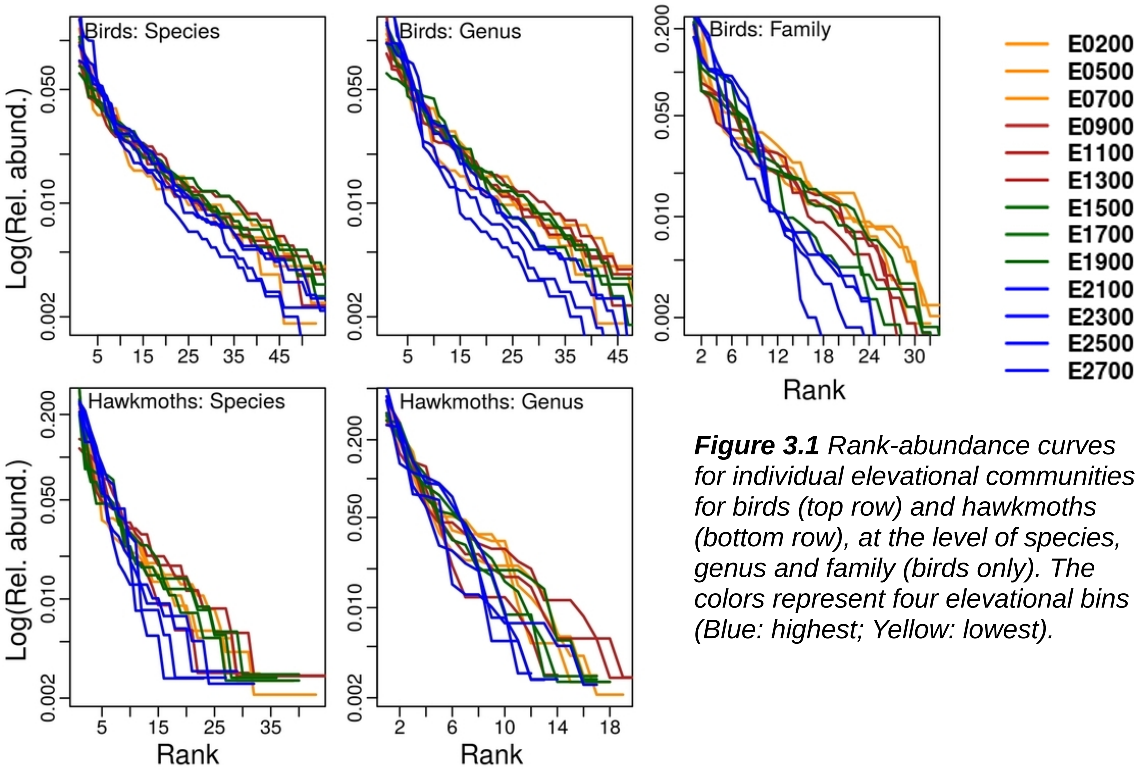


Figure 3.1 *Rank-abundance curves for individual elevational communities for birds (top row) and hawkmoths (bottom row), at the level of species, genus and family (birds only). The colors represent four elevational bins (Blue: highest; Yellow: lowest).*

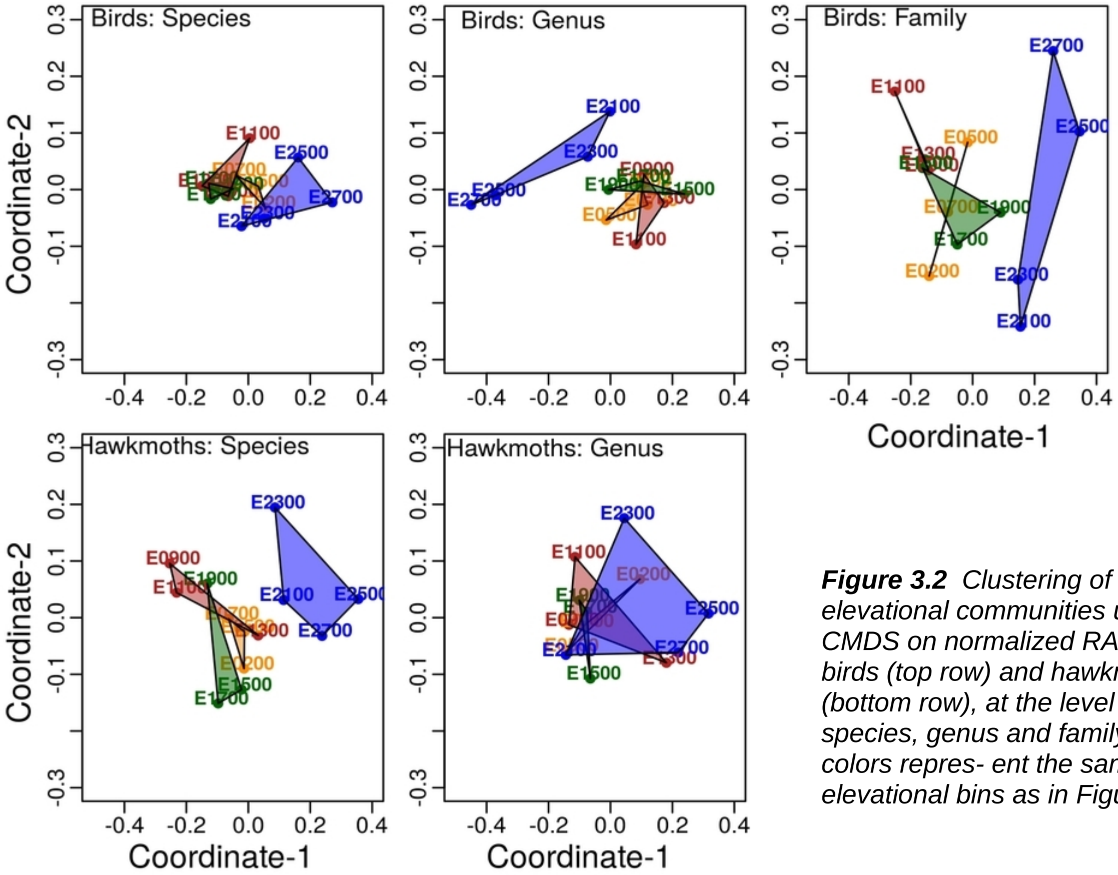


Figure 3.2 *Clustering of elevational communities using CMDS on normalized RACs, for birds (top row) and hawkmoths (bottom row), at the level of species, genus and family. The colors repres- ent the same four elevational bins as in Figure 3.1.*

Fattorini 2005; Etinenne & Olff 2004; Fattorini 2007).

3.2 Objectives

We carried out three exercises with the observed SADs of birds and hawkmoths:

1. identify the SAD model which best fits the observed data, and investigate its variation with taxon and elevation.
2. investigate the change in evenness of the community with taxon and elevation.
3. Identify the correlation of evenness with other community parameters (only species richness).

These exercises were carried out at different taxonomic levels including species, genus and (for birds only) family.

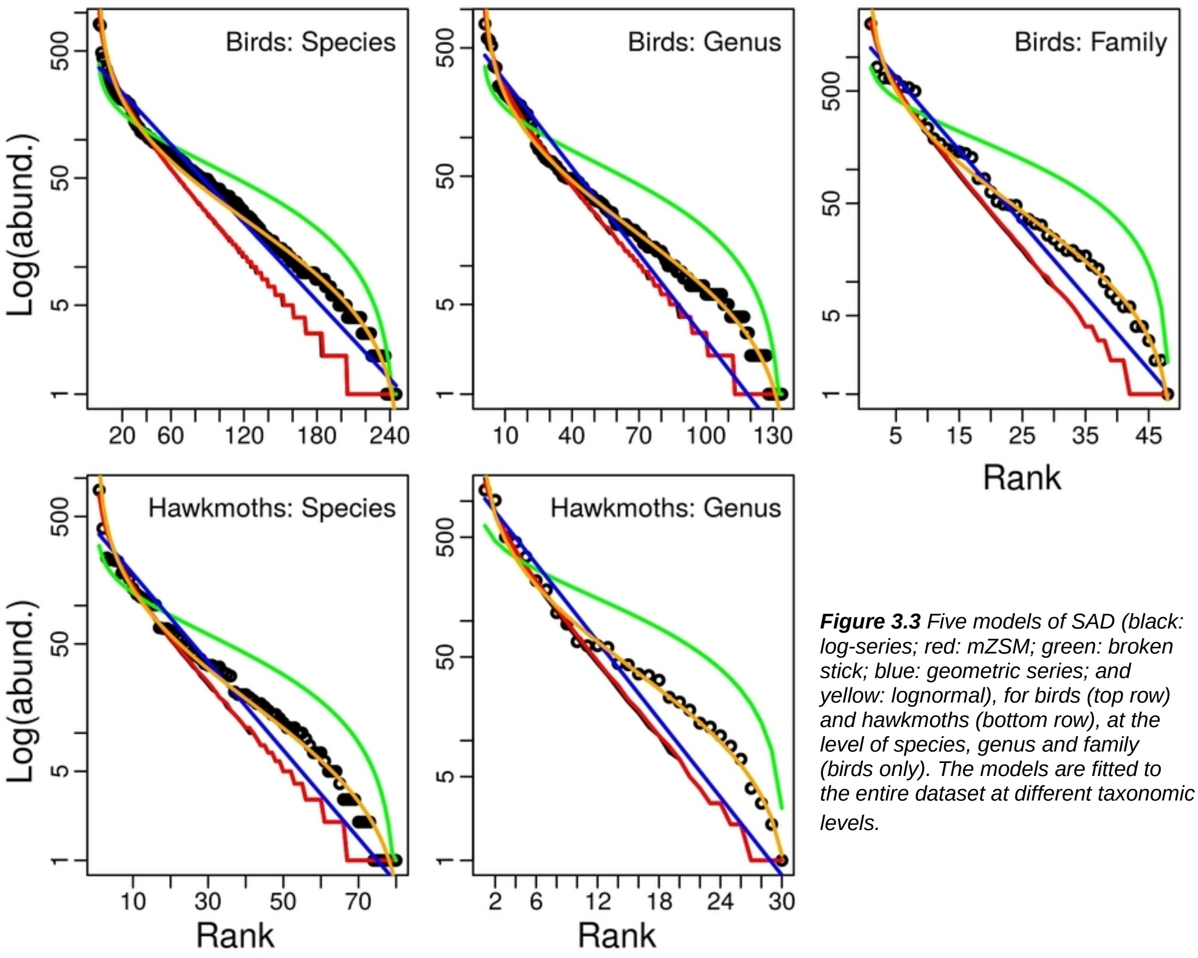


Figure 3.3 *Five models of SAD (black: log-series; red: mZSM; green: broken stick; blue: geometric series; and yellow: lognormal), for birds (top row) and hawkmoths (bottom row), at the level of species, genus and family (birds only). The models are fitted to the entire dataset at different taxonomic levels.*

In the absence of measures of environmental variables across the elevational gradient in our study site we did not develop any hypothesis prior to the field effort. Published studies have suggested that communities at higher elevations, where the environment is expected to be more variable day-to-day and year-to-year (Ulrich et al. 2016) and of lower productivity (Arellano et al. 2017), are better approximated by RACs with a steeper slope (i.e. more uneven abundances of species); that the log-series would be a better fit than log-normal. In contrast, the less variable and more productive environment at lower elevations are expected to host a more even community.

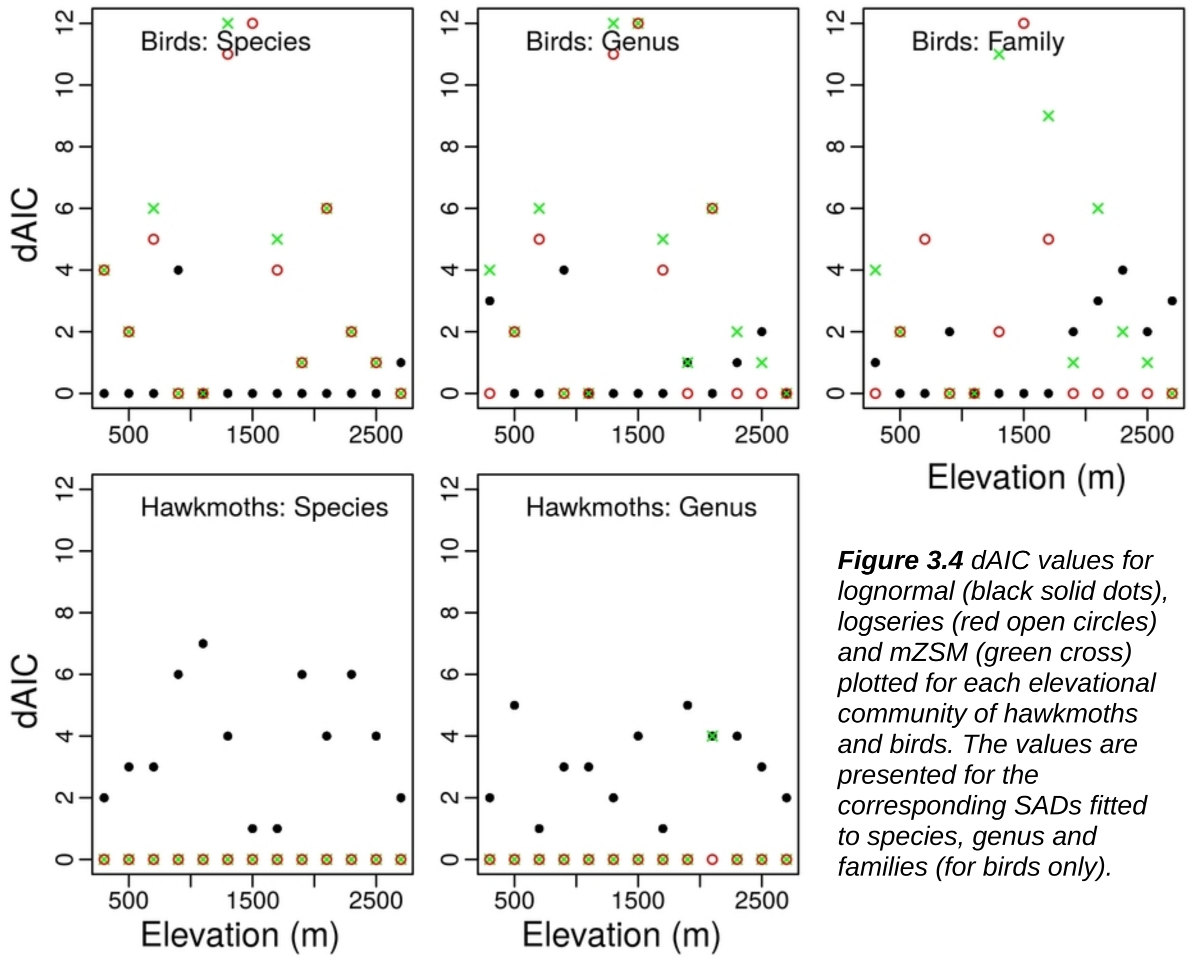


Figure 3.4 *dAIC values for lognormal (black solid dots), logseries (red open circles) and mZSM (green cross) plotted for each elevational community of hawkmoths and birds. The values are presented for the corresponding SADs fitted to species, genus and families (for birds only).*

3.3 Analysis and Results

Figure 3.1 shows the RACs at different elevations for birds and hawkmoths, separately at the level of species, genus and family (only for birds). The RACs at the genus and family level are based on the number of individuals belonging to that class. It is clear from the figure, even visually, that the highest elevations (blue color) have steeper RACs, for both hawkmoths and birds, and at all taxonomic levels.

Following Saeedghalati et al. (2017) we repeated all analyses using normalised RACs as well. We normalized the RACs using the *maxRank* normalization method (R package

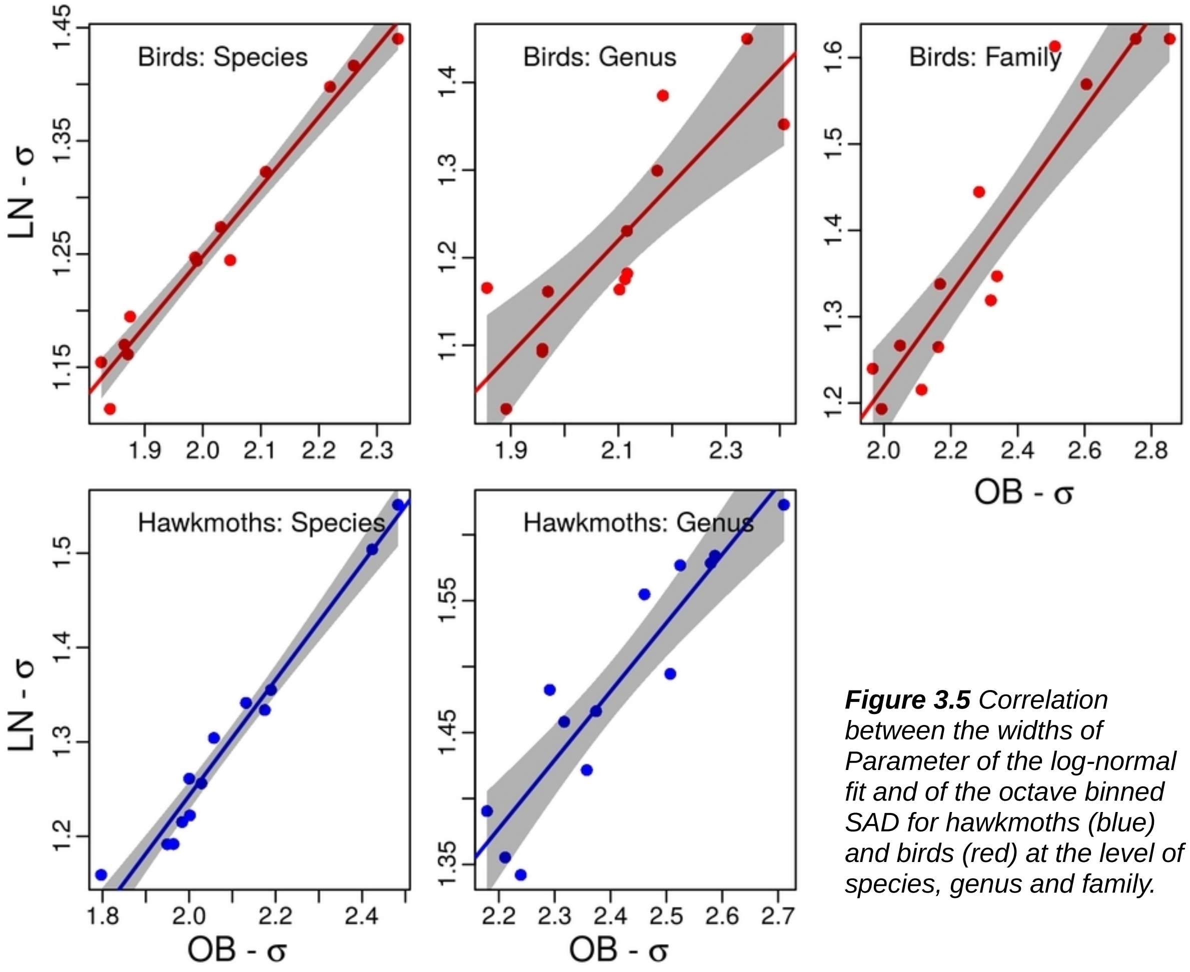


Figure 3.5 *Correlation between the widths of Parameter of the log-normal fit and of the octave binned SAD for hawkmoths (blue) and birds (red) at the level of species, genus and family.*

Fit	Slope	p value	r^2
Bird: Species	0.62 ± 0.03	< 0.001	0.97
Bird: Genus	0.65 ± 0.12	< 0.001	0.71
Bird: Family	0.54 ± 0.06	< 0.001	0.86
Hawkmoth: Species	0.61 ± 0.03	< 0.001	0.97
Hawkmoth: Genus	0.52 ± 0.06	< 0.001	0.85

RADanalalysis and 1000 sub-samples to determine the average and standard distribution of the rank abundance vector. Following their recommendation, we obtained Manhattan distance between elevational communities, obtained from normalized RACs. These were used in classical Multi Dimensional Scaling (cMDS). This ordination method is used to

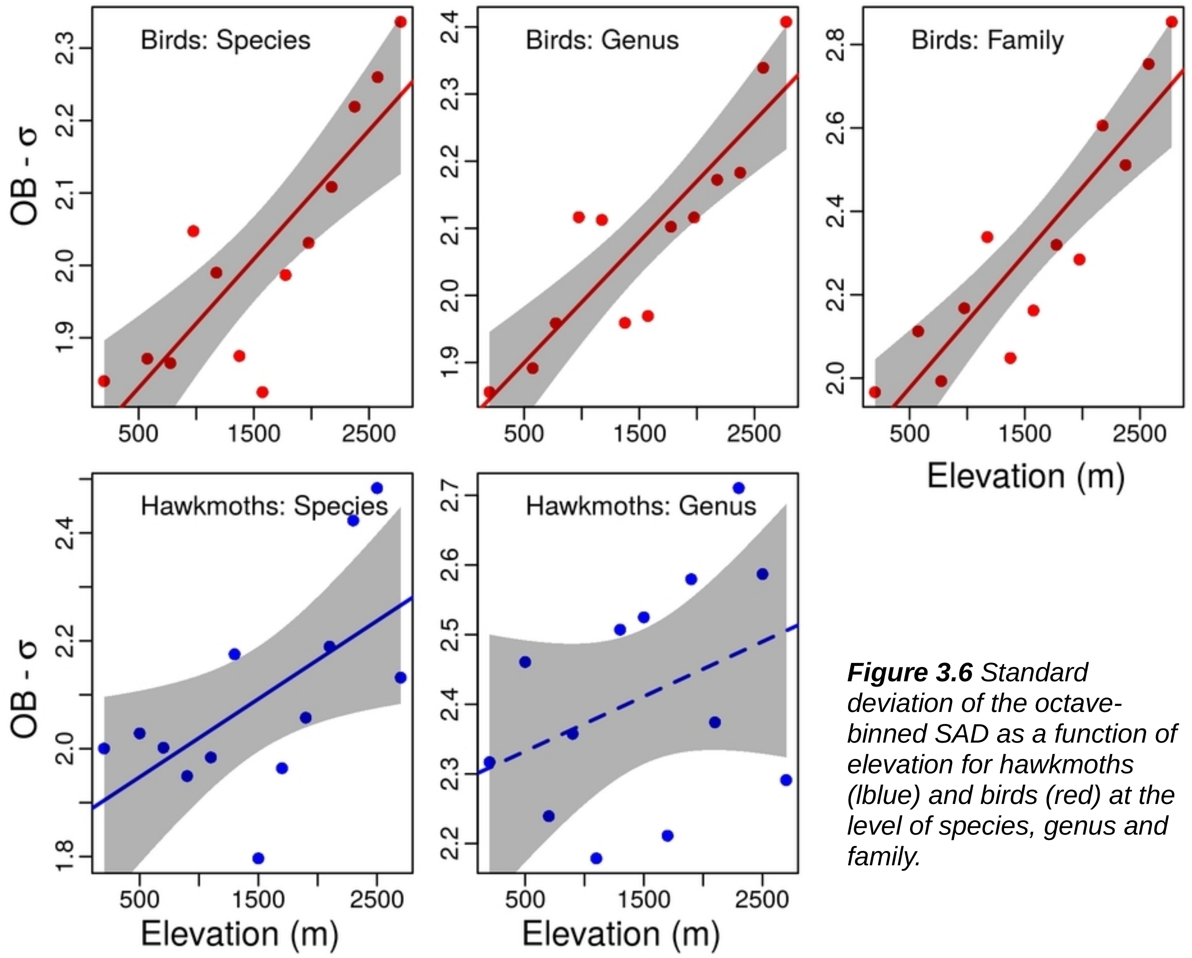


Figure 3.6 *Standard deviation of the octave-binned SAD as a function of elevation for hawkmoths (lblue) and birds (red) at the level of species, genus and family.*

Fit	Slope	p value	r^2
Bird: Species	1.78 ± 0.35	< 0.001	0.68
Bird: Genus	1.80 ± 0.29	< 0.001	0.76
Bird: Family	3.21 ± 0.48	< 0.001	0.79
Hawkmoth: Species	1.45 ± 0.58	0.030	0.30
Hawkmoth: Genus	0.79 ± 0.06	0.201	0.07

depict the results of the Manhattan distances in a graphical and visually easy manner to facilitate the detection of any observed elevational clusters. The cMDS plots are shown in Figure 3.2. Elevational communities, except for the highest, are all clustered close to each other. We fitted 5 of the most commonly used models to our data using the R package

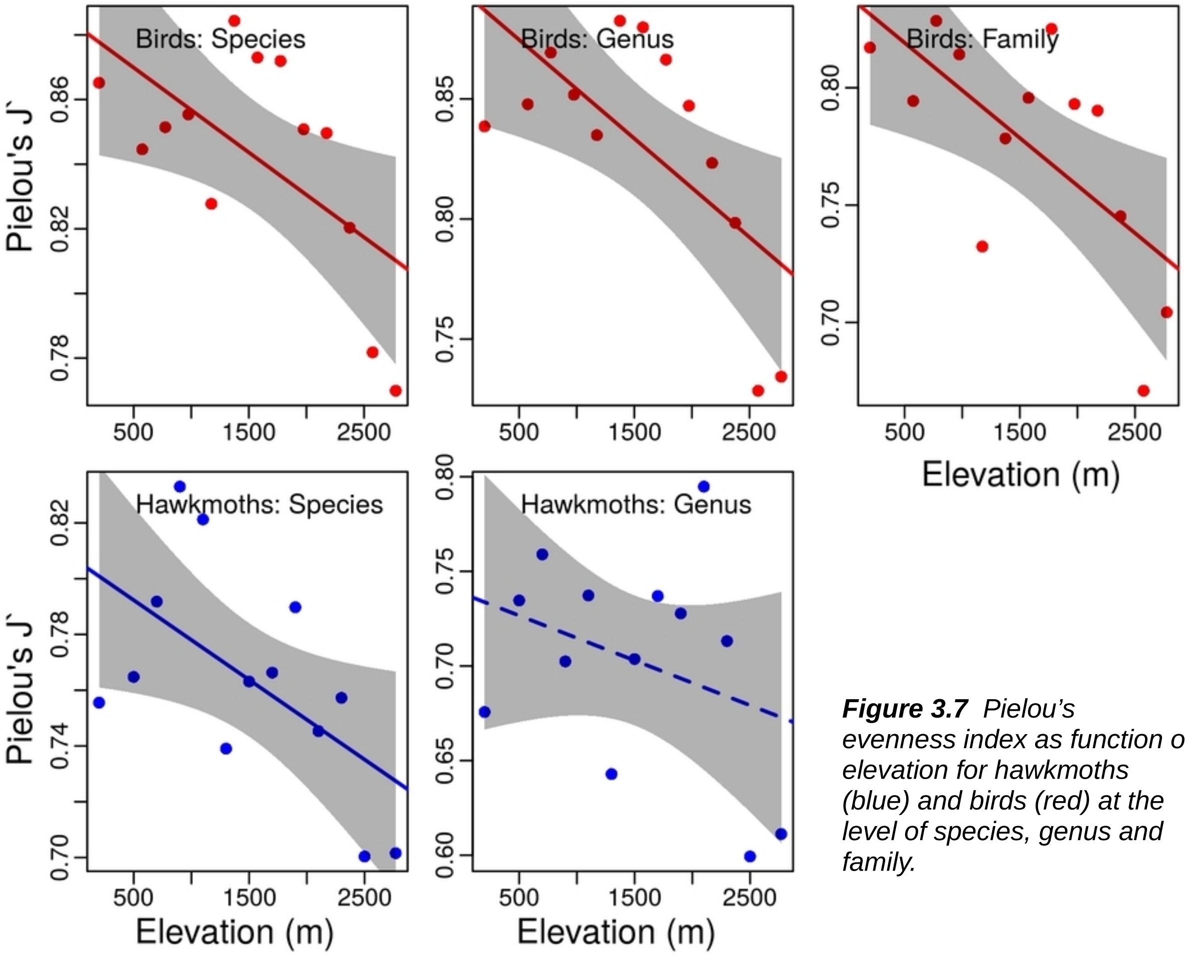


Figure 3.7 *Pielou's evenness index as function of elevation for hawkmoths (blue) and birds (red) at the level of species, genus and family.*

Fit	Slope	p value	r^2
Bird: Species	-2.62 ± 1.02	0.025	0.32
Bird: Genus	-4.11 ± 1.40	0.014	0.38
Bird: Family	-4.05 ± 1.36	0.012	0.39
Hawkmoth: Species	-2.86 ± 1.20	0.036	0.28
Hawkmoth: Genus	-2.37 ± 2.03	0.267	0.03

sads and the maximum likelihood criterion (Prado et al. 2014): the most-even broken stick (MacArthur 1957), Log-normal (Preston 1948), Log-series (Fisher et al. 1943), Zero-sum-multinomial (Hubbell 2001) and the least-even Geometric-series (Motomura 1932). Model comparisons were made using Akaike's information criterion (AIC) instead of other metrics

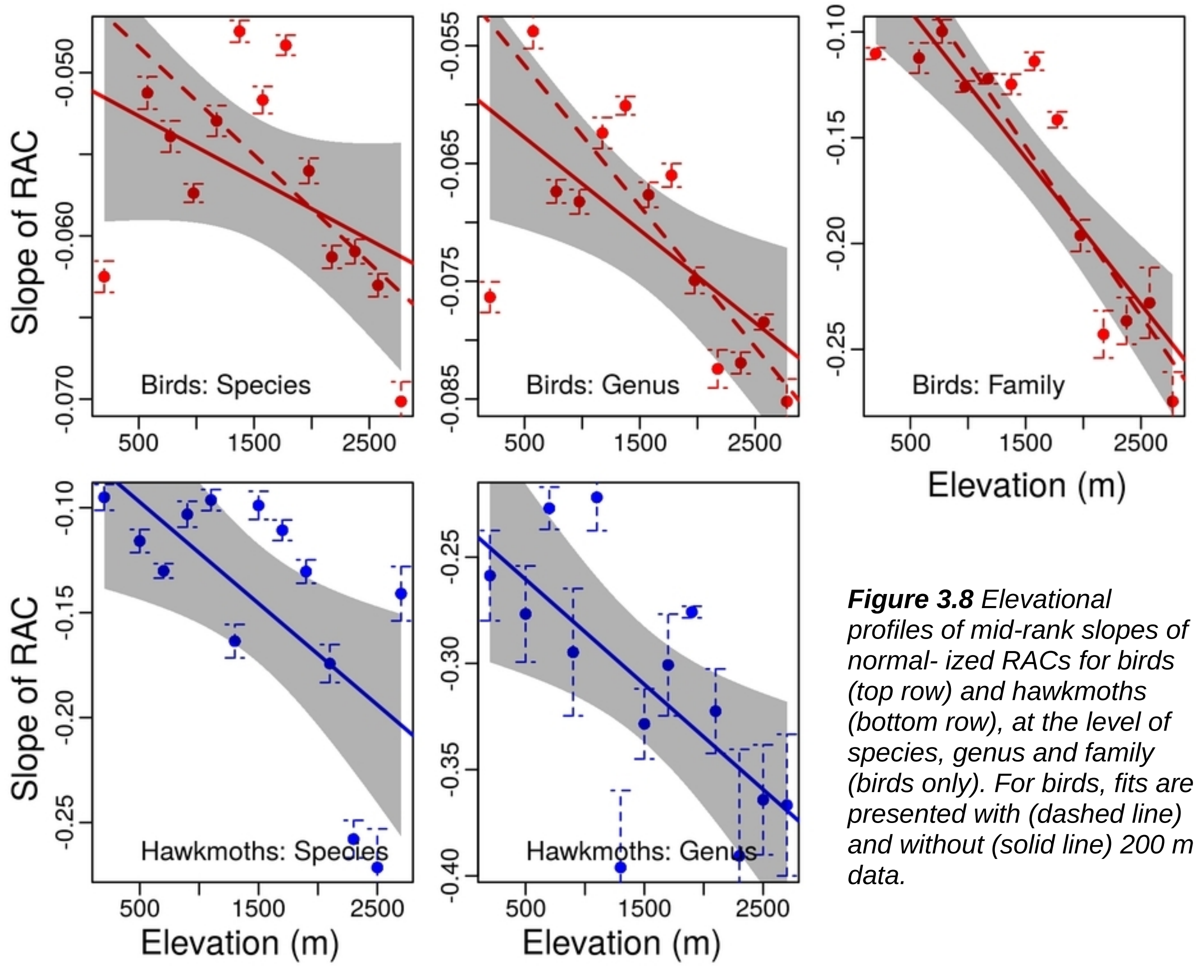


Figure 3.8 *Elevational profiles of mid-rank slopes of normal- ized RACs for birds (top row) and hawkmoths (bottom row), at the level of species, genus and family (birds only). For birds, fits are presented with (dashed line) and without (solid line) 200 m data.*

Fit	**Slope x 10^{-5}**	**p value**	**r^2**
Bird: Species (with 200 m)	-0.38 ± 0.21	0.11	0.14
Bird: Species (without 200 m)	-0.66 ± 0.20	< 0.01	0.46
Bird: Genus	-0.79 ± 2.70	0.01	0.38
Bird: Family	-6.92 ± 1.05	< 0.01	0.78
Hawkmoth: Species	-4.83 ± 1.69	0.02	0.37
Hawkmoth: Genus	-4.94 ± 1.63	0.01	0.41

such as Chi-square or correlation parameters (e.g.Matthews et al. 2014). The 5 models were fitted to the regional data set of N = 4,731 for hawkmoths and N = 15,746 birds (Figure 3.3), as well as to individual elevational communities. We applied the “species” abundance distribution models to higher taxonomic levels – genera and families – as well

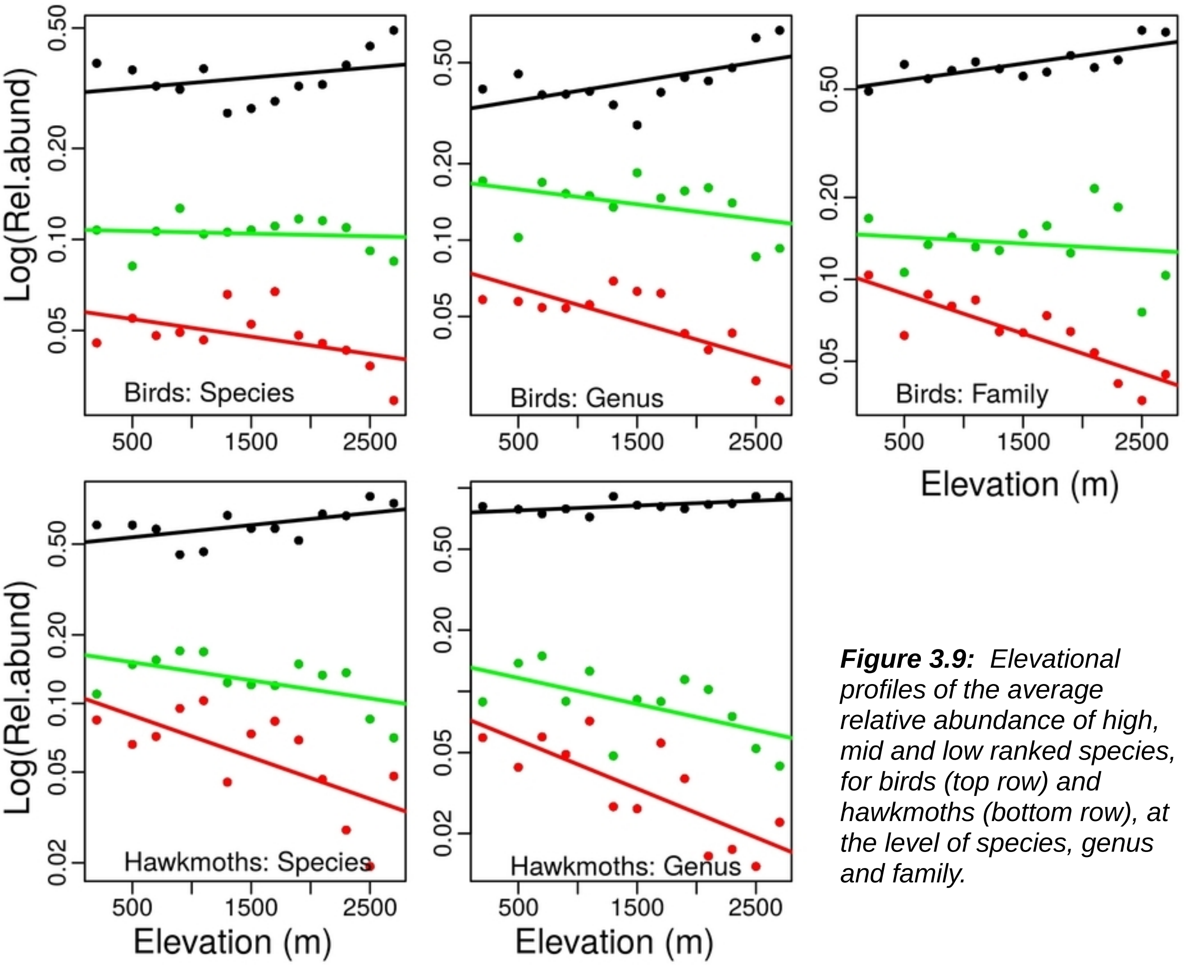


Figure 3.9: *Elevational profiles of the average relative abundance of high, mid and low ranked species, for birds (top row) and hawkmoths (bottom row), at the level of species, genus and family.*

Fit		**Slope x 10^{-5}**	**p value**	**r^2**	**Ranks**
Hawkmoth: Species	High	6.71 ± 2.59	0.025	0.32	1-5
	Mid	-2.17 ± 0.94	0.041	0.27	8-12
	Low	-2.12 ± 0.71	0.012	0.40	15-20
Hawkmoth: Genus	High	3.04 ± 2.34	0.219	0.05	1-5
	Mid	-0.11 ± 1.53	0.941	-0.09	7-10
	Low	-0.94 ± 0.54	0.110	0.15	11-13
Bird: Species	High	2.98 ± 1.99	0.162	0.09	1-5
	Mid	-0.46 ± 0.40	0.280	0.02	15-20
	Low	-0.46 ± 0.28	0.130	0.12	30-35
Bird: Genus	High	-8.41 ± 2.86	0.013	0.39	1-5
	Mid	-1.93 ± 0.88	0.051	0.24	10-15
	Low	-1.27 ± 0.32	< 0.005	0.56	25-30
Bird: Family	High	6.33 ± 2.38	0.022	0.34	1-5
	Mid	-1.73 ± 1.26	0.197	0.06	7-10
	Low	-2.56 ± 0.37	< 0.001	0.79	11-13

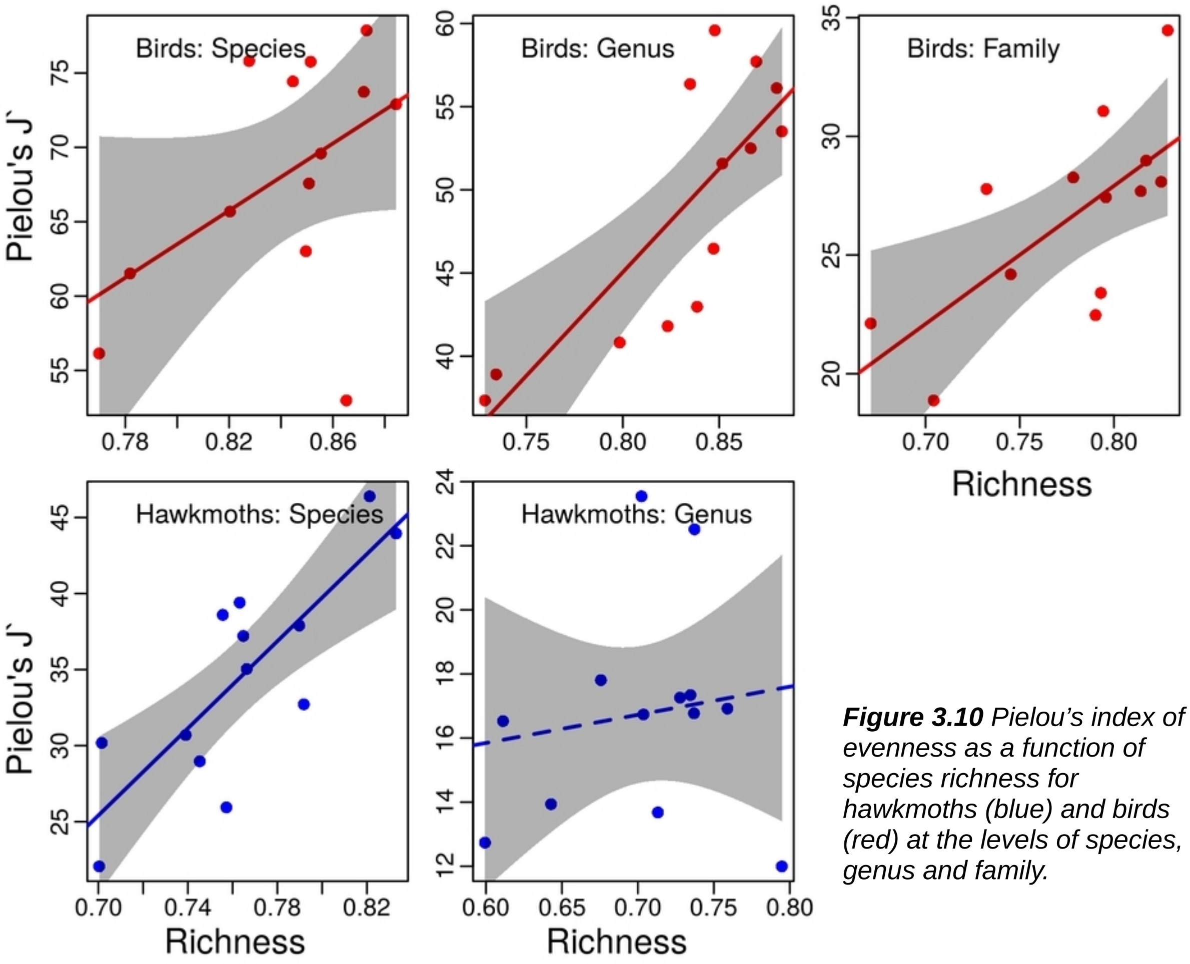


Figure 3.10 *Pielou's index of evenness as a function of species richness for hawkmoths (blue) and birds (red) at the levels of species, genus and family.*

Fit	Slope x 10^{-2}	p value	r^2
Bird: Species (with 200 m)	0.21 ± 0..11	0.09	0.17
Bird: Species (without 200 m)	0.39 ± 0.11	< 0.01	0.53
Bird: Genus	0.51 ± 0.12	< 0.01	0.60
Bird: Family	0.80 ± 0.26	0.01	0.41
Hawkmoth: Species	0.45 ± 0.10	< 0.01	0.62
Hawkmoth: Genus	0.25 ± 0.50	0.63	-0.07

(e.g. Stark et al. 2003). dAIC values of the fit in Figure 3.4 show that Log-series and mZSM (Neutral theory) models were the best fit for all hawkmoth communities at both species and genus level. Birds are a more mixed bag with the Log-normal dominating the communities. It is to be noted that the Log-series is a limiting case of mZSM, and the

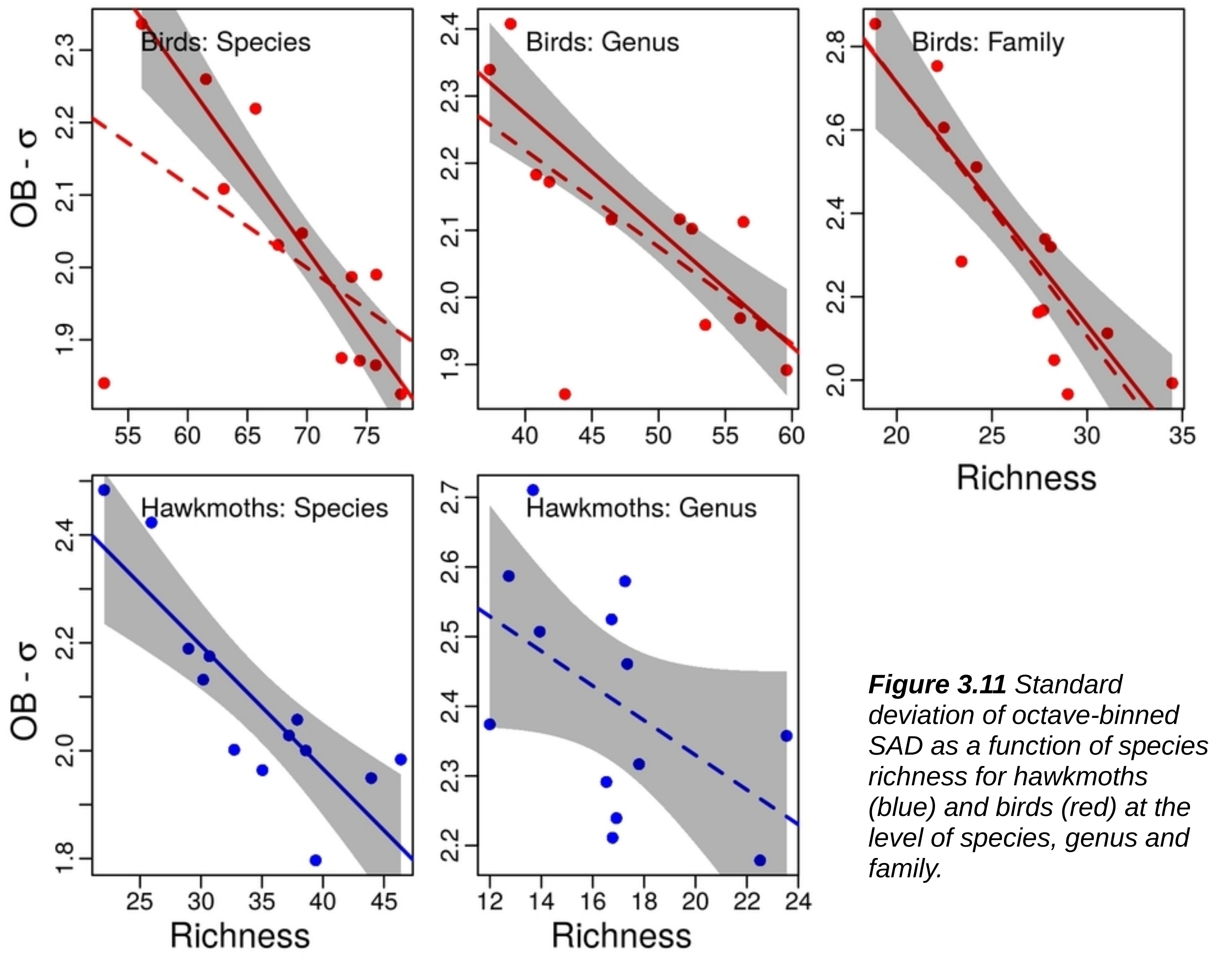


Figure 3.11 *Standard deviation of octave-binned SAD as a function of species richness for hawkmoths (blue) and birds (red) at the level of species, genus and family.*

Fit	Slope x 10^{-2}	p value	r^2
Bird: Species (with 200 m)	-1.14 ± 0..54	0.062	0.22
Bird: Species (without 200 m)	-2.31 ± 0.29	< 0.001	0.85
Bird: Genus	-1.44 ± 0.46	< 0.005	0.42
Bird: Family	-6.08 ± 0.98	< 0.001	0.76
Hawkmoth: Species	-2.29 ± 0.45	< 0.001	0.67
Hawkmoth: Genus	-2.49 ± 1.26	0.074	0.20

parameters of the two models converge as sample size increases. We investigated the evenness of communities using several measures: (i) the slope of the rank abundance curve, (ii) width of the fitted Log-normal function (Magurran 2004), (iii) width of the octave-binned SAD, and (iv) Pielou's index of evenness (Pielou 1966). Overall the Log-normal was the best fit for the pooled (i.e. regional) dataset across all three investigated taxonomic levels (Figure 3.3). Therefore, we used the fitted parameter, σ of the Log-normal model (LN-σ) to compare model-based evenness across all communities. We also estimated model-independent evenness using the standard deviation of the octave-binned SAD (OB-σ), i.e. without fitting any model. In both these cases a higher value of dispersion of the distribution would correspond to a more uneven community. Figure 3.5 shows the strong correlation between LN-σ and OB-σ. Figure 3.6 shows a clear trend of increasing unevenness with elevation. We also estimated evenness using Pielou’s index for evenness (J`) which is mathematically equal to the ratio of Shannon diversity index (H`) and the maximum possible value of H`. Value of J` lies between 0 (low evenness) and 1 (high evenness – equal abundance of all species). Figure 3.7 shows that Pielou's index of community evenness reducing with elevation. The three indices of evenness (width of fitted log-normal, width of octave binned SAD and Pielou’s index of evenness) allow us to infer evenness in a model-independent and a model dependent manner. Since in general, Log-normal was a good fit to all elevational communities, using it’s parameter as an index of evenness is justified. Hwever, since this index shows a similar trend with elevaation, as does the Pielou’s index (which is model-independent) further adds to the confidence in the observed pattern.

Figure 3.8 shows a plot of the middle-rank slopes of normalized RAC versus elevation, calculated from the inner 70% of the ranks (10th – 85th percentile). This approximately corresponds to the ±1 standard deviation of a normal distribution. For birds, fits are presented for data with and without 200 m elevation. The fits for the unnormalised RAC data were similar. The plots show a significant steepening of slope with elevation.

We carried out a similar analyses for the three most speciose bird families to facilitate a direct comparison with the hawkmoths: *Leiothrichidae* = 26 species, *Muscicapidae* = 26 species and *Picidae* = 14 species. The presence of very few species in these families at the lowest elevations precluded any meaningful comparison with hawkmoths.

We also calculated the average relative abundance in 3 different rank regimes. These ranks were determined by the lowest number of taxonomic units in an elevational community for each taxon. These are plotted against elevation in Figure 3.9. In both birds and hawkmoths, the relative abundances of the dominant species (high ranks) increased somewhat with elevation. The fraction of the middle and especially the lower ranks decreased with elevation.

Figures 3.10 and 3.11 show plots of Pielou's index of evenness and OB-σ against rarefied species richness, respectively. Both show that evenness increases with species richness. Gambin α parameter showed no pattern with elevation, which essentially meant the lack of a trend from Log-normal to Log-series across the elevations. On the other hand we have enough sample size in each community to actually determine the best fit using dAIC, as previously shown. Therefore, we have not explored the Gambin parameter any further.

3.4 Discussion

Models of SAD are directly related to processes of community assembly (MacArthur 1957; Fisher 1943; Preston 1948; Tokeshi 1994; Hubbell 2001; McGill et al. 2007; Chen et al. 2012). Theoretical as well as empirical studies use these models to investigate the relative importance of niche vs neutral mechanisms (Hubbell 2001; Magurran & Henderson 2003; Sugihara et al. 2003; Volkov et al. 2005, 2007; Sizling et al. 2009; Chave et al. 2002; Dumbrell et al. 2010; Harpole & Tilman 2006; Cheng et al. 2012).

Investigations of SADs along environmental gradients have typically either fit a model and tested the change of model parameters (Ulrich et al. 2016; Arellano et al. 2017), or confined themselves to largely qualitative descriptions of the change in RACs between different sites (e.g. Whittaker 1965; James & Rathbun 1981; Ellis & Betts 2011). The steepness (slope) of the rank abundance curve has been used as an alternative to alpha diversity or evenness indices to characterise environmental gradients (Foster & Dunstan 2010; Chan et al. 2015; Drake 2014). Unlike beta diversity, SADs can also be used to demonstrate the response of a community pattern along an environmental gradient even when the different communities have no species in common.

3.4.1 Commonality across taxonomic levels

Models of SADs are essentially constructed from the process governing niche partitioning. In this context it makes sense to investigate SADs using functional guilds of species, e.g. *Ctenidae* family of spiders (Uetz 1976); fruit feeding functional group of butterflies (DeVries 1997); dung beetles of subfamily *Scarabaeinae* (Escobar 2004); arbuscular mycorrhizal fungi of phylum *Glomeromycota* in Dumbrell 2010b; functional guilds of C3 or C4 pathways (Harpole et al. 2006). But most studies have not constrained themselves along such a niche axis and have generally specified their study set by taxonomic levels (and not functional guilds). Abundance distributions at the species level have received much more attention than at other taxonomic levels (for analysis at genus and family levels see, for example, Warwick 1988a; Somerfield & Clarke 1995; Olsgard et al. 1998; Olsgard & Somerfield 2000; Stark et al. 2003). The latter are restricted to microbial groups where species delineation is problematic.

The advantages of limiting such analyses to taxonomic levels higher than a species is evident. The tribe of taxonomists is dwindling across the world. A survey of 2,938 taxonomists with expertise across all major domains of life revealed that synonyms are a major problem at the species level, but much less so at higher taxonomic levels (Mora et al. 2011). Enumerating abundances of all organisms down to a fine level of taxonomic resolution takes considerable resources and expertise. Additionally, the larger sample size at higher taxonomic levels makes for more robust inference. But, it remains to be shown that patterns in relative abundance distributions are the same whether at the level of species, genus or family. Our results show that all measures of evenness vary with elevation in a similar manner for both birds and hawkmoths at the level of species, genus and families (birds only).

3.4.2 Models of SAD

The appropriateness of the fitting model is an issue while deriving parameters from a SAD. *A-priori* there is no reason to select one theoretical model over the other, and the best fit to the data decides the model used; and this can change from study to study. Most observed

SADs can be fit by either the Log-normal or Log-series, independent of the mechanistic explanation. Log-normals are thought to represent stable and closed communities while Log-series should dominate in open, dispersal-dominated communities (Ulrich et al 2016).

A comparison of the 5 most commonly used models showed that within each elevational community the Zero-sum multinomial model provided the best fit for hawkmoths, while for birds the Log-normal was the best fit for the largest fraction of communities (Figures 3.4). This difference may even be related to the larger number of species from many families in birds (Ulrich et al. 2016). Interestingly, the Log-normal was the best fit by far for the regional SAD, i.e. by combining all elevations, for both birds and hawkmoths (Figure 3.3).

Whittaker (1975) and Hubbell (1979) initiated the idea that plant community SADs change along productivity gradients, with increasing Log-normality at higher productivity. Log-series was linked to severe, unstable or disturbed (Gray 1979; Death 1996; Maire et al. 2012) environments of lower productivity. Although our data do not contain direct information on forest conditions, our results do not corroborate these hypotheses, if low elevations are considered more productive and stable. Arellano et al. (2017) used the metric Gambin alpha to discriminate between Log-series (lower alpha) and Log-normal (higher alpha). We did not see any trend of Gambin alpha with elevation.

While Figure 3.1 suggests a gradual change in the shape from the lowest to the highest elevations Figure 3.2 clearly shows that the highest elevations cluster separately from the rest.

3.4.3 Evenness of abundance

Studies of patterns in diversity across elevational gradients mostly focus on species richness, ignoring community evenness (but see Graham 1983; Fauth et al. 1989; Wang et al. 2011; Wang et al. 2017). Recent studies have shown that richness and evenness might respond differently to similar changes in the environment (Wang et al. 2017). In fact, community evenness has been shown to be more sensitive to environmental changes than species diversity (Wilsey & Potvin 2000; Wittebolle et al. 2009). A change in community dominance may play a more important role in altering the functional properties of a community which in turn impacts ecosystem processes and functioning (Goldbold et al. 2011; Caliman et al. 2011; Wohlgemuth et al. 2017).

Most studies have shown a strong decline in evenness with latitude which is consistent with the hypothesis that stable, more productive habitats contain more even communities with more equitable abundance distribution (Ulrich et al 2016). A meta-analysis by Zhang et al. (2016) demonstrated a positive correlation between evenness and productivity, while Silva et al. (2010) found evenness positively correlated with decreased climatic seasonality. Macro-detritivore diversity showed a marked decrease in evenness towards late succession (Schrama et al. 2017). The passerine bird community at high elevations had the highest species richness but the lowest evenness (He et al. 2017). The reasons for such observations can be linked to either the niche or neutral dynamics. Neutral models of community assembly link steep species dominance curves to limited dispersal (Zillio & Condit 2007), while niche-based approaches involve pronounced differences in competitive strength with regard to a few limiting resources (Tokeshi 1993).

All the four metrics that we used to quantify community evenness show that both hawkmoth and bird communities become more uneven at higher elevations. We have also shown that the standard deviation of the octave-binned SAD, a model-independent parameter, shows the same trend as the standard deviation from a Log-normal fit (Figure 3.5); i.e. we may be able to use the model independent parameter even in cases where the Log-normal is not an appropriate model. Figure 3.9 also shows an increase in the abundance of the highest ranks, with a corresponding decrease in the rarest species – again a sign of increasing unevenness.

The relationship between (species) richness and evenness (RRE) is predicted to be positive such that species poor communities will be dominated by a few dominant species whereas species rich communities will have more equitable abundances reflecting the higher competitive strategies (Veech et al. 2003; Wang et al. 2017). However, as some recent reviews suggest, observed RREs do not follow a consistent pattern. Soininen et al.

(2012) in their meta-analysis of aquatic datasets showed that only 71 out of 229 datasets (31%) showed significant relationships between richness and evenness, indicating that richness and evenness reflect independent components of biodiversity. It has been suggested that a positive RRE may be driven by organismal traits such as body size and dispersal ability (Reynolds 2006, Wang et al. 2017). Pielou's index has been criticised for its dependence on species diversity (e.g. Smith & Wilson 1996), and this is seen in our data as well in Figure 3.10. However Jost (2010) has demonstrated that J' is an excellent measure of "relative" evenness across communities. We see from Figure 3.11 that the positive relationship between evenness and species richness is seen in OB-σ as well. It is to be noted here that OB-σ was calculated from normalized RACs (Saeedghalati et al. 2017), which compensates for species richness across all RACs being compared.

3.5 Summary

1. The SAD of regional pool for both hawkmoths and birds are well fit by a Log-normal distribution. However, hawkmoth communities at individual elevations all follow the profiles predicted by Log-series or the zero-sum multinomial. The data is more mixed for birds.
2. We have shown that evenness of species abundances within a community decreases with elevation for hawkmoth and birds along a 2600 m elevational gradient. This result is consistent across multiple metrics of evenness including one which is model independent. This is consistent with previous findings and hypothesis that stable, more productive ecosystems with high species richness have more even communities, while unstable, variable and less productive environments are characterised by uneven communities.
3. Evenness was strongly correlated with taxonomic richness indicating higher niche partitioning and competitive interactions at low elevations.
4. The above results are seen at the level of species, genera and the families (investigated only for birds) indicating strong and consistent underlying principals operative across hierarchical taxonomic classes.

Chapter Four

Elevational Patterns in Alpha and Beta Diversity

4.1 Introduction

Elevational gradients exhibit dramatic changes in many environmental variables over short distances. Multiple mountains across the globe provide replicate systems with varying climatic, spatial, historical and biotic settings. The differences in the response of ecological communities to these factors forms the basis for assessing the relative importance of different causative factors. This also makes studies of elevational patterns in species richness important for understanding the response of ecological communities to global climate change (Parmesan 2006).

While conceptually simple, actual investigations of elevational gradients of diversity continue to challenge investigators (Szewczyk & McCain 2016), almost a century after it was first attempted. A global analysis of elevational gradients in diversity of birds shows four patterns in nearly equal frequency: monotonic decline, low-elevation plateau followed by a decline, low-elevation plateau with a mid-elevation peak, and (unimodal) mid-elevation peak (McCain et al. 2009). Ant diversity patterns' commonly exhibit a monotonic decrease, low-elevation plateau followed by a decline and a mid-elevation peak (Szewczyk & McCain 2016). Equal support was found for monotonic decrease and mid-elevation peaks in a global meta-analysis of elevational species richness patterns of bats (McCain 2007). An investigation of Lepidopteran family *Sphingidae* along nine tropical transects, using presence-absence records and range interpolations, revealed hump-shaped distribution at all locations, however the diversity peak varied amongst locations (Beck & Kitching 2009). Separating the “universal” determinants of diversity patterns from the idiosyncrasies of each taxon and locality has been a focus of this field during the last decade (Rahbek 2005; McCain 2007; McCain 2009; McCain & Grytnes 2010; Szewczyk & McCain 2016; Dong et al. 2017; Xu et al. 2017).

No single measure of diversity adequately quantifies all its different properties such as species richness, evenness in abundances, range sizes and overlap, turnover, vulnerability, functional trait diversity, phylogenetic diversity, etc (Colwell & Coddington 1994; Rosenzweig 1995; Southwood & Henderson 2000; Hawkins 2001; Magurran 2004; Hayek & Buzas 2010). The most appropriate metric is not always obvious and would ultimately depend on the specific objectives, but this ability to examine diversity in different ways helps in a better understanding of how ecosystems function (Magurran 2010). The focus of the current chapter is on the taxonomic diversity of communities of hawkmoths and birds along an east-Himalayan elevational gradient spanning 2600 m.

The diversity metric (whether taxonomic, phylogenetic or functional) may be evaluated at three different geographical scales, though there is no specific (numerical) spatial scale value associated with the three. Whittaker (1972) coined the terms *alpha, beta* and *gamma* diversity for the local, inter-community and regional/large geographic scales. For the current study the alpha diversity of any elevation was calculated from all individuals which were recorded at screens (or transects) at one or a few locations within an elevational band. Beta diversity refers to the change in community composition between two elevational bands. We have not dealt with Gamma (or regional) diversity in this study.

4.1.1 Alpha diversity

Alpha diversity is widely described in terms of two related but different terms, *species richness* and *species diversity*. Species richness is the total number of species observed or estimated (Colwell and Coddington 1994; Magurran 2004) and is the simplest measure of diversity. At its most basic it is a compilation of the presence-absence data for species in an area (a checklist). Building upon this, many workers have developed sophisticated estimators of *true* species richness from the observed value (Burnham and Anderson 1976; Chao 1984; for a review see Colwell and Coddington 1994 and Magurran 2004). Brose et al. (2003) have provided a comparative analysis on the efficacy and robustness of different estimators. Species diversity (index) incorporates species richness and their relative abundances into a single statistic. However, this index often does not reflect the actual number of species in the community.

Estimators of species richness fall into the parametric and non-parametric categories. Non-parametric estimators, which are independent of the underlying distribution of species abundance, are known to be more robust to differences in sample sizes, species richness and evenness and have performed better and yielded values very close to the true species richness in simulated datasets (Burnham and Overton 1978, 1979; Chao 1987; Palmer 1990; Colwell and Coddington 1994; Magurran 2004; Brose 2003).

Species diversity indices can be either a parameter of a species abundance model (e.g. Fisher’s alpha; Fisher 1943), or a simple measure that makes no assumption about the underlying species abundance distribution (e.g. Simpson’s diversity index; Simpson 1949).

4.1.2 Beta diversity

Beta diversity quantifies the differences in species composition between sites (Whittaker 1972; Alahuhta et al. 2017). The diversity of the metrics of beta diversity is even more forbidding than that of alpha diversity with more than two dozen measures in use (Wolda 1981; Legendre & Anderson 1999; Koleff et al. 2003). They can be broadly classified into two categories: classical metrics (that use measures on alpha and gamma diversity to quantify beta), and multivariate measures based on distance matrices (Legendre et al. 2005; Anderson et al. 2011; Legendre & De Càceres 2013). There have been several detailed reviews of the concepts, metrics and their performance in the last two decades (Legendre and Legendre 1998; Vellend 2001; Koleff et al. 2003; Jurasinski et al. 2009; Tuomisto 2010; Magurran 2011)

The Bray-Curtis index of similarity (Bray & Curtis, 1957) was one of the first metrics to incorporate differences in species abundances (compared to previous metrics based on presence/absence data) and is still popular today (Blake 2007; Kraft et al. 2011; Zinger et al. 2011; Myers et al. 2013; Ashton et al. 2016; Catano et al. 2017). It is a modified version of the popular Sørensen index that allows incorporation of species relative abundances and is sometimes called the quantitative Sørensen index. In a review on measures of beta diversity, Clarke and Warwick (2001) reported that the Bray-Curtis index was the only one meeting all of their six criteria: (a) the value should be 1 when two samples are identical; (b) value should be 0 when two samples have no species in common; (c) a change of measurement unit should not affect the value; (d) the value should not change when a species is added to or removed from a third sample; (e) addition of other localities should not change the dissimilarity values between the previous localities; and (f) the index should reflect differences in abundance (Clarke and Warwick 2001; Magurran 2004).

Beta diversity patterns along an elevational gradient can be approached in two ways. The first kind investigates the pattern in beta diversity along the elevational gradient, comprising questions like: Does the beta diversity pattern mimic the alpha diversity pattern? Is the pattern consistent for different taxa? Does the pattern mimic the latitudinal pattern? The second category of questions deal with the distance-decay of similarity; in this the attribute distance between the localities, whether elevational, geographic or environmental, is considered rather than the absolute value of the attribute. Distance-decay generally refers to the slope of the relationship between the similarity in species composition between two communities and the distance separating them. As the difference in elevation increases between the communities, so should their compositional difference. Distance-decay slope is affected by a large number of organismal traits such as the body-size, dispersal ability and niche width and is expected to be steeper for organisms with weaker dispersal ability and/or narrower niches (Alahuta et al. 2017). Questions raised by such analyses are: Is the slope of distance-decay plot significantly different across taxa? Is the difference (if any) in accordance with what we know about the dispersal abilities or niche breadth (specializations) of these two contrasting taxa?

Beta diversity can be partitioned into two additive components namely, species replacement (or turn-over) and community nestedness (or species loss) (Baselga, 2010, 2013). Causative mechanisms of species turnover can be related to both environmental filtering and competition (Melo et al. 2009; Kraft et al. 2011; Alahuta et al. 2017). Species nestedness is usually associated with processes such as connectivity and environmental filters (Baselga 2010).

4.1.3 Correlates of Diversity

The processes responsible for elevational diversity patterns are still poorly understood. The many hypotheses proposed for the various observed patterns include geometric constraints (via the Mid-Domain Effect; MDE), temperature (via the Metabolic Theory of Ecology; MTE), area (via the Species-Area Relationship; SAR) and precipitation (via the elevational climate model; ECM), among others.

The geometric constraint model assumes that the elevational ranges of species are bounded by two hard limits beyond which species' ranges do not extend. Certain distributions of ranges will result in a maximum overlap towards the middle of the elevational range, known as the Mid-Domain Effect (**MDE;** Colwell & Hurtt 1994). Colwell and Hurtt (1994) proposed several models that simulate range size and randomise range placement within one-dimensional bounded geographical domains (e.g. an elevational gradient). Based entirely on stochastic processes these null models produce symmetrical curves with a mid-domain peak in species richness.Shuffling species ranges randomly has been criticized by some authors as species ranges are a result of important ecological interactions between species and the environment (Hawkins & Diniz-Filho 2002; Laurie & Silander 2002).

The metabolic theory of energy (**MTE;** Allen et al. 2007) proposes that biochemical reactions and metabolic rates, which depend on temperature, drive ecological and evolutionary processes and, hence, speciation may increase with temperature. Thus, temperature can directly influence richness independently of its impact on plant productivity. MTE was shown to be a strong predictor of elevational richness patterns in reptiles (McCain 2010), ants (Sanders et al. 2007; McCain & Szewczyk 2016) and birds (McCain 2009). The MTE predicts a monotonic decline in diversity along an elevational gradient corresponding to an adiabatic lapse rate of ~0.6˚C per 100 m elevation.

The elevational climatic model **(ECM)** was proposed by McCain (2007) by identifying productivity as a correlate from a meta-analysis of elevational patterns of bat diversity. The model estimated productivity using a combination of temperature and precipitation. The ECM predicts unimodal diversity patterns on arid mountains and decreasing or low-plateau trends on humid mountains. On arid mountains, increased run-off from the summit and dry climate at the base renders the mid-elevations as zones of highest water availability, and hence maximum productivity. On wetter and more humid mountains temperature becomes the driving force and determines the diversity patterns by itself. The species area relationship (**SAR)** predicts a linear relationship between area and species richness (Rosenzweig 1995). Studies of elevational gradients in species richness fall into two categories: regional studies that summarize known distributions within a large geographical region typically encompassing a complete mountain range (Szewczyk &

McCain 2016), and local-scale studies based on a single transect survey scheme (Rahbek 1995, 2005; Romdal & Grytnes 2007). Area can have a direct or indirect effect in both cases. It should be noted that the relationship of area with elevation can be complex (Elsen & Tingley 2015).

4.2 Objectives

We have addressed the following questions in this chapter:

1. Comparison of the elevational pattern of alpha diversity of hawkmoths and birds using different metrics.
2. Correlations between alpha diversity and area (SAR), geometry (MDE), temperature (MTE) and precipitation (ECM) using linear and multivariate analyses
3. Comparison of elevational patterns of beta diversity for hawkmoths and birds
4. Partitioning of the beta diversity into turnover and nestedness components.

4.3 Analysis

4.3.1 Alpha diversity

We quantified alpha diversity using rarefied (observed) species richness, estimators of t*rue* species richness (Chao's and ACE), Fisher's diversity index (Fisher's alpha) and Simpson's diversity index (D) (Chao 1987; Chao & Lee 1992; Hurlbert 1971; Fisher 1943; Gini 1912; Simpson 1949). The same may be obtained from *R 3.3.1:* ***Vegan*** *2.2-3: specpool, rarefy, fisher.alpha and* ***Inext*** *2.0-12: ChaoSimpson.* There are no suitable (i.e. without high anthropogenic modification) and accessible areas in EWS below 200 m elevation. We sampled the moths in a degraded distant corner of EWS about 20 km from the 500 m location. We had to go a few more kilometres and across a major river valley for sampling birds at 200 m elevation. The diversity at 200 m is very low in our data, especially in birds. In fact, the diversity at 200 m is even lower than that at 2700 m. Therefore, we have presented results with and without the 200 m data.

There is also the issue of formal errors for the different metrics. The error bars on rarefied species richness is not straight-forward and by the nature of the procedure becomes zero at either end. Furthermore, the errors in different parts of the curve are correlated. We also suspect that the formal, formula-based errors on Fisher's alpha are much smaller than that from ecological stochasticity. Perhaps, this is why so few published studies actually report formal errors for diversity measures. Therefore, one can only estimate errors on parameter values from residuals obtained by fitting the data to a specific model.

Elevational profile of diversity broadly follow 4 shapes which may be quantified as follows: **(a)** monotonic decrease: fitted by a straight line with 2 parameters, **(b)** symmetric mid-elevation peak: inverted parabola with 3 parameters, **(c)** low elevation (asymmetric) peak: inverted parabola truncated toward low elevation, with 3 parameters, and **(d)** low plateau following by a monotonic decline. The last category may also be fitted by an inverted parabola except that the fitted peak would be much closer to zero elevation and the error bars on it would be larger. Therefore, the observed elevational profile can be assigned to one of the 4 shapes by fitting a straight line or a parabola. We emphasise here that the claim is not that these are the correct models for fitting; our prescription is just a quantitative discriminant instead of assigning one of the 4 shapes in a subjective manner.

4.3.2 Correlates of diversity

A. Mid-Domain Effect (MDE): The expected species richness profile was obtained by using *R 3.3.1: **rangemodelR** 1.0.1: rangemod1* which implements the simulations by Rahbek et al. (2007). This procedure preserves the empirical range size frequency distribution (RSFD; Colwell et al. 2004 and references therein). The regression of observed values on the expected (simulated) values, based on the average of 10,000 simulations, was used to estimate r^2 of the fit (Colwell et al., 2004; McCain, 2004).

B. Metabolic Theory of Energy (MTE): Temperature measurements for all elevations in the study region were obtained from *Aniruddha Marathe (ATREE, Bangalore)*.

C. Species-Area Relationship (SAR): The area in each elevational band was calculated using a digital elevation model of Arunachal Pradesh. Ideally, the area should be calculated inside a region within which the target taxon is panmictic. On the other hand panmixis will be a function of the vagility of a species within the taxon being studied. The problem is even more acute when dealing with a vast linear mountain system such as the

Himalayas. Many studies have dealt with area as a causative mechanism of elevational diversity profiles, yet few studies have justified the choice of a particular geographical extent for calculating the elevational area. Some studies (e.g. Szewczyk & McCain 2016) have used mountain ridges and major watersheds isolating the focal sampling locations within a 30 km radius as the boundary for “local” area estimation. In the absence of any justification for a value of the geographic radius we tested the correlation of the estimated diversity with elevational areas within 10 km, 50 km, 100 km and 200 km radius of the study site.

D. Precipitation Elevation Model: The precipitation data was obtained from Price et al. (2014). Univariate correlations of predictor variables with diversity were calculated for each dataset (hawkmoths and birds) and Pearson’s r^2 values were used as a measure of hypothesis support. Additionally we performed a multivariate analysis implementing generalized linear models (linear link, Gaussian error distribution) using Akaike information criterion (AICc; Burnham & Anderson 2003) for model selection.

4.3.3 Elevational patterns in beta diversity

Many dissimilarity indices (e.g. Morisita-Horn) can be particularly sensitive to the abundance of an extremely dominant species (Magurran 2004). We therefore performed a square root transformation of the abundance matrices of both hawkmoths and birds before calculating the dissimilarities. We also generated distance matrices according to the Chao index (Chao et al. 2005) and the quantitative Jaccard dissimilarity index (also known as the Ruźcika Index; Legendre 2014), which are both commonly used in literature. Dissimilarities were computed using R 3.3.1: **Vegan** 2.2-3: *vegdist*. We assessed the correspondence between all three distance matrices using Mantel’s test (Mantel 1967). We generated NMDS ordination diagrams using these distance matrices to identify any clustering of elevations. The ordination diagrams for the 3 indices were compared using a PROcrustean randomization TEST (PROTEST) (Jackson & Pere-Neto 2000) (*R 3.3.1: vegan 2.2-3: procrustes).* Significance of clustering was done using ANOSIM.

The Bray-Curtis dissimilarity was partitioned into its two additive antithetic components, turnover and nestedness (Baselga 2013), using *R 3.3.1: betapart 1.4-1: bray.part.* We

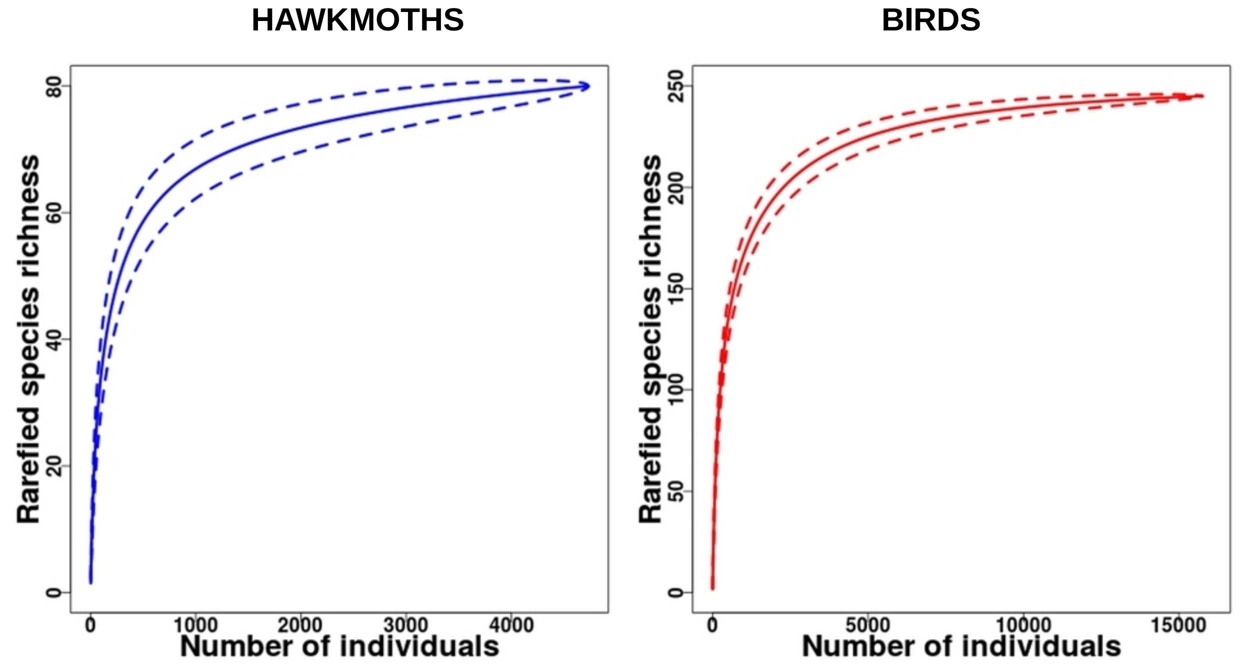


Figure 4.1 *Rarefaction curves for hawkmoth (leftl) and bird (right) species for the regional assemblage.*

investigated the elevational patterns in beta diversity and it’s two components were investigated using the slope and the correlation coefficient. The distance decay of assemblage similarity, or equivalently, the increase in dissimilarity (d) with increase in elevational distance (s) was fitted using the model $d = 1 - a * e^{b * s}$

4.4 Results

4.4.1 Elevational patterns in alpha diversity

Figure 4.1 shows the rarefaction curves for hawkmoths and birds for the data pooled for the entire regional assemblage. Figure 4.2 shows the same for each elevational community. The 95% confidence intervals from the procedure are shown by the dashed envelope and the vertical bars, respectively.

The next 3 figures show the elevational dependence of observed species richness and rarefied richness (Figure 4.3), Fisher's alpha and Simpson's indices (Figure 4.4) and Chao's and ACE estimator of true species richness (Figure 4.5)

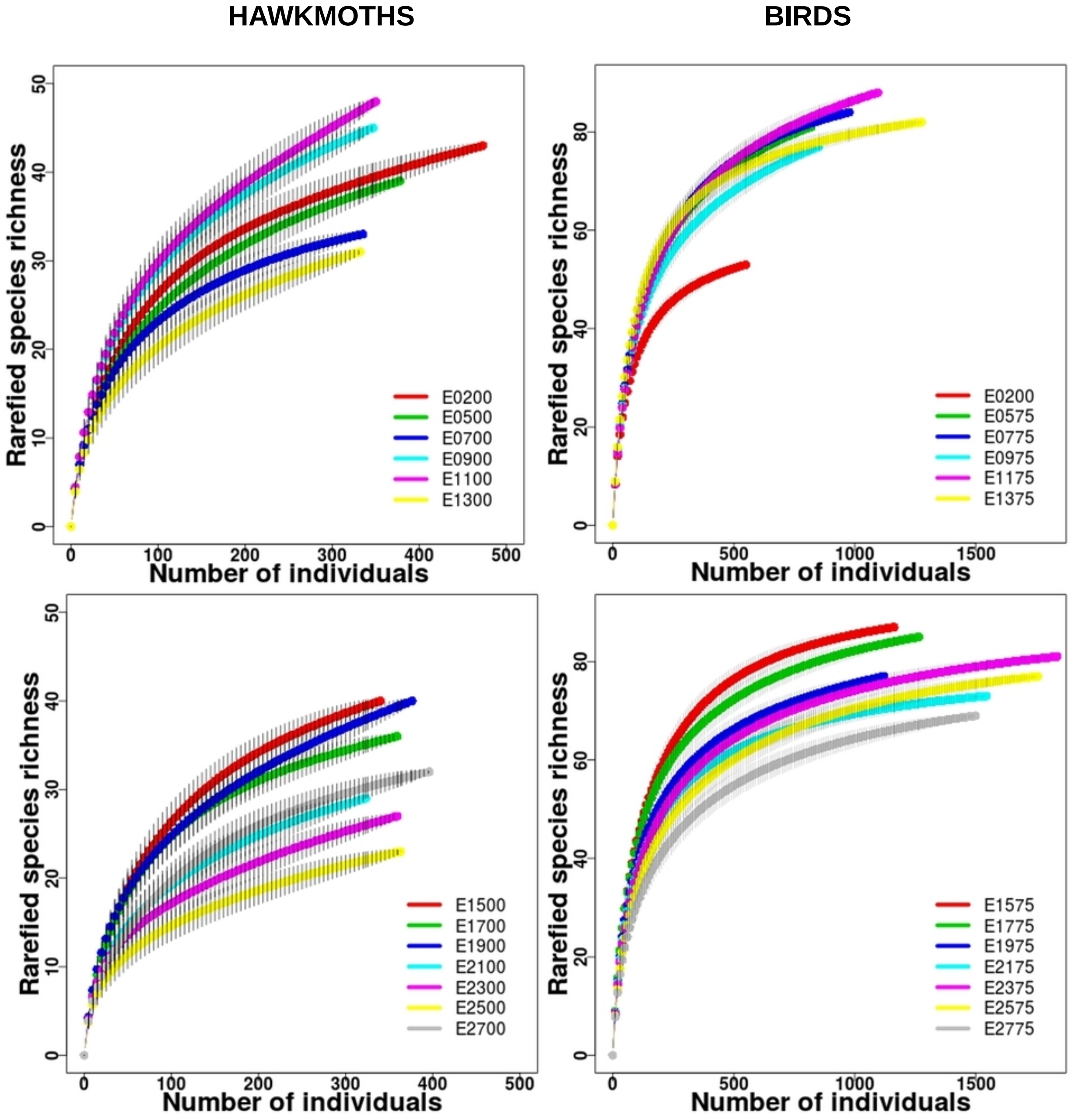


Figure 4.2 *Rarefaction curves for hawkmoths (left) and birds (right) for each elevational community. Colors represent different elevations.*

At first glance, the scatter of the data above 200 m elevation (grey symbols) was too large for anything other than a linear fit. However, smoothing the data over 3 elevations (coloured symbols) reduced the noise and clearly indicated a curvature in the profile and hence a parabolic fit. Including the data at 200 m also indicates a parabolic fit, even though we are not certain if it should be part of the profile, for reasons explained earlier.

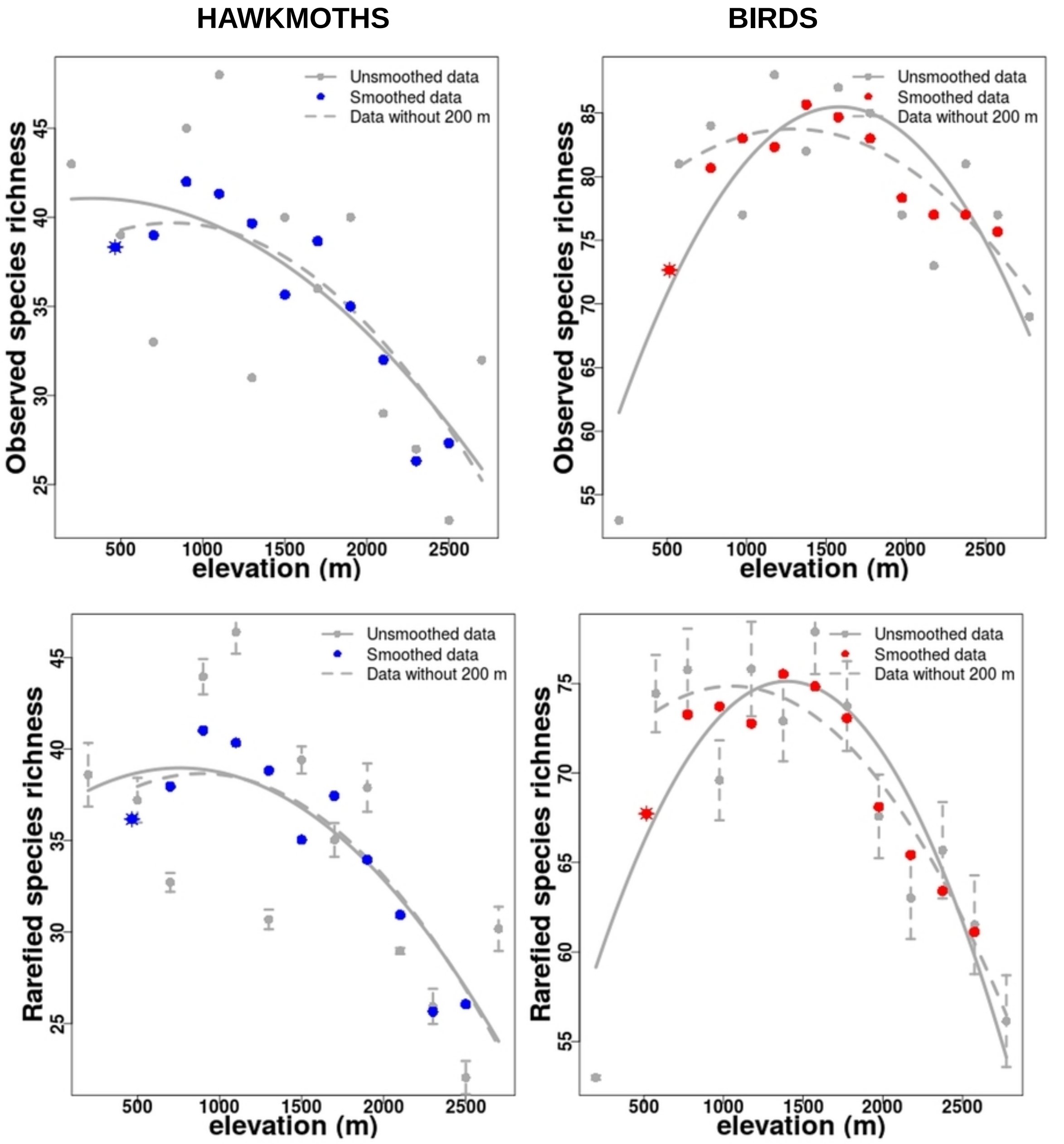


Figure 4.3 *Elevational profile of species richness – observed (top) and rarefied (bottom) – for hawkmoths (left; blue) and birds (right; red). Rarefied richness was calculated for N = 322 and 548 individuals for hawkmoths and birds. The raw data are shown as grey dots while the colored dots are moving averages over 3 elevation bins. The solid lines are parabolic fits using all elevations, while the dashed lines exclude the 200 m data.*

Nevertheless, it is very unlikely that it is so severely underestimated that its proper value will change the parabola into a straight line. Even without the 200 m data point the rarefied species and Fisher's alpha plots show clear departure from a straight line. The shapes of the fits of different metrics are compared in Figure 4.6 by shifting the peak of each curve to a value of 1.0, and scaling the curves to have the value of 0.0 at 2700 m.

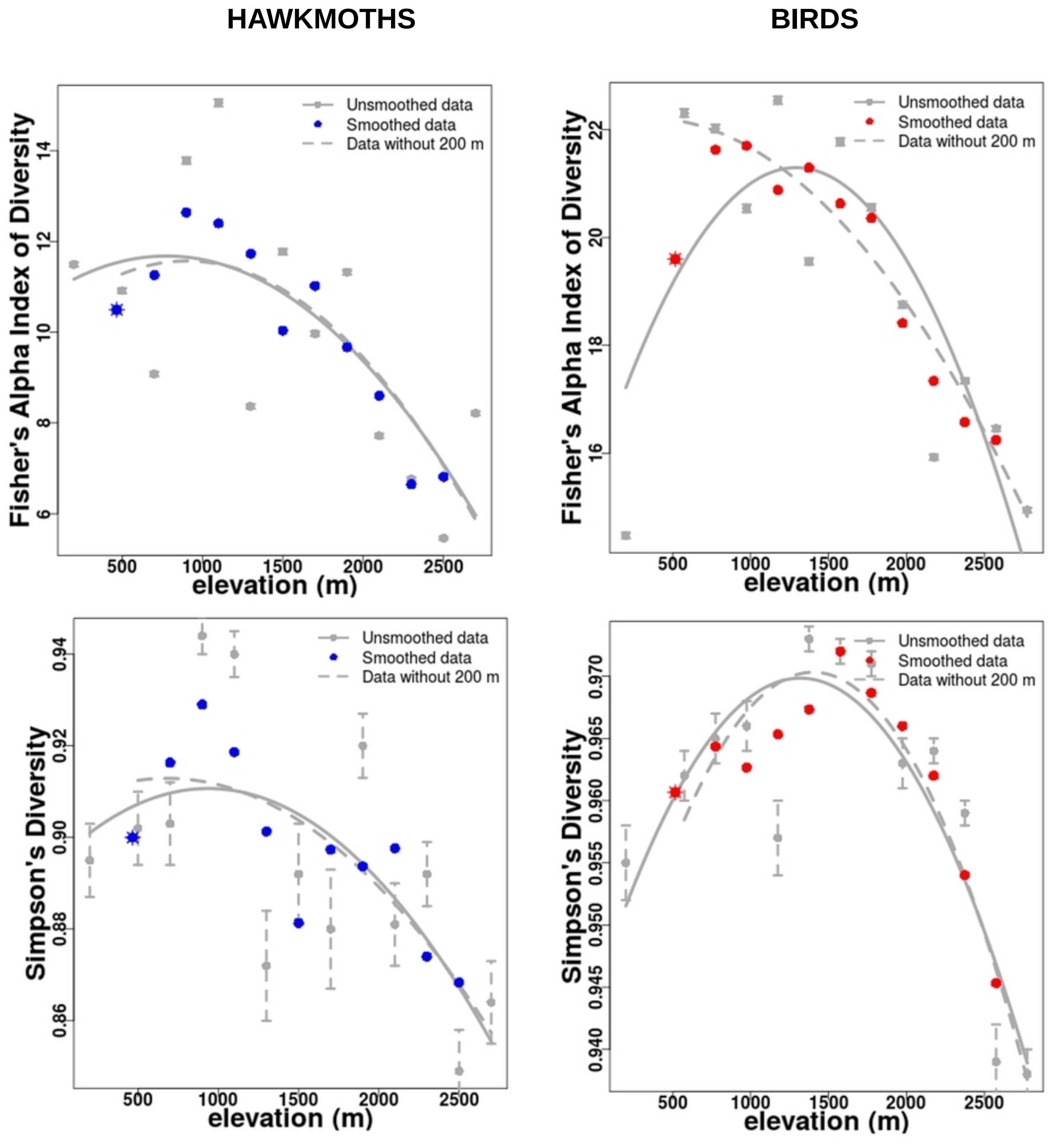


Figure 4.4 *Elevational profile of species diversity index – Fisher's alpha (top) and Simpson's (bottom) – for hawkmoths (left; blue) and birds (right; red). The raw data are shown as grey dots while the colored dots are moving averages over 3 elevation bins. The solid lines are parabolic fits using all elevations, while the dashed lines exclude the 200 m data.*

Table 4.1 lists the parameters of the best fit curves. It includes the coefficients of a parabolic fit, the standard deviation of the residuals, and the elevation of the peak. The dispersion in the peak elevation value was derived by fitting curves to 1000 simulated data sets which were generated by adding to the fit value at each elevation a random noise from a normal distribution with the same standard deviation as the observed residuals. The

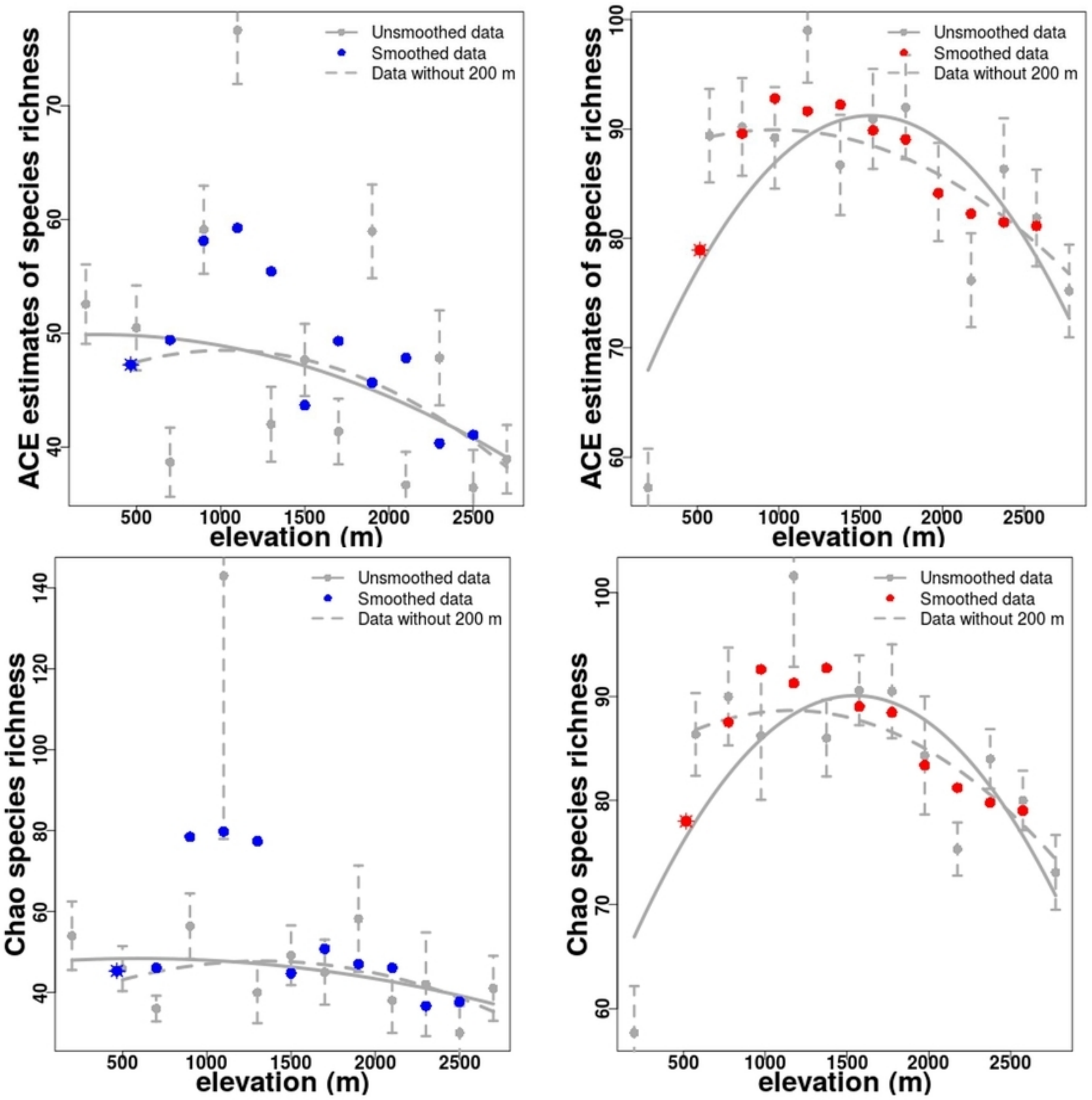


Figure 4.5 *Elevational profile of true species richness – Abundance-based Coverage ACE (top) and Chao's (bottom) – for hawkmoths (left; blue) and birds (right; red). The raw data are shown as grey dots while the colored dots are moving averages over 3 elevation bins. The solid lines are parabolic fits using all elevations, while the dashed lines exclude the 200 m data.*

simulated peak elevations do not follow a normal distribution which justifies the use of simulation to derive the dispersion. The table also lists the “overall” peak elevation obtained by averaging values from different metrics. It should be noted that, since all the metrics were obtained from the same data, combining these will not reduce the error in the estimate of the mean. Nevertheless, it is likely that the biases in each metric will be offset to some extent by the averaging process. The mean elevation of the peak was about 1100

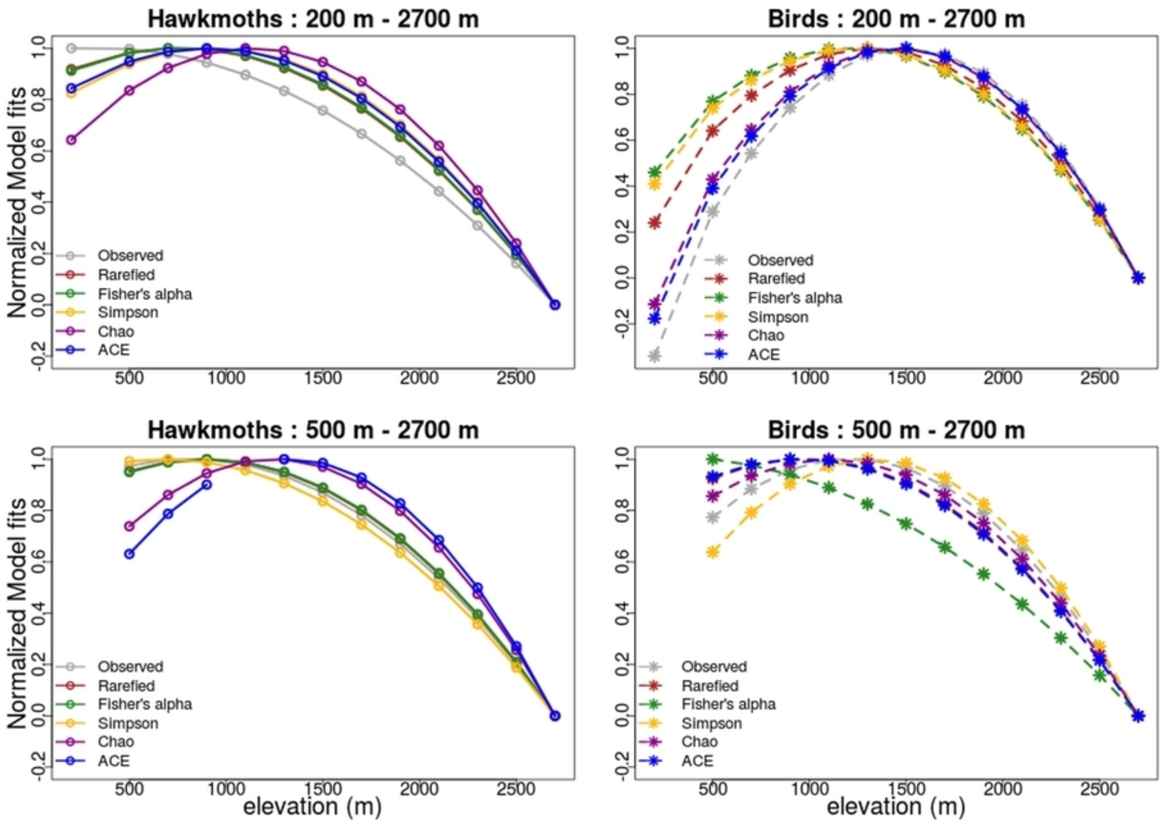


Figure 4.6 *Comparison of the shapes of the diversity profiles of different metrics. The profiles were scaled and shifted to achieve a value of 0.0 at 2700 m and 1.0 at the peak.*

m for hawkmoths and at 1500 m for birds, with a larger dispersion for hawkmoths than for birds. This lower peak and larger dispersion for hawkmoths would be consistent with a profile described in literature as a low-plateau mid peak.

In Figure 4.7 we have plotted the elevational profile of species richness using only the mean value of a species' elevational range; i.e. we have “contracted” a species' range to just its mean value, which is its optimal habitat in some sense. Surprisingly, hawkmoths and birds differ strikingly in this, with the former revealing a mid-elevation peak consistent with the other alpha diversity profiles whereas the bird data showed a flattish profile.

For reasons elaborated in Chapter 2 we did not augment the 2014 hawkmoth data with the data from 2013. Figure 4.8 shows that the elevational profiles from 2013 and 2014 are qualitatively similar and illustrates the reason for extending the sampling to 200 m in 2014,

	Metric	a	b	c	Fit Peak	Median Peak	15 - 85 %ile	Mean Peak
Hawk moths with 200 m	**Observed**	40.8 ± 6.1	1.8 ± 9.3	-2.7 ± 4.1	327	830	0 - 2534	
	Rarefied	36.7 ± 5.5	6.0 ± 8.4	-3.9 ± 2.8	758	879	0 - 1249	**1046 ± 179**
	Fisher's α	10.8 ± 2.2	2.4 ± 3.5	-1.5 ± 1.1	775	958	0 - 1326	
	Simpson's	0.89 ± 0.02	0.03 ± 0.04	-0.02 ± 0.01	938	925	0 - 1372	
	Chao	44.1 ± 29.8	31.7 ± 45.6	-13.9 ± 15.1	1135	1296	616 - 1836	
	ACE	48.7 ± 11.5	9.4 ± 17.6	-5.2 ± 5.8	908	1173	382 - 2055	
Hawk moths without 200 m	**Observed**	36.9 ± 9.8	6.6 ± 13.7	-4.1 ± 4.3	815	963	139 - 1345	
	Rarefied	35.0 ± 9.0	8.1 ± 12.5	-4.6 ± 3.9	891	1327	227 - 2800	**1247 ± 127**
	Fisher's α	10.1 ± 3.7	3.2 ± 5.1	-1.7 ± 1.6	903	1041	294 - 1364	
	Simpson's	0.90 ± 0.04	0.02 ± 0.05	-0.01 ± 0.02	681	1302	388 - 2004	
	Chao	36 ± 48.7	41.9 ± 67.8	-16.8 ± 20.8	1245	1354	728 - 1738	
	ACE	44.7 ± 18.7	14.7 ± 26.1	-6.7 ± 8.0	1100	1209	444 - 1570	
Birds with 200 m	**Observed**	54.0 ± 6.4	39.8 ± 9.4	-12.6 ± 3.0	1582	1504	910 – 2112	
	Rarefied	53.4 ± 4.6	31.1 ± 6.8	-11.1 ± 2.2	1400	1479	961 – 2003	**1502 ± 54**
	Fisher's α	15.6 ± 1.9	8.8 ± 2.8	-3.4 ± 0.9	1292	1425	819 – 2013	
	Simpson's	0.9 ± 0.0	0.04 ± 0.0	-0.01 ± 0.0	1319	1568	843 – 2341	
	Chao	60 ± 7.5	43.5 ± 11.0	-14.3 ± 3.5	1522	1504	956 - 2078	
	ACE	60.2 ± 7.7	42.1 ± 11.3	-13.7 ± 3.6	1540	1533	1008 - 2042	
Birds without 200 m	**Observed**	74.1 ± 7.6	15.0 ± 10.0	-5.8 ± 2.9	1287	1487	813 - 2072	
	Rarefied	68 ± 5.4	13 ± 7.1	-6.2 ± 2.1	1052	1459	781 - 2151	**1475 ± 26**
	Fisher's α	22.1 ± 2.1	0.8 ± 2.7	-1.2 ± 0.8	330	1453	798 - 2119	
	Simpson's	0.94 ± 0.01	0.05 ± 0.01	-0.01 ± 0.02	1789	1519	877 – 2264	
	Chao	81.1 ± 9.5	16.2 ± 12.5	-6.9 ± 3.7	1180	1476	784 - 2072	
	ACE	85.9 ± 8.3	10.4 ± 11	-5.1 ± 3.2	1032	1466	774 - 2145	

***Table 4.1** Parabolic fits to different diversity metrics with elevation for hawkmoths and birds: Diversity = a + b (Elev/1000) + c (Elev/1000)^{2}. **Fit Peak** is the fitted peak elevation. **Median Peak** and **15-85 %ile** are the median and 15th and 85th percentiles of the fitted peaks from 1000 simulated data sets with the same residue statistics as the original. **Mean Peak** is the mean and standard deviation of the Median Peak values of the different metrics.*

despite the lack of suitable habitat within EWS. All the moths are from the single family *Sphingidae. So* we have also plotted the observed species richness for the 5 most speciose and the 6 most abundant bird families in Figure 4.9. The numbers were chosen to approximately match the number of hawkmoth species.

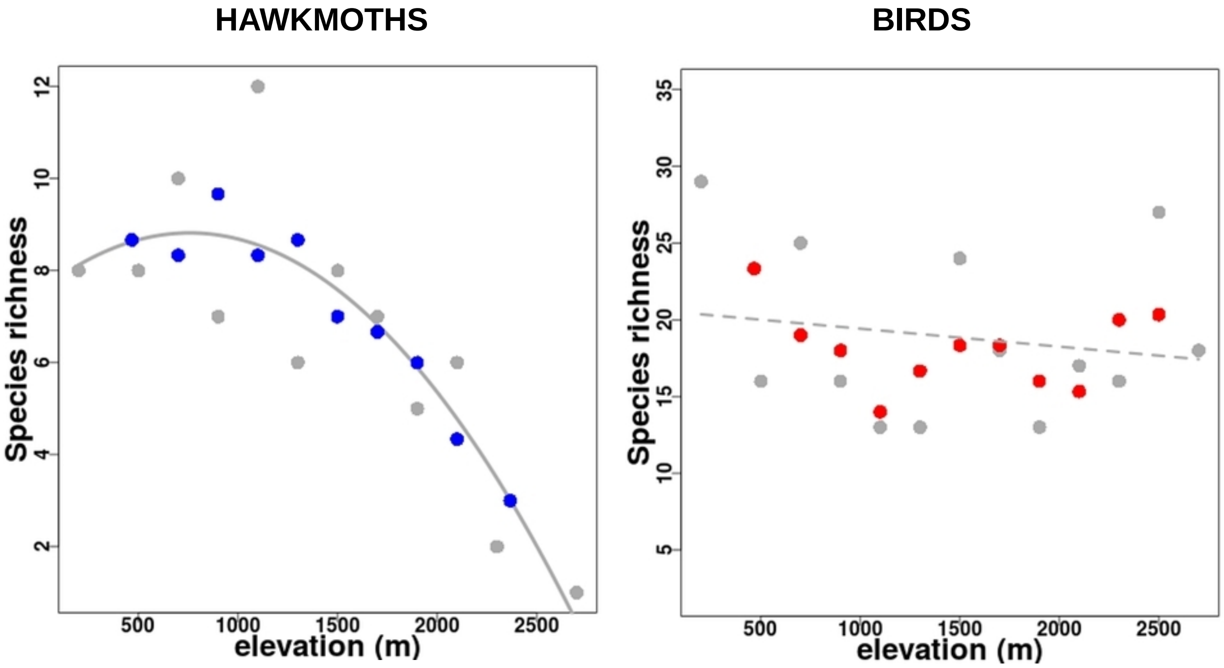


Figure 4.7 *Observed Species richness as a function of elevation using only the "Optimum Elevation" for a species, i.e. Each species is only counted at its mean elevation.*

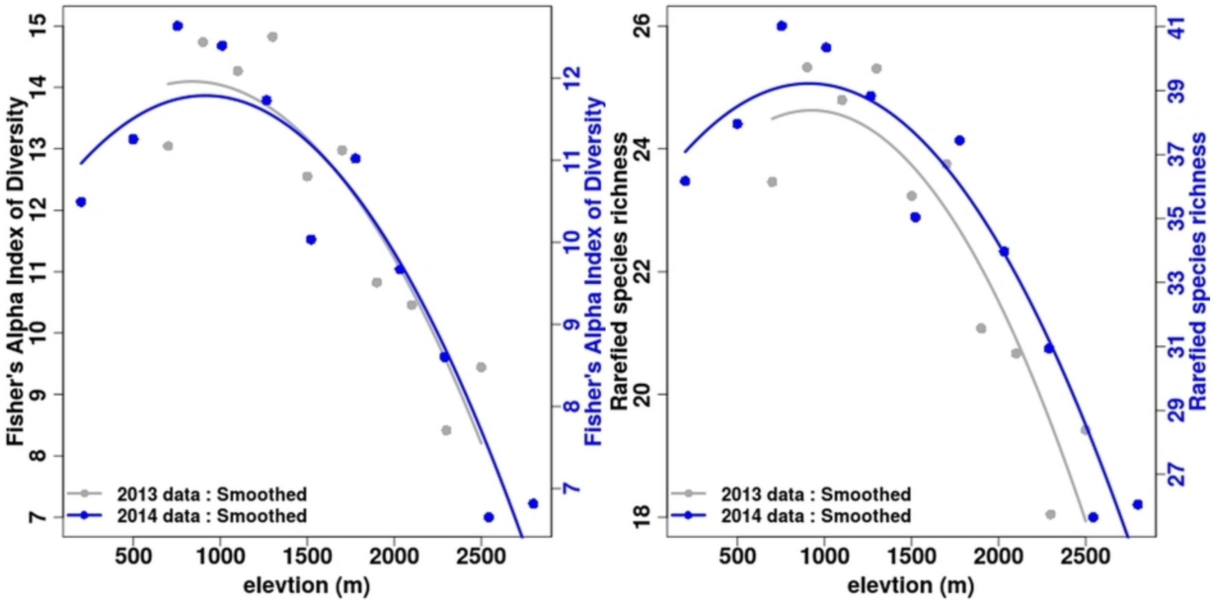


Figure 4.8 *Comparison of elevational profile of alpha diversity – Fisher's alpha and rarefied species richness – for hawkmoths between the years 2013 (grey) and 2014 (blue) Rarefied richness was calculated at* n_{2013} *= 67 and* n_{2014} *= 322 individuals.*

	Radius (km)	**r^2**	**p-value**	**slope**
Hawkmoths	10	0.09	0.1	0.26
	50	0.1	0.1	-1.3
	100	-0.01	0.1	-0.47
	200	-0.09	0.1	0.02
Birds	**10****	**0.80**	**<0.05**	**0.34**
	50	0.02	0.1	-0.55
	100	-0.1	0.1	0.07
	200	-0.03	0.1	0.15

Table 4.2 *Linear regression scores for α- diversity with area, using 4 values of radii*

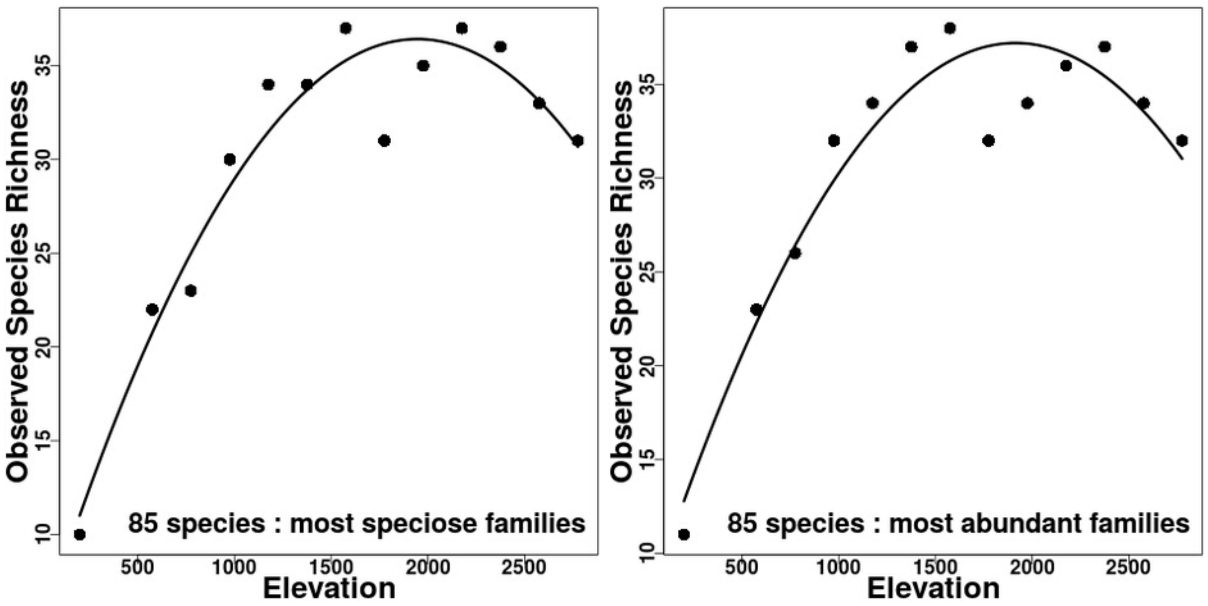


Figure 4.9 *Alpha diversity with elevation for the most speciose and abundant families that together constitute ~80 species (to match the number of species in the hawkmoth data). Observed species richness is plotted here as the number of species at the lowest elevations was too small for secure estimation.*

4.4.2. Correlates of elevational patterns in alpha diversity

We calculated elevational area within radii of 10 km, 50 km, 100 km and 200 km from the centre of EWS to investigate its correlation with Fisher's alpha. The coefficients of the linear fits to the data are shown in Table 4.2. Only the relationship between bird diversity and the elevational area within a 10 km radius shows a significant correlation; diversity

	Predictor	r^2	p-value	slope
Hawkmoths	Area (10 km)	0.09	0.1	0.26
	Temperature*	**0.11**	**<0.05**	**0.37**
	Precipitation*	**0.11**	**<0.05**	**0.003**
	AET*	**0.27**	**<0.05**	**0.005**
	MDE Richness	0.11	0.1	0.11
Birds	**Area* (10 km)**	**0.80**	**<0.05**	**0.34**
	Temperature (with 200 m)	0.16	0.1	0.30
	Temperature* (without 200 m)	**0.78**	**<0.05**	**0.55**
	Precipitation (with 200 m)	0.21	0.1	0.002
	Precipitation* (without 200 m)	**0.71**	**<0.05**	**0.003**
	AET (with 200 m)	**0.05**	**0.2**	**0.004**
	AET (without 200 m)*	**0.72**	**<0.05**	**0.009**
	MDE Richness*	**0.31**	**<0.05**	**0.10**

***Table 4.3** Results of linear regression of Fisher's α on 4 correlates of diversity; significant values are highlighted in bold.*

	Predictor	Df	Sum of Sq	RSS	AIC
Hawkmoths	*Step: AIC = 22.04 Hawkmoths ~ MDE + AET*				
	<none>			44.63	22.04
	Precipitation	1	1.67	42.95	23.53
	Temperature	1	1.79	43.17	23.53
	Area (10 km)	1	0.16	44.48	23.99
	MDE	1	16.55	61.19	24.13
	AET	1	35.90	80.53	27.70
Birds	*Step: AIC = 8.9 Birds ~ Temperature + Area*				
	<none>			17.29	9.7
	Temperature	1	4.45	21.74	10.68
	AET	1	0.24	17.04	11.52
	MDE	1	0.13	17.15	11.60
	Area	1	62.50	79.79	27.58

***Table 4.4** Stepwise AIC based model selection; AET and MDE emerged as the best model for hawkmoths, while Temperature and Area were best predictors in case of birds.*

	Bray-Curtis (Hawkmoths)		Bray-Curtis (Birds)	
	Mantel's r	**p-value**	**Mantel's r**	**p-value**
Chao	0.83	< 0.001	0.98	< 0.001
Jaccard	0.99	< 0.001	0.99	< 0.001

Table 4.5 *Mantel statistics for correlation of distance matrices between Bray-Curtis, Chao and Jaccard dissimilarity indices.*

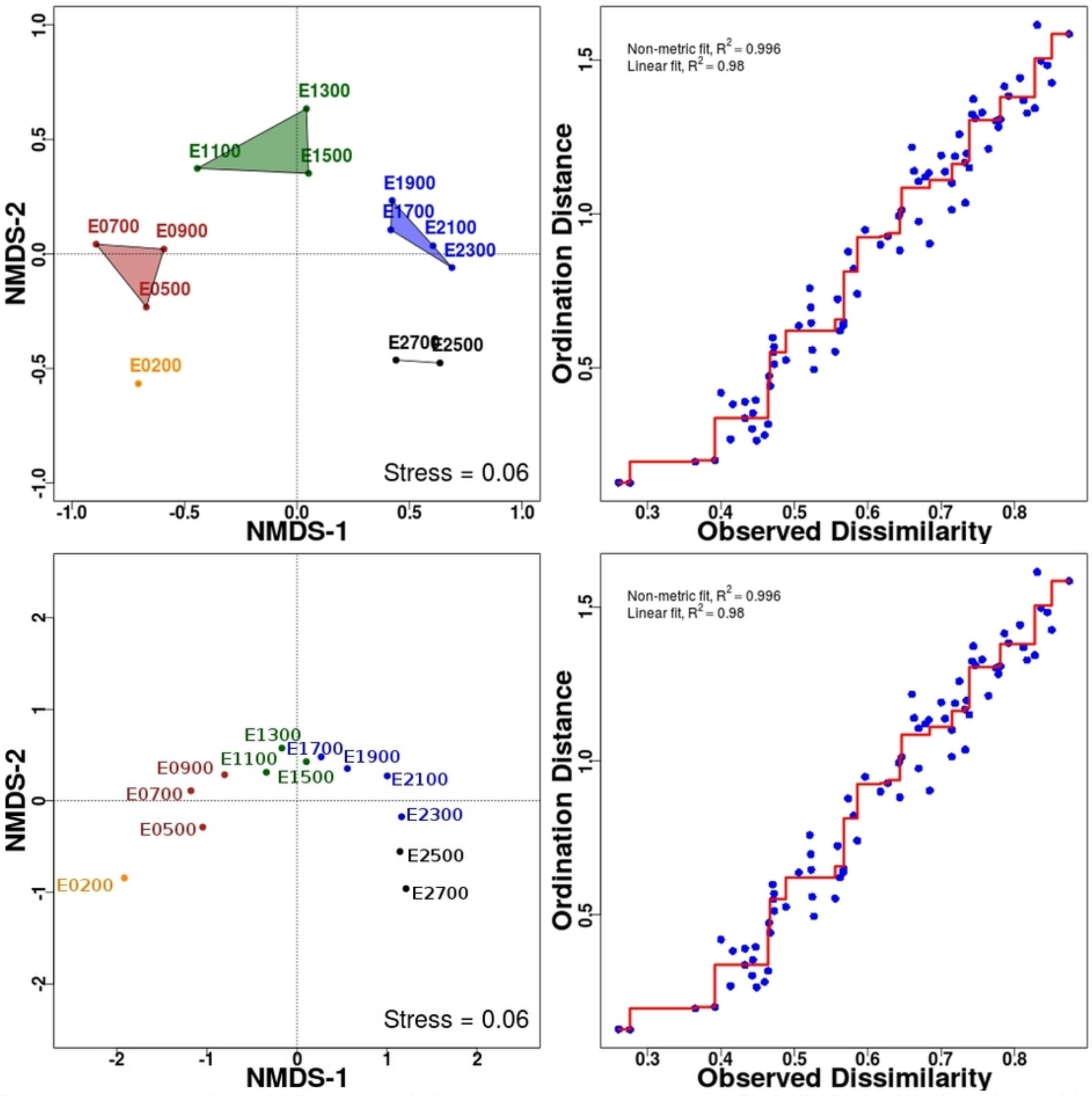


Figure 4.10 *Nonmetric Multidimensional plots on Bray-Curtis index of dissimilarity for hawkmoth and bird communities with associated stress plots.*

	Bray-Curtis (Hawkmoths)		Bray-Curtis (Birds)	
	Corr. Coeff	**P-value**	**Corr. coeff**	**p-value**
Chao	0.92	< 0.001	0.98	< 0.001
Jaccard	0.98	< 0.001	0.97	< 0.001

Table 4.6 *Similarity between the NMDS ordinations using Bray-Curtis, Chao and Jaccard indices (using Procrustes rotation and 999 permutations)*

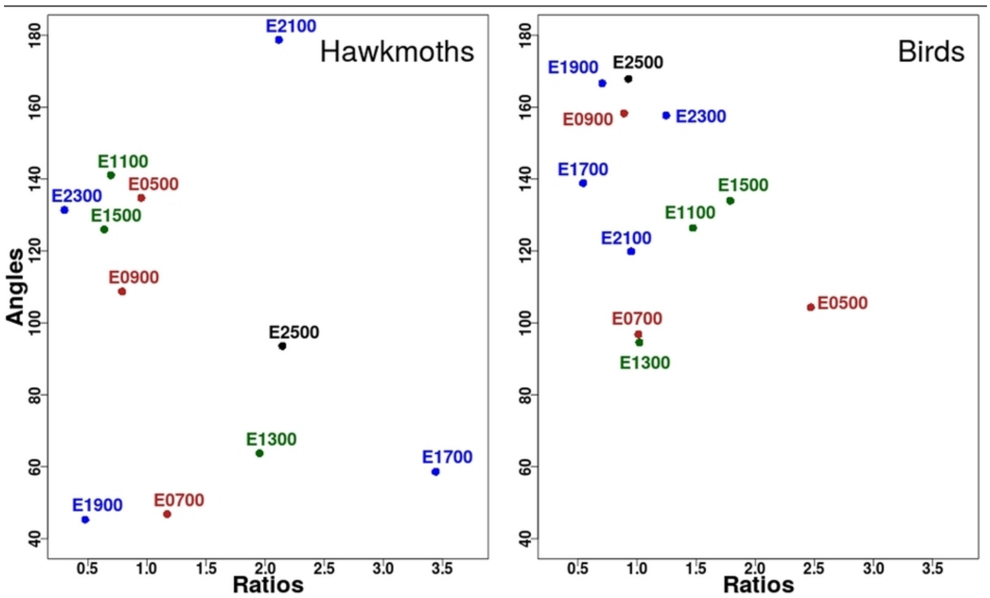


Figure 4.11. *Angle at each elevational vertex in the NMDS plane plotted against the ratio of lengths of the two arms enclosing the angle*

varies as area to the power 0.34.

The linear regression of diversity with temperature, precipitation and simulated MDE is listed in Table 4.3. Hawkmoth diversity shows a significant correlation with temperature and precipitation but not with MDE richness. On the other hand bird diversity is correlated with MDE richness but not with temperature and precipitation. However, the lack of correlation seems to change with the data from 200 m elevation. Removing this results in a correlation with temperature and precipitation as well. The results of a step wise multiple regression of diversity with all the correlates is shown in Table 4.4.

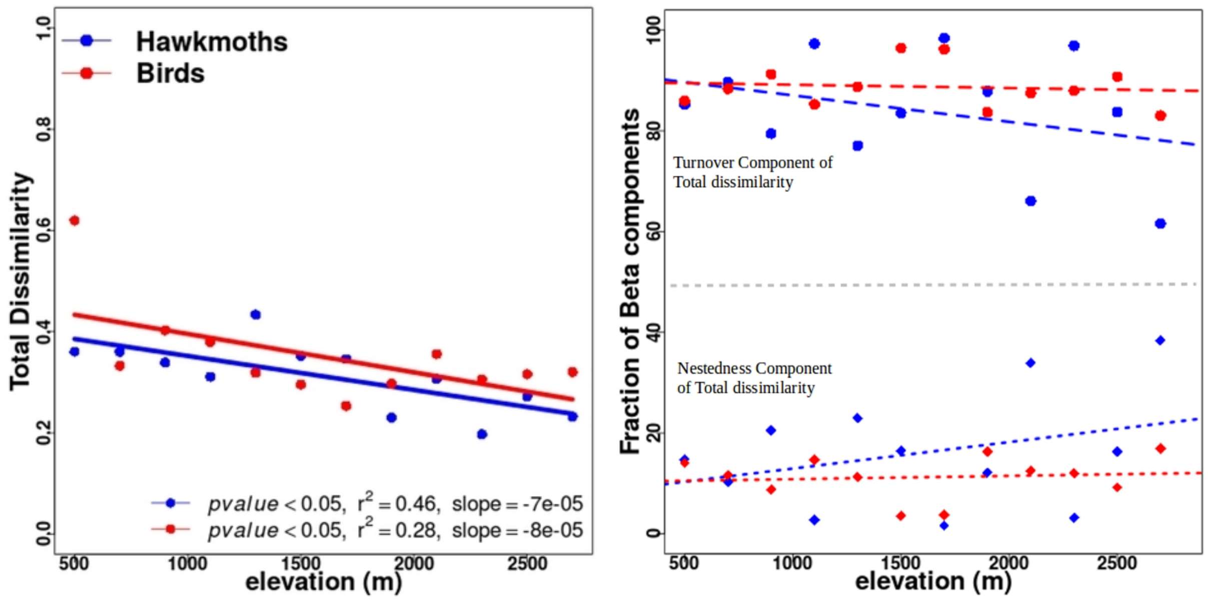


Figure 4.12 *The change of beta diversity with elevation for hawkmoths (blue) and birds (red).* ***a)*** *Total dissimilarity, and* ***b)*** *Turnover (circles) and Nestedness components (diamonds) as percentages of the total. The slopes of the linear regression and the Z- and p-values for no-difference between birds and hawkmoths are listed below.*

	Slope Hawkmoths x 10^{-5}	**Slope Birds x 10^{-5}**	**Z-statistic**	**p-value**
D_{Total}	–6.7 ± 2.09	–7.6 ± 3.34	0.22	0.41
$D_{Turnover}$	–5.3 ± 4.23	–6.6 ± 1.88	-0.10	0.51
$D_{Nestedness}$	3.5 ± 1.37	–7.2 ± 7.76	0.68	0.32

4.4.3 Elevational patterns in beta diversity

The Mantel statistic showed that the dissimilarity matrices calculated using Bray-Curtis, Chao and Jaccard dissimilarity indices are highly correlated (Table 4.5). Similarly, the NMDS diagrams made using these 3 measures were also highly correlated (Table 4.6). Therefore, we only present the rest of the beta diversity results for the abundance-based and widely used Bray-Curtis dissimilarity index. The NMDS plots (Figure 4.10) show that elevational communities seem to be in 5 clusters in hawkmoths (separated by colour on the plot), while they are strung out in a smoothish arc in birds. ANOSIM could not discriminate between the two, and returned statistically significant clustering for both.

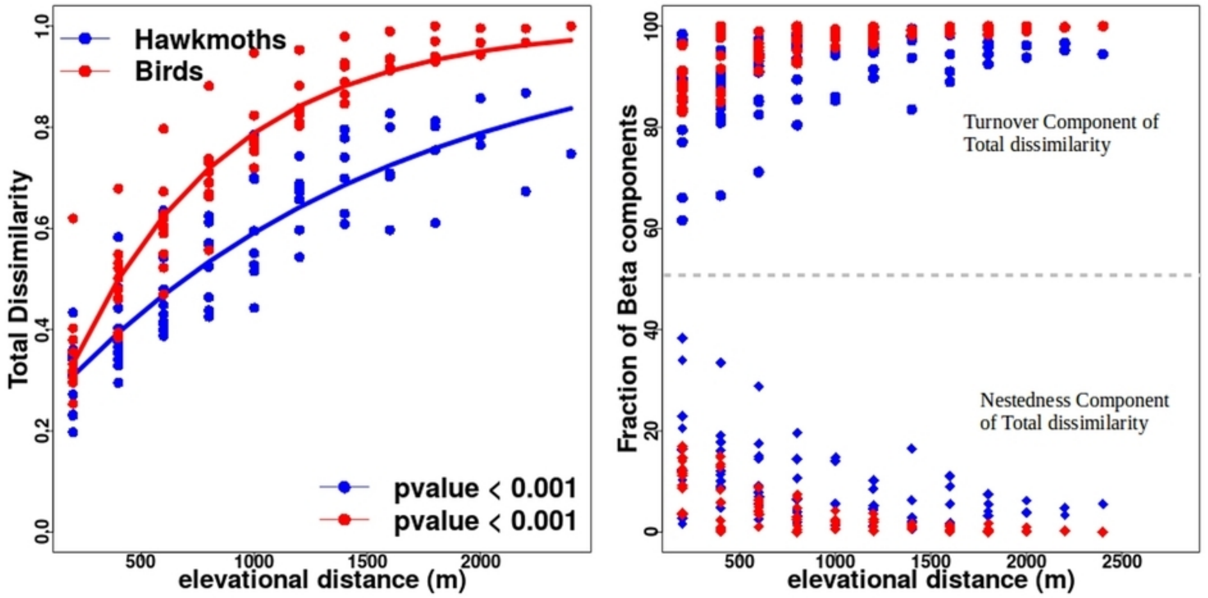


Figure 4.13 *The change of beta diversity with elevational distance for hawkmoths (blue) and birds (red):* ***(a)*** *total dissimilarity, and* ***b)*** *Turnover (circles) and Nestedness compo- nents (diamonds) as percentages of the total. The fitted exponential indices (b) and the Z- and p-values for no-difference between birds and hawkmoths are listed below.*

	b: Hawkmoths x 10^{-4}	**b: Birds x 10^{-3}**	**Z-statistic**	**p-value**
D_{Total}	–6.6 ± 0.43	–1.4 ± 0.08	8.67	< 0.001
$D_{Turnover}$	–6.3 ± 0.43	–1.4 ± 0.07	9.85	< 0.001
$D_{Nestedness}$	–3.0 ± 1.40	–1.1 ± 0.02	2.90	< 0.001

However, ANOSIM simply measures the pairwise differences within and across groups and should return a significant signal for actual clustering (like in hawkmoths) and for elevations strung out sequentially along a curve (like in birds). Therefore, we constructed a simple discriminant between the two patterns. Essentially, if elevations are string out sequentially along a smooth curve the angle at a vertex (i.e. elevation) made with the two adjacent elevations should be close to 180 deg, whereas this angle should be lower within a cluster (within which it is likely to be dominated by noise). Similarly, the ratio of the two lengths, i.e. of the vertex with the adjacent elevations on the NMDS, should extend to higher values within a cluster. Figure 4.11 shows the distribution of these quantities, and hawkmoths, as expected, extend to lower angles and larger ratios.

The total dissimilarity between adjacent elevations was negatively correlated with elevation for both hawkmoths and birds (Figure 4.12). Species *Turnover* dominated the beta diversity signal and decreased with elevation while *Nestedness* contributed very little. A Fisher's r-to-z comparison showed that the difference between hawkmoths and birds was not significant. The statistics of the dissimilarity profile are listed in Table 4.7

The dependence of Bray-Curtis dissimilarity and its two additive components, Turn-over and Nestedness, on elevational distance (i.e. $\Delta E = E_i - E_j$) for all pairs of elevational communities are shown in Figure 4.13; here, for example, $\Delta E = 200$ is obtained by all community pairs separated elevationally by 200 m: 300-500 m, 500-700 m, 700-900 m, etc. The exponential index is significantly steeper for birds than for hawkmoths.

4.5 Discussion

Biodiversity is a multi-dimensional property of ecological communities. Although there are many studies of alpha diversity patterns along elevational gradients, few have investigated different components and metrics of alpha and beta diversities, and even fewer have done so in a comparative framework across two different organismal groups at the same place and time. In this study, we have explored multiple facets of biodiversity of two different species rich taxa, birds and hawkmoths, and across the same elevational gradient spanning 2600 m in the eastern Himalayas. Our work highlights the utility of systematic and simultaneous collections across different organismal groups to understand the complexity of processes shaping diversity patterns.

4.5.1 Species richness

In general, bird species numbers were much higher than hawkmoth throughout the study area. This is expected, as the bird dataset spans 50 families whereas hawkmoths represent just one family of a hyper-diverse group *Lepidoptera*. Nevertheless, the comparison is justified given the large difference between the global diversity for the class *Aves* (10,303 species) and class *Insecta* (2-30 million species). Even Lepidoptera (moths and butterflies) comprise over 300,000 species. Continual taxonomic revisions, discovery of new species, hybrids and sub-species leave most insect groups with highly dynamic boundaries between heirachical taxonomic levels. We intend to extend this research to other families within Lepidoptera, and also other taxa outside Lepidoptera.

Our data reveal an exceptionally high diversity of birds (S_{obs} = 245), comparable to the other avifauna hot-spot of the world – the Andes of South America (Blackburn et al 2001; Blake 2000; Jankowski et al. 2009; Bencke et al. 1999). This was recorded in a sampling area of only about 20 ha (48 elevations x 100 m length x 40 m width) but spanning 200-2800 m. The checklist for the area is in excess of 400 bird species including winter migrants. The species richness of the region, and its importance as a global hotspot, has been noted previously by several researchers (Orme et al 2005; Price et al. 2003; Price 2012; Rasmussen and Anderton 2005). This area has the highest density of range-restricted bird species (Orme et al 2005) and the highest number of Oscine passerines in the world (Price et al. 2012). The importance of the region for conservation is based not just on the number of species present but also on high beta diversity and the presence of several threatened and endangered species e.g. Temminck's Tragopan, Blyth's Tragopan, Ward's Trogon, Great Pied Hornbill, Rufous-necked Hornbill, Chestnut-breasted Hill-Partridge, etc (see Athreya 2006a for more records).

Hawkmoth species richness (S_{obs} = 93) from EWS is comparable to the neighbouring hawkmoth "hotspots" in south-east Asia and Indo-Australian archipelagos – 123 in Northern Vietnam, 157 in Northwest Thailand, 135 in central Thailand, 109 in Malaysia (Beck & Kitching 2006). It should be noted that our numbers are based on sampling of just a few nights at a dozen elevations on just one hill slope. This was the first systematic effort in the region. The only published checklist of hawkmoths from the region reports 27 species from adjacent Bhutan (Singh & Kitching 2014); the low number is undoubtedly indicative of the effort which needs to be made. Sustained sampling over the next few years should see a substantial jump in the recorded hawkmoth diversity of the area.

The above numbers are similar to our observed species richness (hawkmoths = 93 & birds = 245) and the estimated richness (Chao) varies between 111-127 for hawkmoths and 276-303 for birds. We interpret the pattern in alpha diversity with elevation using only rarefied species numbers and Fisher's diversity index as (a). estimators of richness (Chao

& ACE) gave very large standard errors using the standard formulae despite our large sample sizes, and (b) their estimates were anomalously high at 1100 m.

4.5.2 Elevational profiles in alpha diversity

The elevational pattern in species richness was for long believed to mirror the latitudinal gradient due to the similarity in their temperature gradients. This belief was first challenged by Rahbek (1995) who demonstrated that the perception was a result of an overemphasis on a few studies showing the expected decline in species richness. Empirically, the most frequent pattern was, in fact, a mid-elevation peak or a hump-shaped curve. Later, Rahbek (2005) showed that about 80% of the studies showed the hump-shaped curves when data was corrected for non-standardized sampling and incompletely sampled gradients, and this is the currently popular paradigm (Kessler et al. 2011; Beck & McCain 2017).

In our study, both hawkmoths and birds exhibited a mid-elevation peak in diversity. The hawkmoths had a lower peak and a broader distribution than birds. The unsmoothed data at 200 m resolution does not at first glance does not require a peak in profile. However, smoothing the data over 3 elevation bins clearly brought out the peaked nature of the profile in all cases except one (Fisher's alpha for birds in the absence of 200 m data).
Within Lepidoptera, previous studies have reported several patterns: a monotonic decline (e.g. Sphingidae: Beck & Kitching 2009; butterflies: Acharya & Vijayan 2015; Geomteridae: Axmacher et al. 2004), hump-shaped (Sphingidae: Beck & Kitching 2009; Geometridae: Beck & McCain 2017; butterflies: Gallou et al. 2017), a flat profile (Brehm et al. 2003, 2016). While we fitted parabolas to all the Eaglenest (EWS) hawkmoth profiles we interpret the shape as a low elevation peak in the region of 1000 m. It is to be noted that the elevation extends up to 3250 m on the same mountain and up to 5000 m within a radius of 50 km. The unavoidable truncation of the parabola at zero elevation and the low elevation of the peak makes it quite similar to the low-plateau-mid-peak (LPMP; e.g. McCain, 2010). We also note a lack of data below 700 m would have resulted in a linear fit to the profile. Our simulations of the fit using observed residual statistics showed a very long tail of the peak elevation distribution to zero elevation (Table 4.1). We wonder if the flat profile of (Brehm et al. 2003, 2016) is related to their lowest sampled elevation being 1040 m. Beck

& Kitching (2009) have shown the diversity profile along 9 elevational gradients in the Indo-Australian region. Seven of them show a low elevation peak. Lack of data below 700-1000m would have rendered all of them as monotonic declines. Ashton et al (2016) have studied the diversity of moths in neighbouring south-west China and find that species richness decreases monotonically with elevation. However, their data is essentially limited to 3 elevational bands centred on 1000 m, 2300 m and 3500 m. Once again, we suggest that the lack of a low elevation peak may be due to the lack of data below 800 m. In fact, there is a hint of a down-turn in diversity in their plot in the few data points below 1000 m.

The patterns reported for bird diversity along elevational gradients have been more varied with nearly equal frequencies of decreasing, low plateau, low plateau with a mid-elevation peak and unimodal with a mid-elevation peak patterns (McCain 2009). Our results on the diversity profile of birds in Eaglenest are in agreement with previous published studies from the region (Price et al. 2014), but do not support McCain’s theory of elevational-climate model (McCain 2009). This pattern is discussed more in the next subsection on the correlates of diversity.

We also looked at the elevational profiles using just the central/mean value of the species' ranges. In some sense, the central value of a species range is the “optimal” habitat for a species. Several species have been shown to have the highest intraspecific diversity and abundance in the middle of their range (e.g. Kirkpatrick & Barton 1997). The elevational profiles of species richness for moths and birds are strikingly different, in contrast to the similarity of elevational profiles using abundance distributions. While moths continue to show a low elevation peak, the elevational profile of birds is essentially flat. This can be reconciled with the profiles of the rest of the metrics if the birds have elevational ranges skewed towards the lower elevations.

There have been a few multi-taxon studies of diversity profiles along the same elevational transect and carried out at about the same time. Some of these studies have focussed exclusively on plant families (e.g. Grau et al. 2007; Turtureanu et al. 2013), while some have compared a faunal or microbial diversity profile to that of a plant taxon (e.g. Mori et al. 2013; Bryant et al. 2008). Of course, plant groups contribute to the diversity of an area but plants also shape the “background” habitat which impact faunal diversity profiles. In that sense the comparison of plant and faunal diversity profiles can be viewed as a cause-effect relationship. On the other hand, our comparative study of hawkmoths and birds involves two less intimately connected taxa which are more likely to sample different dimensions along factors which influence diversity.

Some of the cross-taxon comparisons have included birds and bats in Peru (Patterson et al, 1998), moths and ants in Costa Rica (Colwell & Rangel 2010), leaf-miners, moths and leaf-miner parasitoids in Australia, butterflies and mammals in North America, Geometrid and Sphingid moths in Borneo, ants, moths and mammals in Costa Rica, and ants, butterflies and birds in New Guinea (all in Colwell et al. 2016).

In terms of a direct comparison between an ectotherm and an endotherm (as in our study) only two of the above are of relevance: the Costa Rican and New Guinean data from Colwell et al (2016). Their North American dataset also compares an ectothermic group (butterflies) with an endothermic group (mammals), but the data was compiled over 50 years and we are not sure of the impact of climate change over this time scale. Qualitatively, our results are similar in that the diversity peak for ectothermic lepidoptera are at a lower elevation than for the endotherm (marginally in Costa Rica, and considerably in New Guinea). We discuss their results further in the next section.

4.5.3 Correlates of elevational profiles in alpha diversity

Elevational profiles of diversity have been shown to exhibit little support for a single ‘best’ univariate predictor (Brehm et al. 2007; Beck & Kitching 2009). The correlates usually investigated can be grouped into four main categories: climate, space, evolutionary history and biotic processes (McCain & Grytnes 2010). We have also encountered a few papers discussing the role of connectivity as a spatial factor, perhaps due to the difficulty in quantifying connectivity across the elevations in montane ecosystems given periodic climate change and differences in the vagility of species in a community. Speciation rates, extinction rates, clade age and phylogenetic niche conservatism are theoretically and, in some cases, empirically linked to diversity (e.g. Rohde 1992; Allen et al. 2002; Stephens &

Wiens 2003; Wiens et al. 2006; Mittelbach et al. 2007). Biological processes including competition (e.g. Terborgh & Weske, 1975), source–sink dynamics, ecotone effects (e.g. Terborgh 1985; McCain 2004), habitat heterogeneity (e.g. MacArthur & MacArthur 1961) and habitat complexity (e.g. Terborgh 1977) have also been proposed but rarely tested.

Studies have shown that species richness patterns are a complex interplay of several, forces which makes identification of realistic mechanisms rather difficult, at best. For instance, temperature coupled with water availability had the highest support in a multi-gradient study of land birds (McCain 2007; 2009), however it was difficult to tease apart the direct influence of water and temperature from plant productivity. High correlation between organisms with specific moisture requirements such as the amphibians (Muller et al. 2013), and precipitation has been reported, but again it has proved to be difficult to separate water availability from plant productivity.

For Lepidoptera, net primary productivity was found to be the strongest predictor for the mid-elevation peaks of Geometrids (Beck & McCain 2017) while area of the altitudinal band was more strongly correlated with species richness patterns of Sphingidae (Beck & Kitching 2009). Both environmental and geometric factors were deemed likely to contribute to the hump-shaped distribution of Geometrids in Costa Rica (Brehm et al. 2007).
Distribution of host plants and forest habitat boundaries or ecotones have been demonstrated to play a major role in diversity patterns and peaks. A study of plant species in Bhutan (27.514ºN, 90.433ºE) adjacent to the study site identified a peak in diversity of plant species between 1000-1299m (Ashton 2003) which may be responsible for a peak in diversity of other taxa as well (Acharya et al. 2011). Many previous studies have attributed a peak in species richness across multiple taxa to a peak in productivity (Gaston et al. 2000; Ding et al. 2005, 2006; Whittaker et al. 2010; Acharya et al. 2011).

A large number of methodical and comprehensive studies on multiple mountain systems across the globe would be necessary to separate out the contributions of these multiple confounding factors. Meta analyses (McCain 2009a; Beck & McCain 2017) have attempted to address this issue. However, the paucity of data at the lowest elevations in many (lepidopteran) studies, perhaps because these elevations suffer the most from anthropogenic influences, is likely to strongly bias the result given the preponderance of low elevation peaks in the diversity profiles of this taxon.

Our results on the correlates of diversity of hawkmoths and birds are in accordance with previous results that the mid-elevation peak has little support for a single ‘best’ univariate predictor. Temperature and precipitation both show high support in univariate and multivariate analysis, however contrary to the major prediction of the MTE (a monotonic decline in diversity), we observed a mid-elevational peak suggesting the interplay of multiple causative mechanisms, which is perhaps also reflected in the observed high vegetation diversity at about 1300 m in neighbouring Bhutan (Ashton 2003).

For birds, Elevational-Climatic Model (ECM) has been used as an explanation of monotonic decline in diversity along wet-humid mountains (McCain 2007, 2009). The model did not find support in the avi-fauna of our study region, which was located in a region of high precipitation, and exhibited a clear mid-elevation peak. We found support for models that contained area as an explanatory variable, as well as for area as a univariate predictor. However, as mentioned previously, defining regional boundaries represented by local transect surveys is difficult and we find standardizing diversity for area premature in the current context. MDE was supported in multivariate analyses as an additional factor, but never as the main driver, however we find it difficult to unambiguously statistically separate effects of these multiple factors in explaining the observed patterns of mid-elevational peaks. Further, the set of available environmental and productivity measurements is limited at best in the poorly investigated tropical eastern Himalayas (which is rugged and difficult to access) where suitable data do not yet exist.

Previous multi-taxon studies have, in a traditional manner, attempted to explain the observed ‘peak location’ discrepancy using the popular approach of multivariate analysis i.e. regressing species richness on multiple environmental and geometric constraint variables. Explanations are then based on linking the empirical pattern with taxon specific aspects of life history that the ‘best’ environmental correlate explains (e.g. differential water dependence for liverworts, mosses vascular plants and ferns; Grau et al. 2007).

In an advancement over this frequentist approach, Colwell et al. (2016) proposed the integration of geometric constraints with environmental and historical correlates in their midpoint attractor model to explain taxon-specific attributes of patterns of species richness. The notion of bounded geometric constraints plays a significant role in this model and environmental and historical factors are incorporated implicitly as species' optimum elevation or as an underlying unimodal "*favourability*" gradient, which will be specific to each elevational transect and to each taxon. The relative strength of this attractor changes at every point along the domain, representing different optimum elevations for different species' range midpoints. The model predicted taxon-specific peaks in richness for a wide variety of taxa along the same gradient including a comparison of endothermic and ectothermic taxa. They stress that while the location of peak will be an emergent property of the taxon's ecology, a direct prediction of this peak, given a taxon's life history, might be complex at best since the environmental, historical and evolutionary factors that underlie midpoint attractors in nature are likely to be complex (Colwell et al. 2016). Our results were qualitatively similar to theirs (lower elevation diversity peak for ectotherms compared to endotherms in Costa Rica and New Guinea). Investigating their predictions for hawkmoths and birds in our dataset is part of a future plan.

Additionally, climatic history or palaeoclimate has also been proposed as a major driver of species richness patterns by oscillating thermal zones along the mountain slopes. Rapid rate of extinctions at the highest elevations and at the sea-level during glacial minima and maxima respectively has been shown to produce mid-elevation peaks for different taxa (Colwell & Rangel 2010). Our results, however, are contrary to the expectations of this stochastic, evolutionary model, in that a single insect family (*Sphingidae*) revealed a broader peak whereas the Avian class with 50 families yielded a narrow or sharper peak. The model parameter that dictates this property is the optimal level of founder species (which are correlated to the taxonomic level of the study group) and a lateral area effect. We can currently only speculate on the importance of such effects due to the lack of complete time-calibrated phylogenies (for hawkmoths) and climate reconstructions.

4.5.4 Elevational patterns in beta diversity

Organisms perceive and react to their environment depending on their resource requirements, dispersal ability, interspecific interactions and other life-history traits (Addicott et al. 1987; Kotliar and Wiens 1990, Mac Nally 2004, Nally et al. 2004). It follows that ecological specialization and spatial/geographical distribution will be correlated, and beta diversity should be greater among organisms with relatively specialized resource requirements than among relative generalists (Rabinowitz 1981; Gaston & Kunin 1997).

Our results on compositional similarity amongst communities (Figure 4.10) suggests that hawkmoths can be grouped into 5 elevational clusters. Ashton (2003) identified 5 different regimes of elevation in plant species distribution in neighbouring Bhutan: (below 900 m), 1000-1300 m, 1600-1900 m, 1900-2200 m and 2500-2800 m. These zones are quite similar to the elevational clusters seen in the hawkmoth data and are perhaps indicative of the strong dependence of herbivorous insects on the underlying vegetation structure.

Such elevational clusters were not observed in birds communities which showed a smooth locus of elevational communities across the NMDS plane . Possibly, birds are less directly linked to the plant species composition than hawkmoths, as their resource pool makes them any one amongst herbivores, insectivores, nectarivores, frugivores or granivores.

A decline in beta diversity along latitudes has been reported by several studies (Janzen 1967; Koleff & Gaston 2001; McKnight et al. 2007; Qian 2009; Kraft et al. 2011, etc). Stevens (1992) extended the hypothesis to altitudinal gradients stating that beta diversity should decline along mountains for the same reasons as towards higher latitudes. The climate is generally more variable at higher elevations (Huey 1978; Morin & Chuine 2006), and so high-elevation species may have wider climatic niches, and disperse farther than in the more stable climates of lowlands (Janzen 1967). While, at lower elevations and latitudes, lower climatic tolerance and, hence, faster allopatric speciation may result in narrower niche breadth, smaller ranges, and higher interspecific competition (Huey 1978, Morin & Chuine 2006, McCain 2009, Morin & Lechowicz 2013), and higher beta diversity.

Beta diversity patterns have mostly been studied using presence-absence data (and not species abundances), which limits insight into the underlying causative processes. Abundances are being increasingly used to estimate the turnover and nestedness components of beta diversity (Gaston and Blackburn 2000; Baselga 2010). These two components, which are due to different community processes, provided an additional dimension to the understanding of the structure and formation of ecological communities.

In a study on phylogenetic beta diversity of mammals using a global dataset, Peixoto et. al (2017) revealed that beta diversity across higher latitudes is mostly a result of lineage loss, whereas at higher elevations it is linked to lineage turnover. By analyzing global patterns of the contribution of phylogenetic beta diversity components, they show that dispersal determines the response of different lineages to geographical and environmental barriers.

In our study, we found that beta diversity reduced with elevation for both birds and hawkmoths (Figure 4.12). The compositional change was dominated by turnover with less than 20% attributable to nestedness at most elevations. This is in accordance with previous studies along tropical montane gradients (Bishop 2015 and references therein) which have attributed the high diversity to high species specialization or local adaptations leading to a relatively high turnover.

The decrease in compositional similarity of communities with increasing distance has been well documented (Nekola & White 1999; Nekola and Brown 2007; Soininen et al. 2007; Hillebrand et al. 2008). However, there is little consensus on the rate and extent of this decline across organismal groups and geographic/environmental gradients. In a meta-analysis of 401 distance-decay relationships Soininen et al. (2007) showed that it is higher for organisms that are actively mobile than among passively dispersed organisms. Hillebrand et al. (2008) remarked that this rate was greater for smaller organisms as they respond more intensively to fine scale variation in the environment due to their shorter generation times (Gillooly et al. 2002). Additionally, larger organisms are generally more vagile, which results in homogenization across greater distances (Soininen et al. 2007).

Two main explanations have been proposed for distance-decay of similarity. Tilman (1982) extended the niche theory to suggest that compositional differences between communities will increase with environmental distances, irrespective of their geographic proximity, as a result of species differences or competitive sorting of species with different physiological abilities. Composition at any site can thus be predicted from the environment because species differ in their ability to perform under different environmental conditions (Nekola & White 1999; Tuomisto et al. 2003; Gilbert & Lechowicz 2004). Neutral theory, by contrast, predicts that the decay of community similarity is caused by limited dispersal, independent of environmental differences between sites (Hubbell 2001; Astorga et al. 2012). Variation in rates of decrease in compositional similarity can be due to either differences in landscapes or in organismal dispersal abilities. It predicts that community similarity will decay with distance even if the environment is completely homogenous (Hubbell 2001).

It is now believed that these two concepts represent the extremes of a continuum and most natural ecological communities are structured by a combination of the two (Gravel et al. 2006; Astorga et al. 2012). However, since environmental and geographic distances are typically highly correlated, testing these hypotheses has been problematic and regressing community similarity against environmental and spatial distance remains the only way to determine their relative roles (Tuomistro et al. 2003; Gilbert & Lechowicz 2004). In Eaglenest, we found that the rate of species turnover with elevational distance was significantly higher for birds than for hawkmoths. This contradicts previous patterns (from meta analyses) that suggested higher turnover for smaller organisms with shorter generation times (Gillooly et al. 2002 ; Hillebrand et al. 2008). Many tropical forest bird species are known to have low mobility and are typically sedentary (Moore et al. 2008 and references therein). Anecdotally, tropical ornithologists have long known that certain bird species were very reluctant to cross water, pastures or sometimes even natural trails separating forest patches. Recently, experimental evidence from Amazonia suggests that many species rarely move across narrow gaps created by roads or natural trails but move readily through continuous forest and, less commonly, across small forest gaps (Moore et al. 2008). Unlike tropical birds, hawkmoths of south-east asia have demonstrated considerable dispersal abilities, colonizing widely throughout the Indo-Australian archipelago (Beck et al. 2006; Beck & Kitching 2007). As of now we have no basis for translating dispersal ability into elevational expanse; and the degree of confidence with which taxonomic boundaries have been delineated vary greatly between birds and hawkmoths. Therefore, our results will require the support of many more patterns from montane systems across the world before any useful attempt at understanding the underlying processes can be made.

4.6 Summary

1. Both birds and hawkmoths show a peaked diversity profile in multiple measures of alpha diversity, although, the peak was lower and broader in hawkmoths.

2. Interestingly, when each species was only represented by the mean elevation of its distribution while calculating the diversity the bird profile turned out to be much flatter, while hawkmoths continued to show a mid-elevation peak.
3. Our work has also brought out the crucial importance of low elevation data (below 700 m) in identifying the true profile. Data from this low elevation region is often unavailable in many studies as these elevations are subject to enormous anthropomorphic changes across the world.
4. The beta diversity reduced with elevation in a similar manner in both hawkmoths and birds. The change was dominated by species turn over rather than nestedness. On the other hand, there is some indication from NMDS analyses that elevational communities of moths are clustered into 5 groups while those of birds showed a smoother transition in community composition across the gradient. This may reflect the tighter linkage between lepidoptera and host plant species.
5. Birds showed a more rapid replacement of species with elevational distance.
6. The primary result from this study is that the elevational profiles of diversity of birds and hawkmoths are similar in some respects but different with others. This melange of similarity and dissimilarity of diversity patterns suggests a complex interplay between environmental factors and taxon-specific life history traits. It should also serve to focus attention on the subtle differences in the ecological parameters and processes being probed by the different metrics. The importance of coeval multiple-taxon studies along the same gradients has been highlighted before (e.g. Soininen et al. 2007).

Chapter Five

“Bergmann's Rule”

Taxonomic diversity, largely alpha diversity at the species level, has been the focus of most research in diversity patterns. However, other aspects of diversity – phylogenetic, morphological, functional traits – are very useful in understanding the important role of interspecific variations in community assembly and species coexistence (see Cisneros et al. 2014). In this and succeeding chapters we explore patterns of diversity of two functionally important morphological traits: body and wing dimensions.

5.1 Introduction

Directional variation in traits, exhibited either within or across (phylogenetically) closely related species, has often been shown to correlate with spatial (e.g. latitude, longitude, altitude, depth) or environmental (e.g. temperature, precipitation, salinity, productivity) variables (Gaston et al. 2008). These observations have led to the formulation of several ecogeographic rules which credit the spatial patterns to environmental gradients, of which the one linking latitudinal variation in body size to a general decline in temperature (Bergmann 1847) is most well known. Some of the others include an increase in range size attributed to higher climatic variability at higher latitudes (Rapoport 1982); broad geographic scale variation in plumage pigmentation of birds, believed to be driven by temperature (Gloger 1883); and the latitudinal variation in the number of vertebrae in fish is ascribed to water temperatures (Jordan 1892).

From the time these rules made their appearance (Bergmann 1849; Glogger 1883; Rensch 1948; Mayr 1956) there have been questions raised of their universality across taxa and across regions. Since then, various studies have returned a mixed bag of results – some confirming the rule, others supporting the “anti-rule”, and the rest providing no evidence one way or the other (Foster 1964; Ashton 2002; Sandars 2002; Ashton & Feldman 2003; Meiri & Dayan 2003; Brehm & Fiedler 2004; Lomolino 2005; Purvis & Orme 2005; Bromhan & Cardillo 2007; Dunn & Sandars 2007; Feldman & Meiri 2013; Zamora Camacho et al. 2014; Reimchen & Cox, 2015; Gouveia & Correia 2016; Freeman 2016; Beck et al. 2016). Quite likely the mixed results mean that some environmental factors are important for certain taxa, which follow the proposed rule; another set of environmental factors may be more important for other taxa, which follow the "anti rule"; while in those with no pattern either the previous processes are simply not valid or a complex set of factors may have trade-offs resulting in no observable pattern (Gaston 2008, Shelomi 2012; Gutierrez-Pinto et al. 2014).

Bergmann's rule for trends in body size across broad scale temperature gradients, remains a popular, though contentious, pattern in biogeography (Blackburn et al. 1999; Ashton 2001; Lomolino et al. 2006; Olalla-Tarraga 2011; Shelomi 2017). This popularity can be attributed to the direct implications of body size on many other important processes: physiological – e.g. respiration, reproduction and growth (Peters 1983); macroecological – e.g. size-abundance and size-diversity relationships (Backburn & Gaston 1994; Ritchie & Olff 1999); and evolutionary – e.g. rate of molecular evolution (Gillooly et al. 2005). Body size also scales with many life history traits such as dispersal, age at maturity, longevity, resistance to predation and other stressors (Rowe & Johansson 2000; Ellers & Jervis 2003; Dias et al. 2013, Greenleaf et al. 2007; Moretti et al. 2016). Moretti et al. (2016) present a comprehensive review showing that body size is important in linking organismal performance to environmental conditions or ecosystem processes.

The "rule" itself was formulated much after Bergmann's empirical test of the relationship predicted by thermoregulatory considerations of warm-blooded bird species. Claiming that the original German paper (Bergmann, 1847) was rarely read but widely and usually erroneously quoted, Salewski and Watt (2017) have discussed the content of and intent behind the original paper and "synthesize" a Bergmann's version of the Bergmann's rule as follows: that, all else being equal, *"within species and amongst closely related species of homeothermic animals [….] a larger size is often achieved in colder climates than in warmer ones, which is linked to the temperature budget of these animals"*. More generally, large-bodied homeotherms may be favored in colder climates due to their lower surface area-to-volume ratio and thus better heat conservation, whereas the smaller species would tend to inhabit warmer environments. The rule has been much debated throughout its long history (Watt et al. 2010) and much of the confusion is centered around three points **(a)** Whether the applicability of the rule is to intraspecific or interspecific variation in body size (Blackburn et al. 1999; Shelomi 2012)? **(b)** Is it still a ‘rule’ for a pattern independent of the thermoregulatory mechanism (Olalla-Tarraga, 2011)? **(c)** Is the rule inapplicable to ectotherms (McNab 1971; Watt et al. 2010)?

The opinion that Bergmann's Rule is inapplicable to ectotherms, though widespread in research, is justified only if we accept the classic thermoregulation-based explanations. Olalla-Tarraga (2011) addresses this by pointing to a long standing dictum among ecologists on avoiding the conflation of patterns and processes (Mayr 1963, Cushman et al. 1993, Blackburn et al. 1999, Lawton 1999, Chown and Gaston 1999, Gaston and Blackburn 2000, Ashton 2002). Decoupling the pattern in body size along environmental gradients from the process of thermoregulation allows the exploration of alternative ideas for ectotherms (e.g season length, starvation resistance, predator risk, etc) while still being able to address the validity of the pattern (Rydell & Lancaster 2000; Chown & Gaston 2010; Vinarski 2014 for a review on applicability of Bergmann’s rule to ectotherms).

Proposed originally for homeotherms (mammals and birds), vertebrates have received the most attention in investigations of Bergmann’s clines. Many reviews have attempted to comment on the generality (or lack thereof) of the ‘rule’. A meta-analysis by Meiri et al. (2003) classified 72% birds and 65% mammal species as consistent with Bergmann's Rule. Instead of compiling data from multiple individual studies that may be limited by either the small number of observations, low species numbers or small spatial scales of investigation, Reimer et al. (2017) used a large compilation (275,000 individuals) of digitized museum records spanning 960 species of mammals and birds to conclude that intraspecific Bergmann's Rule is neither a strong nor a general pattern (Reimer et al. 2017). This inconsistency of results from different studies warrants further investigations into the validity of the Rule even for endotherms – the group that led to the original idea.

Shelomi et al. (2012), in a review of the pattern for poikilothermic invertebrates, showed a lack of consensus amongst different studies with a majority of the studies showing no pattern in body size with elevation or latitude. Later, Vinarski (2014) attributed this to insufficient data and the likely involvement of multiple factors making the patterns idiosyncratic to the taxon and the region under investigation. Studies have demonstrated negative body size-temperature relationships, positive relationships and no trends in equal measure (Janzen et al. 1976; Hawkins de Vries 1996; Ashton and Feldman 2003; Chown & Klok 2003; Brehm and Fiedler 2004; Hodkinson 2005; Karl et al. 2008; Hu et al. 2011; Beck et al. 2016). A negative relationship in ectotherms, commonly known as a converse-Bergmann’s cline, is hypothesized to be mediated by season length (Atkinson 1994; Smith et al. 2000). Shorter seasons at colder latitudes and higher elevations restrict the body-size growth due to a reduction in time available for foraging, growth and development. This hypothesis was supported by a general finding that converse Bergmann clines are more commonly observed in larger bodied arthropods, such as Coleoptera and Orthoptera, which require a longer developmental time (Blanckenhorn & Demont 2004; Shemlomi 2012). Positive relationships have been attributed to different mechanisms such as feeding habits (Ochocinska & Taylor 2003), starvation resistance (Arnett & Gotelli 2003; Angilletta et al. 2004b) and recently thermoregulation (Zamora-Camacho et al. 2014).

The latitudinal trend originally proposed by Bergmann (1849) was extended to altitudinal variation after almost a century (Rand 1936). Compression of climatic zones over a short distance makes the study of biodiversity across these gradients manageable (McCain & Grytnes 2010). Historical contingency, and geological and evolutionary histories are more uniform across a montane diversity gradient than across latitudinal gradients.

It is important to understand and emphasise that studies differ in the way Bergmann's rule is investigated (see Gaston et al., 2008, for a review). The simplest is to look for a cline among populations of a species along an environmental gradient – the intraspecific Bergmann's Rule (we refer to it here as ***BR-P***, for an inter-population cline within a species). Sometimes such a study is undertaken using several closely related species, though this should strictly be called the interspecific Bergmann's Rule.

The interspecific investigation, sometimes termed the species-approach (***BR-S***), tests the relationship using species mean values for both trait and the environment variable, i.e. the number of points in the plot would be equal to the number of species (e.g. Freeman 2016; Alhajeri & Steppan 2016; Bai 2016; Beck et al 2016). This is because the data for the location and body size are often from different sources, e.g. body size from museum specimens and ranges from literature with possibly unequal sampling effort across the study (e.g. Gohli 2016). The species may or may not be closely related to each other.

Alternatively, one takes a community-approach (also called the assemblage Bergmann's Rule, by Gaston et al. 2008) in which there is one data point per environmental community. i.e. the trait values of all the individuals in the community, regardless of species, are averaged to find the mean trait for the community. Therefore, the number of data points in the plot will equal the number of communities across the environmental gradient. In the community or assemblage approach, there are two ways in which the community mean can be calculated: one is to weight the regional species mean (often from published sources or museum records) by the species abundance within the community to calculate the community specific mean – often termed the **BR-*CWM*** for Community (abundance) Weighted Mean (e.g. Brehm & Fiedler, 2004); the other is to measure and average the trait values of many or all the individuals in the community regardless of species, to arrive at the community trait mean – ***BR-CIM*** for community-individual-mean.

The last mentioned, ***BR-CIM,*** that we have followed in this work, is qualitatively and quantitatively different from the usual approach in that species identity is ignored to identify the typical body size at that elevation; this “ideal” body size for the community, independent of any species identity, should reflect the sum total of multiple life histories and eco-physiological processes impacting the community. Of course, any test of such a “Community/Assemblage Bergmann's Rule” would be most appropriate when the community is selected to represent a particular set of life history traits – e.g. big bodied hawkmoths, insectivorous birds, etc.

In the rest of this chapter we use the term Bergmann's Rule, without quotes, in its most general meaning of variation of body size with elevation/latitude, whether within a species, or a set of closely related species or at the level of a community of species. We explore the validity of Bergmann's cline in hawkmoths and birds along the same elevational gradient in Eaglenest. Since our data for birds came from published sources (Price et al 2014) we can only investigate the pattern using species means ... like in previous studies. We tested the size-elevation relationship with and without accounting for the phylogenetic non-independence of the species using published phylogeny of the two groups (species level for birds and genus level for hawkmoths). However, since we have estimated the body volume for individual hawkmoths we are able to investigate the pattern at the level of individuals across the entire community and also the intraspecific Bergmann’s Rule.

5.2 Analysis and Results

We assessed the elevational Bergmann's Rule for hawkmoths using all 4 approaches: BR-P, BR-S, BR-CWM, and BR-CIM, since we had individual traits only for moths, but only BR-S and BR-CWM for birds. At 1700 m elevation we could measure the traits for only 27% of hawkmoth individuals (98 out of 359) because of very heavy rain which prevented them from being photographed on the gridded screen. This sample size is in the range 171-418 (median = 260) individuals at other elevations. Therefore, we have calculated the results for hawkmoths with and without the 1700-m community.

Figure 5.1 shows the BR-CWM plots for hawkmoths, including the mean, median, 90th percentile and 10th percentile values at each elevation. The mean and median body mass shows a positive correlation with elevation, while the two percentiles do not.

Figure 5.2 shows the same plots for BR-CIM for hawkmoths. The results are very similar to BR-CWM.

Figure 5.3 shows the BR-CIM relationship between body length and elevation for hawkmoths. We have shown this plot as the body length is the most common surrogate used for body mass in most previous studies. This also shows a significant correlation of both mean and median body length with elevation.

Figure 5.4 shows the BR-CWM relationship for birds. In contrast with hawkmoths all the 4 plots (assemblage mean, median, 10th percentile and 90th percentile) show a very strong *converse-Bergmann* pattern with small sized birds dominating at higher elevations. The two percentile plots suggest that the entire distribution is shifting to lower values (again contrasting with the pattern for hawkmoths).

Figure 5.5 shows the BR-CWM data for birds and hawkmoths in the same plot to bring out the contrast between them.

Figure 5.6 shows the partitioning of body size variation in moths into turnover and intraspecific components and their covariation using *R 3.3.1 : CATI : decompCTRE* (Leps et al. 2011), wherein species turnover dominates the variation.

Figure 5.7 show the mean-normalised and unnormalised value of dispersion of body size (CWM) of birds and hawkmoths with elevation. There is a clear reduction of dispersion with elevation in birds in both cases. In comparison, the mean-normalised dispersion is almost flat for hawkmoths. The pattern is less clear in the case of unnormalised dispersion in hawkmoths. Smoothing over a 3-elevation window brings out a clear “mid-elevation peak” in the dispersion; the unsmoothed data shows no clear trend.

Figure 5.8, shows the BR-S relationship for birds and hawkmoths. The hawkmoths show no dependence on elevation for both the extremes of biomass normalisation of abundance (Figure 2.5). The birds showed a negative correlation between mean body mass and elevation but the same vanished when we analysed the relationship using the Phylogenetic Generalised Least Squares (pGLS) procedure (e.g. Freeman 2016). The pGLS analyses of hawkmoths was constrained by the availability of only the genus level phylogenetic tree (Kawahara et al. 2008). The species level phylogenetic tree for birds was obtained from Price et al. 2014. Pagel’s λ (Pagel 1997) was used to measure phylogenetic

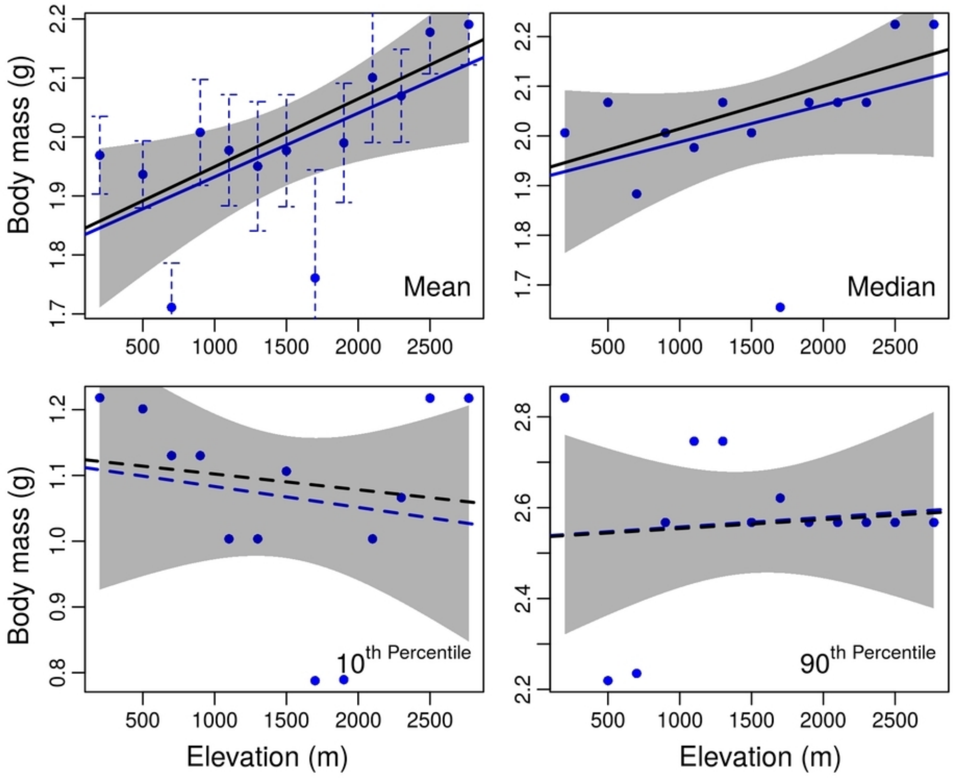


Figure 5.1 Elevational *profile of Community weighted mean (CWM) of hawkmoth body mass. The blue and black lines are the linear regression with and without 1700-m data, respectively. The shaded regions indicate the uncertainty of the fit.. CWM values were calculated using the elevational abundance of a species and its regional mean body volume, in line with the usual practice in many previous studies.*

Fit	Intercept	Slope x 10^{-4}	p.value	r^2
Mean (with 1700 m)	1.82 ± 0.07	1.08 ± 0.41	0.02	0.34
Mean (without 1700 m)	1.83 ± 0.05	1.15 ± 0.31	< 0.005	0.54
Median	1.91 ± 0.08	0.74 ± 0.49	0.16	0.10
Median (without 1700 m)	1.93 ± 0.04	0.85 ± 0.24	< 0.01	0.51
10th Percentile (with 1700 m)	1.12 ± 0.09	-0.32 ± 0.55	0.57	-0.06
10th Percentile (without 1700 m)	1.13 ± 0.08	-0.24 ± 0.48	0.63	-0.08
90th Percentile (with 1700 m)	2.54 ± 0.11	0.21 ± 0.66	0.76	-0.08
90th Percentile (without 1700 m)	2.54 ± 0.12	0.20 ± 0.70	0.79	-0.09

signal. The colour-coded map of body size on the phylogenetic trees are shown in Figure 5.9. We obtained λ = 0.74 for hawkmoths and λ = 1 for birds, indicating strong phylogenetic conservatism in body size. The Brownian motion model of trait evolution, supported by AICc comparison, was used in the analyses (Table 5.1). The table in Figure

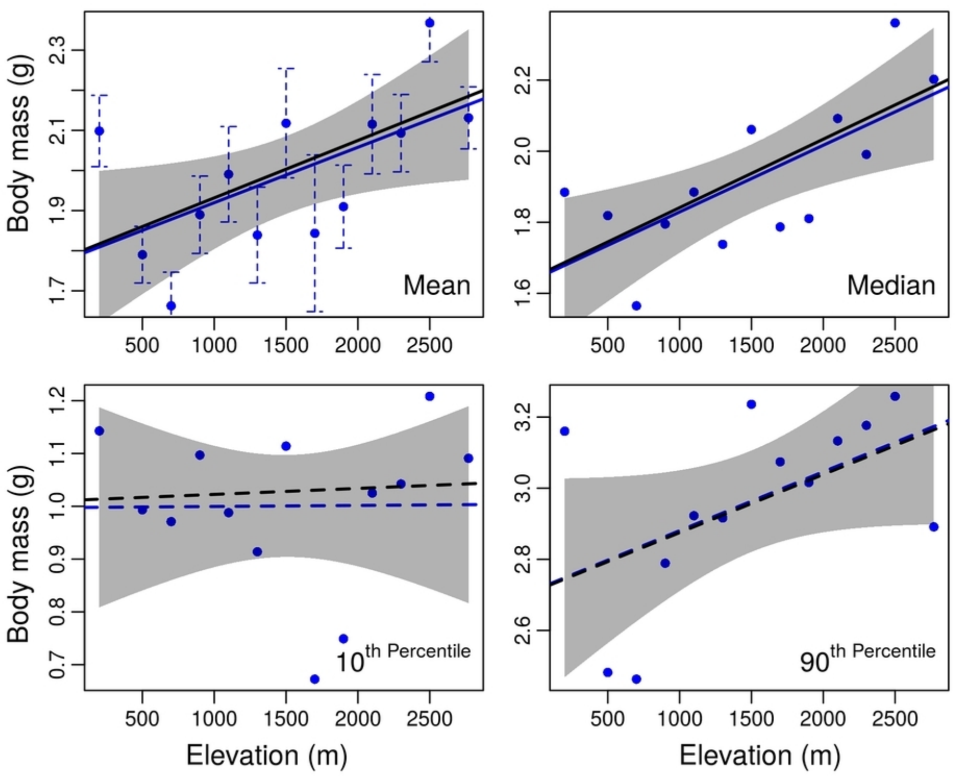


Figure 5.2 *Elevational profile of Community means (CIM) of hawkmoth body mass. The blue and black lines are the linear regression with and without 1700-m data, respectively. The shaded regions indicate the uncertainty of the fit. CIM values were calculated using using the trait values of individuals at each elevation..*

Fit	Intercept	Slope x 10^{-4}	p.value	r^2
Mean (with 1700 m)	1.78 ± 0.10	1.38 ± 0.57	0.03	0.29
Mean (without 1700 m)	1.79 ± 0.10	1.43 ± 0.57	0.03	0.33
Median	1.64 ± 0.10	1.88 ± 0.57	< 0.005	0.45
Median (without 1700 m)	1.65 ± 0.10	1.93 ± 0.56	< 0.005	0.49
10th Percentile (with 1700 m)	1.01 ± 0.09	0.10 ± 0.06	0.97	-0.09
10th Percentile (without 1700 m)	1.01 ± 0.08	0.11 ± 0.45	0.81	-0.09
90th Percentile (with 1700 m)	2.72 ± 0.14	1.66 ± 0.84	0.08	0.19
90th Percentile (without 1700 m)	2.71 ± 0.15	1.63 ± 0.90	0.09	0.18

5.8 shows no significant correlation between body size and elevation for either bird species or hawkmoth genus.

Additionally we explored BR-S for bird species within individual families which had at least 2 species in them. The linear regression coefficients are listed in Table 5.2. Only two familes (*Pellorneidae* & Corvidae) showed significant relationships but their slopes were

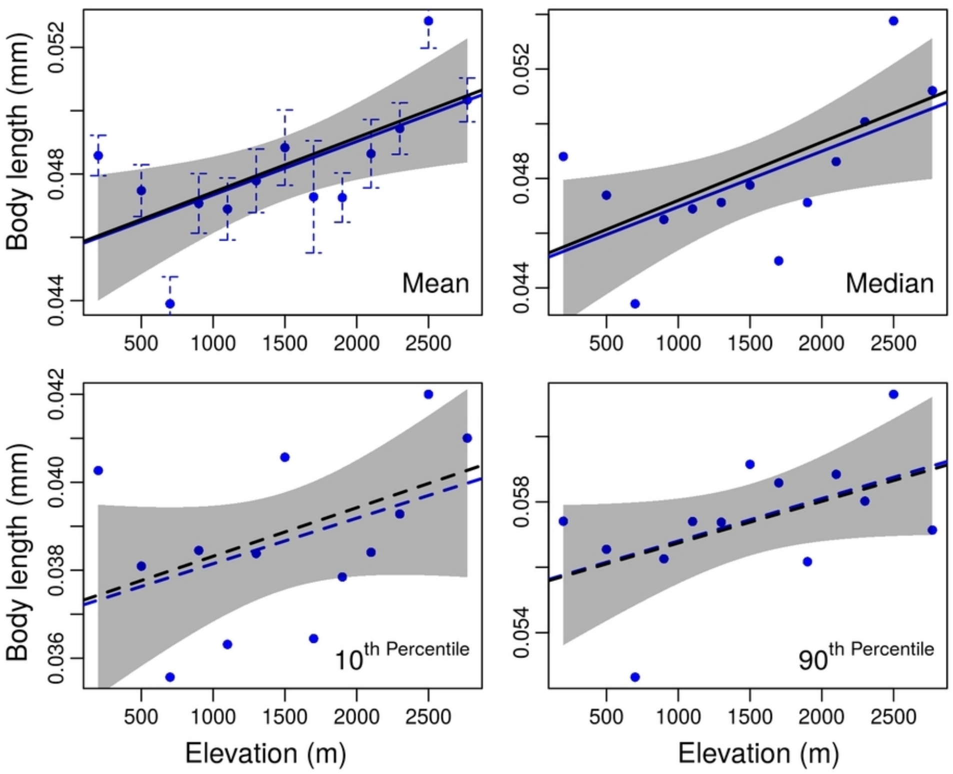
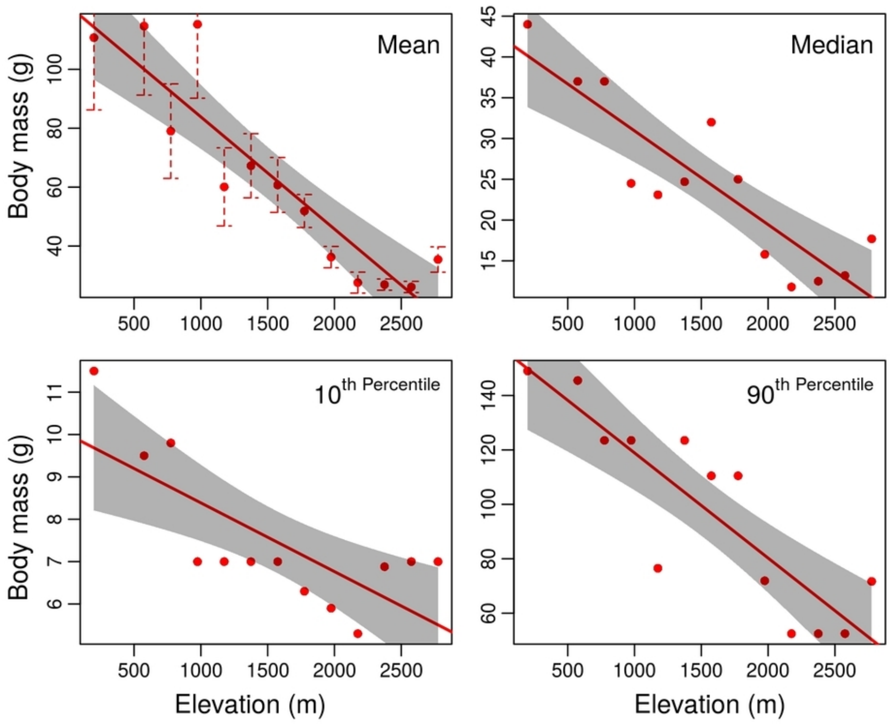


Figure 5.3. *Elevational profile of Community means (CIM) of hawkmoth body length. he blue and black lines are the linear regression with and without 1700-m data, respectively. The shaded regions indicate the uncertainty of the fit. CIM values were calculated using using the trait values of individuals at each elevation.*

Fit	Intercept x 10^{-2}	Slope x 10^{-6}	p.value	r^2
Mean (with 1700 m)	4.57 ± 0.10	1.69 ± 0.59	0.02	0.37
Mean (without 1700 m)	4.57 ± 0.10	1.72 ± 0.61	0.02	0.39
Median	4.49 ± 0.13	2.03 ± 0.79	0.03	0.32
Median (without 1700 m)	4.51 ± 0.12	2.13 ± 0.72	0.02	0.41
10th Percentile (with 1700 m)	3.71 ± 0.11	1.03 ± 0.65	0.14	0.11
10th Percentile (without 1700 m)	3.72 ± 0.11	0.11 ± 0.62	0.11	0.16
90th Percentile (with 1700 m)	5.55 ± 0.11	1.30 ± 0.65	0.07	0.20
90th Percentile (without 1700 m)	5.55 ± 0.11	1.28 ± 0.67	0.09	0.19

not consistent with each other.

We also tested the intraspecific Bergmann's Rule (BR-P) while combining data points from all species to increase the signal, if any. We transformed the elevation and the trait to the deviation from the mean for a species, i.e. $\mathbf{E' = E - \mu_{E\text{-}sp}}$ and $\mathbf{B = (B - \mu_{B\text{-}sp})/\mu_{B\text{-}sp}}$ or $\mathbf{B = (B - \mu_{B\text{-}sp})/\sigma_{B\text{-}sp}}$ for every individual. The combined data for the entire hawkmoth sample is



Fiigure 5.4. ***E****levational profile of Community weighted means (CWM) of bird body mass. The line and the shaded area are the fit and uncertainty of linear regression. The CWM values were calculated using the elevational abundance of a species and its regional mean body volume ... in line with the usual practice in many previous studies.*

Fit	Intercept	Slope x 10^{-6}	p.value	r^2
Mean	122 ± 9	-0.04 ± 0.005	< 0.001	0.82
Median	42 ± 3	-0.01 ± 0.002	< 0.001	0.76
10th Percentile	10 ± 0.8	-0.002 ± 0.0004	< 0.005	0.53
90th Percentile	157 ± 11	-0.04 ± 0.007	< 0.001	0.74

shown in Figure 5.10. It shows a very weak (r^2 = 0.02) but significant relationship ($p < 0.05$) suggesting that the intraspecific variation, at least when averaged over all the species, is quite small, if at all.

5.3 Discussion

Our results provide evidence for strong and contrasting trends of mean community body size with elevation for birds (negative correlation) and hawkmoths (positive). The effect seems to be stronger in hawkmoths when individual trait values are used instead of regional species means. We do not have individual trait data for birds for a similar

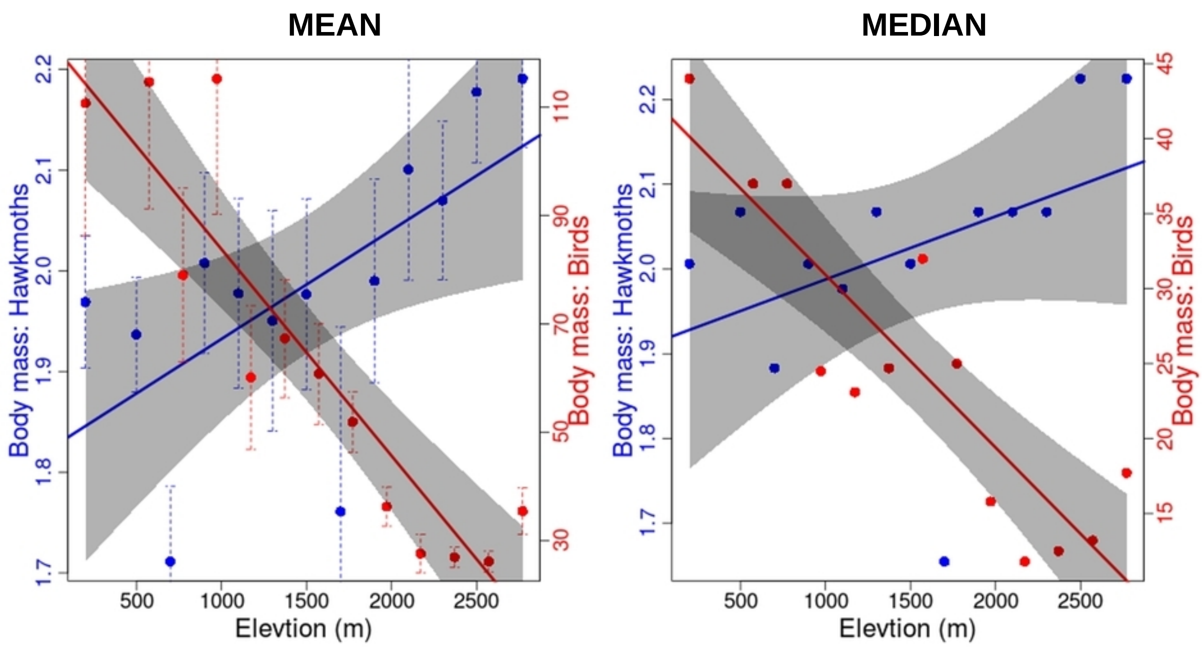


Figure 5.5 *Elevational profile of community mean and median (CWM) for hawkmoths (blue) and birds (red). The plots are the same as in Figures 5.1 and 5.4 and are plotted with a dual-Y axis to facilitate a direct comparison between the two taxa.*

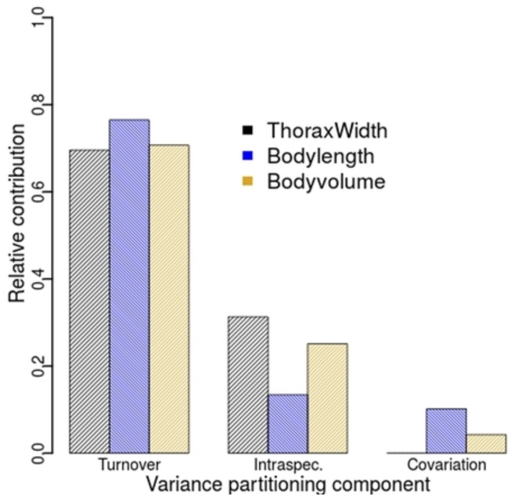


Figure 5.6 *Variance partitioning of thorax width, body length and body volume for hawkmoth individuals showing maximum contribution of species turn over*

analysis. Furthermore, the reduction in assemblage body size in birds seems to be accomplished by a downward shift in the entire distribution of trait values. On the other hand, the increase in assemblage body size in hawkmoths seems to be due to an increase in the upper envelope of the distribution without a change in the lower tail.

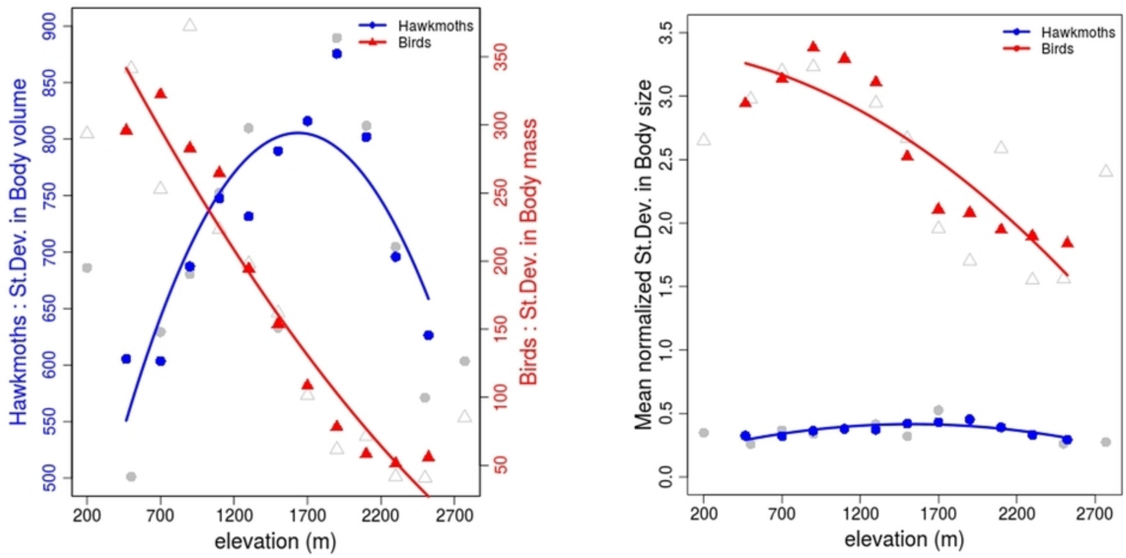
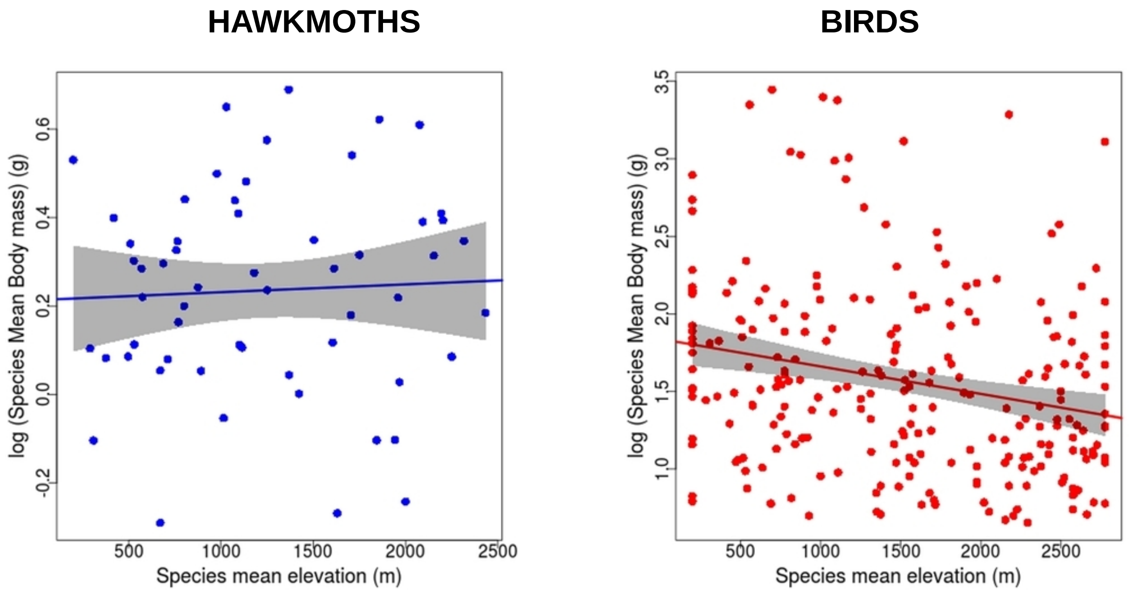


Figure 5.7 *Dispersion in body mass for hawkmoths (blue) and birds (red). Values are presented for standard deviation (left) and mean normalized standard deviation (right).*

Interestingly, the species plot for body size versus elevation shows no correlation in hawkmoths; there is indeed a negative correlation in birds but this vanishes when the data is corrected for phylogenetic relatedness. We also show there is no evidence for intra-familial relationship between body size in birds.

As discussed in the Introduction, the form of the Bergmann's Rule tested may be consequence. In our study there is a clear detection of the assemblage pattern with elevation, but not of the interspecific or intraspecific pattern. One way of understanding the results from the three patterns is to ascribe the change in assemblage mean body size to species tun-over. This indeed is seen in the variance partitioning analysis in the case of moths for which we had individual trait data. It does have an intra-specific component but the same has not been detected at a significant level with individual species.One possible explanation for the observed contrasting pattern for the two taxa is that body size of (endothermic) birds is limited by the need to feed throughout the year. Species at higher elevations can only sustain a smaller body size due to reduced food availability at higher elevations, especially in winter. McNab (2010) has argued that body size trends along



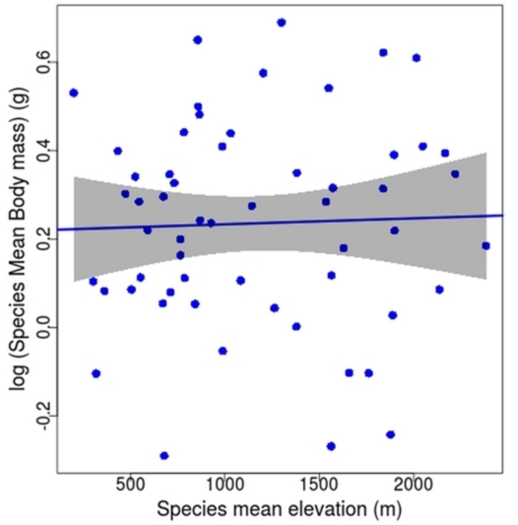


Figure 5.8 *Log of species mean body size (body volume for hawkmoths and body mass for birds) plotted against the species mean elevation (robust mean of abundance weighted elevational range). Figure to the left shows the same plot for hawkmoths using biomass-corrected abundances of each species to calculate optimum elevation.*

Fit	Intercept	Slope x 10^{-5}	p.value	r^2
Hawkmoths	0.21 ± 0.070	1.77 ± 4.96	0.72	-0.02
Hawkmoths (biomass corrected)	0.22 ± 0.068	1.36 ± 5.29	0.80	-0.02
Birds	1.84 ± 0.080	-0.18 ± 0.05	< 0.005	0.56

After accounting for phylogeny from PGLS using Brownian motion model of evolution

Fit	Slope	p.value
Hawkmoths	-0.43 ± 0.43	0.30
Hawkmoths (biomass corrected)	0.0001 ± 0.0008	0.10
Birds	0.003 ± 0.013	0.83

Data		model	AICc
Hawkmoths	Body mass ~ genus phylogeny	Pagel’s Model	343.99
		Ornstein Uhlenbeck	345.43
		Brownian motion	**342.64**
Birds	Body mass ~ species phylogeny	Pagel’s Model	2450
		Ornstein Uhlenbeck	2450
		Brownian motion	**2448**

Table 5.1: *AICc values for trait evolution models*

geographic gradients depends heavily on the abundance, availability and size of resources, a mechanism he termed the “resource rule”.

On the other hand, (ectothermic) hawkmoths are most active and breed during the summer rains. Therefore, winter food availability may not be a constraint when the population, either as eggs or as larvae, are dormant. Their larger body volume may be more effective at retaining heat further into the night when they are most active. Several studies have remarked on the difference between the Bergmann pattern and the Bergmann process. We have shown here a clear difference in the pattern for two taxa with very different life histories, even at the same location. This suggests that different processes are acting on the two taxa, or at least, more than one process is at work and with different impacts on the two.

Endotherms

The original Bergmann's process was based on heat loss as a function of body surface area to volume ratio. While the pattern itself has been seen in many endotherms (review in Meiri et al. 2012) alternative mechanisms such as selection pressure, resource availability, and length of the growing season have been explored (e.g. Teplitsky & Millien 2013).

The Converse Bergmann's Rule seen in birds in our study is in line with previous results: e.g. in certain clades of New Guinean passerine birds (Freeman et al. 2016) and torrent

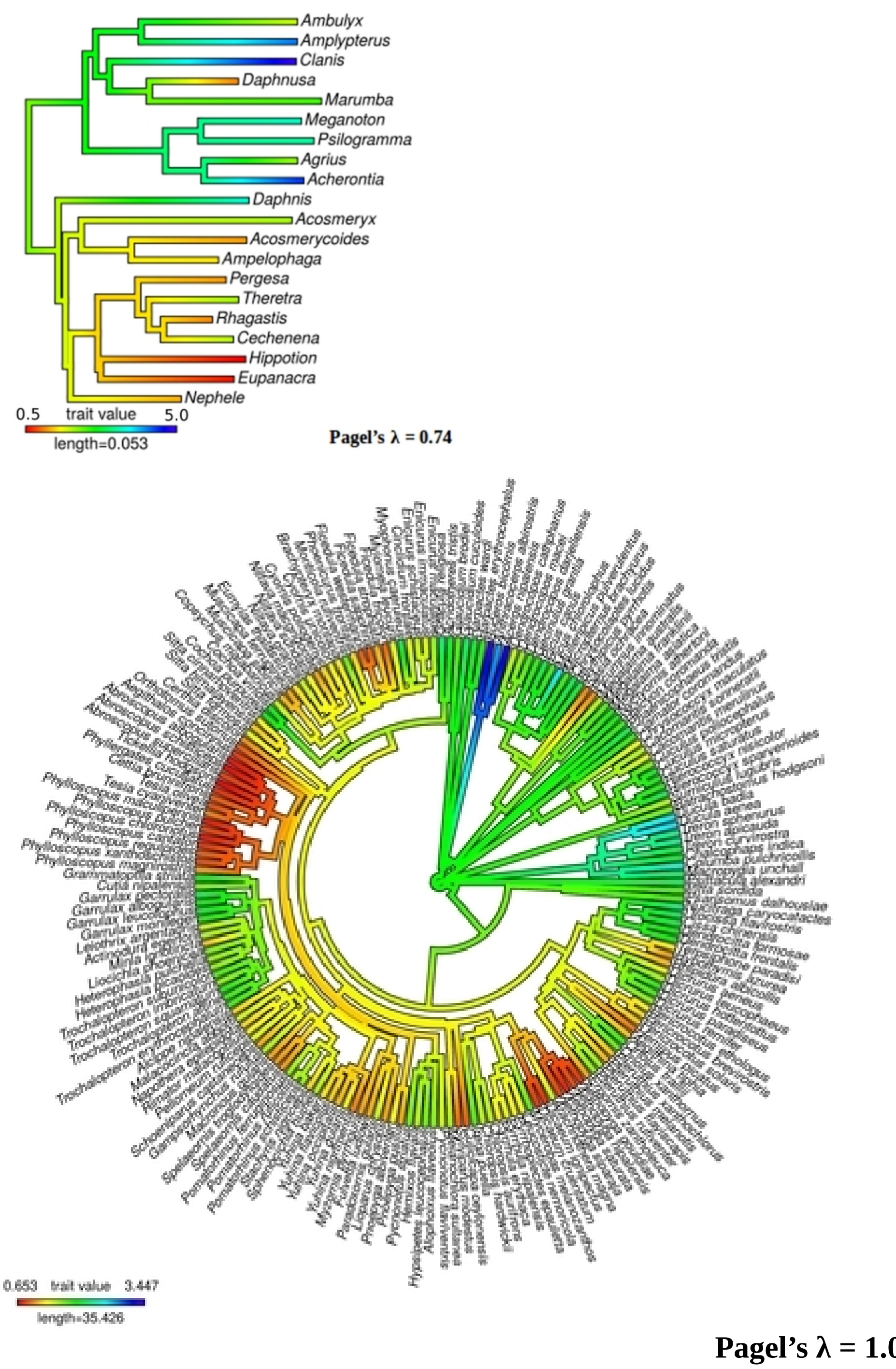


Figure 5.9 *Evolution of Conitnuous trait of log(body mass) reconstructed using 'contMap' function in the phytools R package for hawkmoth genera (left) and bird species (below). The hawkmoth genus level phylogeny was from kawahara et al (2009) while the bird species level phylogeny is from Price et al. (2014). Both groups showed strong phylogenetic conservatism of body mass.*

ducks in the Andes (Gutierrez-Pinto et al. 2014). Clearly, the pattern cannot be a direct result of thermoregulatory consideration here. Rodriguez et al. (2008) suggested that fasting endurance is more important than heat conservation for the smaller mammals at

Family	Slope	Std. Error	$N_{SPECIES}$	P value
Muscicapidae	1	8	26	0.92
Leiotrihidae	-7	11	25	0.55
Picidae	-43	38	14	0.28
Culculidae	12	20	11	0.55
Timaliidae	-3	6	11	0.60
Phylloscopidae	1	1	11	0.24
Scotocercidae	1	1	11	0.46
Columbidae	-10	75	8	0.90
Phasianidae	157	321	8	0.64
Sylviidae	-4	5	8	0.50
Fringillidae	16	2	8	0.53
Pellorneidae	**-9**	**4**	**7**	**0.05 ***
Pycnonotidae	10	8	6	0.29
Zosteropidae	2	2	6	0.34
Dicruridae	-21	17	6	0.28
Corvidae	**41**	**10**	**5**	**0.03 ***
Viereonidae	7	10	5	0.57
Accipitridae	-1156	1027	5	0.34
Campephagidae	1	11	5	0.95
Nectariniidae	-2	6	5	0.79
Bucerotidae	1766	1091	4	0.25
Paridae	-16	5	3	0.18
Sittidae	-2	5	3	0.73
Ramphastidae	11	42	3	0.83
Dicaeidae	2	4	3	0.69
Doubleton Families	-16	19	12	---

Table 5.2 *Linear regression of body mass versus elevation within bird families. Slope values represent change in body mass (g) for every 1000 m elevation. Significant values are highlighted in blue/bold*

higher elevations in the Neotropics. Reduced wing loads, i.e. lower body mass per wing area, may compensate for the lower air density at high elevations (Altshuler & Dudley 2002; Altshuler et al. 2004; Gutierrez-Pinto et al. 2014). Lower oxygen level has been

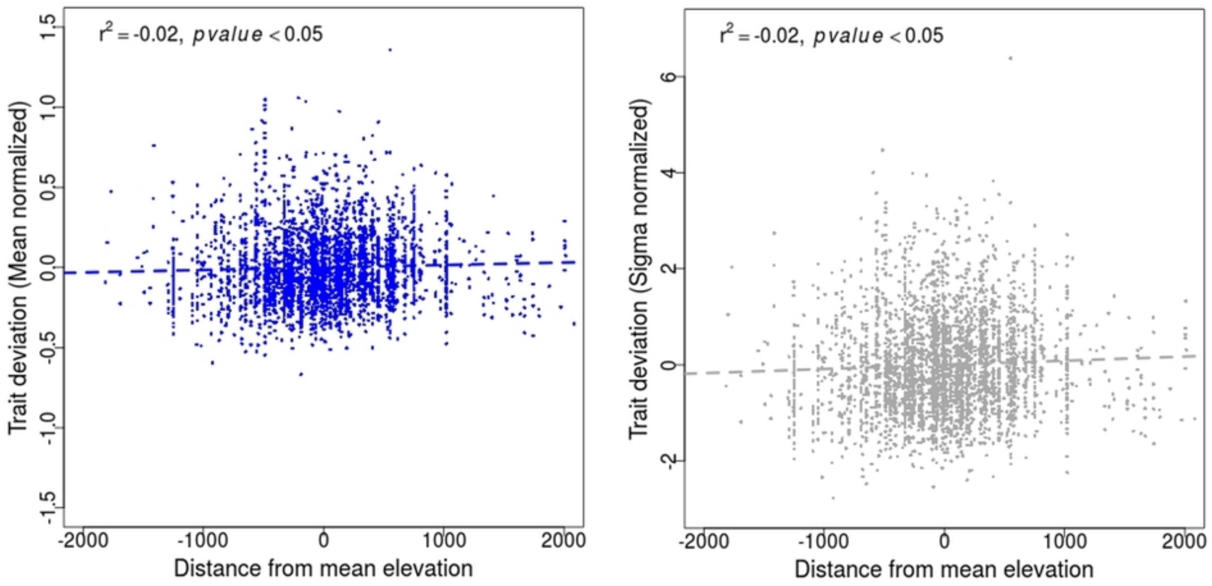


Figure 5.10 *Intraspecific variation in hawkmoth body mass. The data plotted is the normalised body mass deviation from the species mean, which allows for combining data from all species to detect intraspecific variance. Left: fractional change in each species; Right: change in units of standard deviation in each species. Both plots show a very weak but significant correlation.*

demonstrated to decrease digestive efficiency; this may lead to a smaller body size in lizards and mammals (Jin et al. 2006, 2007; Liao et al. 2006). Sun et al. (2016, 2017) have shown heavier hearts and lungs in Eurasian Tree Sparrows at higher elevations in China.

MacNamara et al. (2015) developed a simple optimization model for an endotherm that showed that optimal body size can either increase or decrease with temperature, depending on several important aspects of the animal’s physiology and environment including the incidence of foraging interruptions, predator density, relative likelihood of long food shortages and predator evasion strategy. They also highlighted the importance of considering the different measures of body size (e.g. total mass versus adipose ratios).

Fristoe et al. (2015) showed from theoretical considerations that the interplay between physiological (basal metabolic rates and thermal conductance) and morphological traits allow endotherms to persist in a wide range of temperatures. They concluded that despite the large effect of body size on thermal physiology, size alone only moderately influences the range of environmental temperatures where a species can occur.

Finally, the most recent meta-analysis on the subject by Riemer et al. (2017) notes that the generality of the Bergmann’s rule, as previously suggested by earlier reviews (Meiri et al. 2012) may be influenced by publication bias and selective reporting where studies or individual analyses that do not support Bergmann’s rule are published less frequently. Using data from a large compilation of digitized museum records to evaluate the intraspecific relationship between temperature and mass for 960 mammal and bird species, spanning 275,000 individuals, they demonstrated that Bergmann’s rule is neither a strong nor a general pattern. They also found a greater proportion of species that had significant negative, rather than positive, relationships for latitudinal trends in body size.

Taken together, these results imply that environmental factors other than absolute temperatures might be more important in shaping endotherm communities with respect to the ecologicially important trait of body mass. Our study, though not conducted to explicitly test any particular mechanism for the observed negative relationship between body size of birds and elevation, provides strong support against the classical thermoregulatory mechanism for Bergmann’s clines and warrants further investigations into the likely mechanism governing body size patterns for endotherms.

Ectotherms

As in the case of endotherms, there is no universality of pattern for ectotherms, which demonstrate positive-, negative-, and no-trends in equal measure (Ashton & Feldman 2013; Brehm & Fiedler 2004; Olalla-Tarraga & Rodrigues 2007; Watt et al. 2010; Hu et al. 2011; Zamora-Camacho et al. 2014;Beck et al. 2016). More recently, Blanckenhorn & Demont (2004) and Shelomi (2012) have found that converse Bergmann clines are more commonly observed in larger bodied arthropods, such as Coleoptera and Orthoptera, as these species tend to have longer development times. Other explanations put forward include, but are not restricted to, starvation resistance (Backburn & Hawkins 2004), resource use (Brown & Maurer 1989), host plant distribution in case of herbivores such as moths (Lindstroem et al. 1994), diet specialization (Davies et al. 2012), and phylogenetic conservatism (Wiens et al. 2010; Gaston & Chown 2013).

Even though the thermoregulatory mechanism as proposed by Bergmann for a positive association of body size with temperature is less likely to hold true for ectothermic insects that rely on heat from their environment to thermoregulate, negative associations between body size and temperature demonstrated for several ectotherms have led to explicit investigations into the mechanism (Zamrora-Camacho et al. 2014).

Although a larger ectotherm would retain body heat for a longer time, it would also require a larger time to warm up from an external heat source (Stevenson, 1985). The nett heat gain would depend on the heating- (α) and cooling- (β) capacities as a function of body size (Carothers et al. 1997). Both cases, of $\alpha > \beta$ (e.g. Iberian rock lizard; Carrascal et al. 1992), and $\beta > \alpha$ (*Liolaemus altissimus* and *Psammodromus algirus;* Carothers et al. 1997; Zamora-Camacho et al. 2014), are known in ectotherms. Zamora-Camacho et al. (2014) found that cooling rates in *Psammodromus* decreased significantly with elevation along a 2200m elevational gradient in Sierra Nevada, Spain.

Flying insect taxa, such as the Sphingidae, inhabit a continuum from fully environment-controlled body temperatures to active thermoregulation by wing-muscle activity (Heinrich 1993). Hawkmoths, especially, are known to raise their body temperature well above that of their surroundings using their large wing muscles. They are known to regulate thoracic temperatures to within 2-3ºC of the ambient (Heinrich 1993; Heinrich 1974). Thus, as facultative endotherms, thermal explanations for Bergmann's rule that are normally applied to endothermic vertebrates could potentially operate in the hawkmoths of EWS, which exhibit a positive association between body size and altitude. Bergmann's clines have been reported for other moth families previously (Beck et al. 2017; Brehm & Fiedler, 2004) however temperature as the major mechanism has not found much support.

The many explanations proposed above should not be treated as mutually exclusive (e.g. Rodriguez et al. 2008; McNab 2010; Yom-Tov & Geffen 2001; Pincheira-Donoso & Meiri 2013; MacNamara 2015). Several mechanisms may act in concert with the differential weighting depending on location and taxon (MacNamara 2015). We also note that Martinez *et al.* (2013) have pointed out that some patterns of geographical variation in morphology may have no adaptive basis.

The significant size selection at the level of an assemblage without a corresponding interspecific or intraspecific pattern suggests the role of environmental filters. In the case of birds, the reduction of body mass with elevation is also accompanied by a marked reduction in dispersion of body mass in each elevation. This reduction in dispersion is true even when it is normalised by the mean. In the context of environmental filters this would correspond to a stronger selection effect at higher elevation. We are not aware of any such previous result. The case of hawkmoths is even more peculiar: the absolute dispersion has a mid-elevation peak while the normalised dispersion is more or less flat. The issue of environmental filters vis-a-vis inter- and intra-specific competition in the hawkmoth community is dealt with in greater detail in a later chapter.

5.4 Summary

1. Investigations into Bergmann’s rule (body mass v/s elevation) at the assemblage, inter-specific and intra-specifc scales show differing relationships even within the same data set.
2. At the assemblage level, birds and hawkmoths show strong and contrasting trends with hawkmoths increasing in size with elevation, while birds decrease.
3. At the interspecific level (and intraspecific for hawkmoths), neither show a strong or significant association between body mass and elevation.
4. Species turnover may explain the observed discrepancy across the different levels.
5. Increased body size with elevation for flying insect taxa has been associated with active thermoregulation using flight muscles, where as a selection for smaller body size in endothermic birds may be attributed to limited resources.

Chapter Six

Wing Allometry and Flight

6.1 Introduction

In this chapter, we focus on the relationship between body mass (discussed in the previous chapter) and wing size. The relationship between these two traits determine the flying capabilities of organisms.

Allen's rule is an eco-physio-geographical rule which proposes that the relative sizes of appendages decrease with latitude (Allen 1877; Ray 1960). The selection for smaller limbs, fins, tails, beaks or wings has been attributed to a selection for reduced surface-to-volume ratio that will minimize heat loss and promote thermoregulation in endotherms (Symonds et al. 2010). The rule has received little attention compared to others such as Bergmann’s and Rapoport’s rules (Alho et al. 2011). Empirical support is mostly restricted to latitudinal clines within individual species (e.g. Ray 1960; Fooden & Albrecht 1999; Yom-Tov et al. 2002; Ryland et al. 2017), with very few interspecific studies (e.g. Cartar & Morrison 2005; Nudds & Oswald 2007; Symonds & Tattersall 2010). There has been a revival in recent times in the context of global climate change (e.g. Yom-Tov et al. 2006; Alho et al. 2011).

Most studies of Allen's rule have focused on exposed appendages such as limbs, beaks, antennae, etc., which may have a thermoregulatory role (Rensch 1938; Mayr 1970; Snow 1954; Partridge & Pring-Mill 1977; Laiolo & Rolando 2001; Bull 2006). Wings, apart from being sheathed in insulation like feathers (birds) or scales (lepidoptera), may be involved in selective trade-offs given their important role in flight; for instance, if the body becomes larger in response to decreasing ambient temperatures, the wing area may increase to compensate for it, contrary to Allen’s rule (Schmidt & Nielsen 1972; Hainsworth 1981; Starmer 1988, Alerstam et al. 2007). Flight is a key ecological trait in most birds and insects and used for foraging, predator avoidance and finding mates. While flying an organism must produce enough lift to counteract the downward pull of gravity due to the organism's weight (Norberg 1985; Weinstein 2015). Wing-loading, the ratio of body-mass to wing-area determines the efficiency and ease of flight. Organisms with lower wing-loading have a higher stalling speed associated with greater flight speeds and decreased manoeuvrability (Pennycuick 1971, 1975; Norberg 1985; Nachtigall 1985; Alerstam et al. 2007). Wing-loading is subject to both genetic (evolutionary) and short term (plastic) environmental influences that produce both intra- and inter-specific variation among closely related species (Feinsinger & Chaplin 1975; Gilchrist & Huey 2004).

Johnston (1969) found that house sparrows across Europe show a persistent positive relationship between summer temperatures and wing bone lengths. In contrast, Huxley (1942) showed that in almost 80% of birds in five families of non-migratory North American birds wing length decreased with increasing latitude. Selection for larger body mass without a concomitant increase in wing length has been reported (Snow 1958; Hamilton 1961; Rand 1961; Johnston & Selander 1964, 1972, 1973) and attributed to the benefits of increased size for thermoregulation, especially in the case of endotherms (Blem 1975). These multiple patterns are indicative of the conflicting selection pressures on the wing.

In ectotherms, the theoretical expectations under the thermoregulatory adaptation hypothesis of Allen’s rule are less obvious and is reflected in even fewer studies than in birds. In insects, most appendages, including wings and antennae, are connected to the circulatory system (Chapman et al. 2013), and the constant flow of haemolymph through these appendages can contribute to thermoregulation, as in endotherms. Patterns equivalent to Allen’s rule might thus be expected.

Body temperature in insects may depend on factors other than the relative surface area alone as they are known to exhibit behavioural regulation of temperature such as basking (e.g. Butterflies). Like in birds, the thermoregulatory selection pressures of wings are likely to be in conflict with the requirements of flight: a larger wing area reduces flying effort as well as facilitates take-off at cooler temperatures (Dillon and Frazier 2006, Frazier et al. 2008; Rohner et al. 2018). Low temperature has a negative effect on the wing beat frequency (e.g. in *Drosophila*; Unwin & Corbet 1984) and it is proposed that flying insects adapted to highlands compensate for these effects by reducing wing load (e.g. *Drosophilla melanogaster*: Azevedo et al. 1998), but the generality of such clines awaits confirmation. Whether and under what circumstances the relative size of insect wings increases or decreases with environmental temperature remains unclear.

The relationship between morphological traits are usually investigated in the form of allometric relationships, in which the variation of a particular trait is expressed as a scaling power law with respect to some other trait (usually body size or mass), i.e. $\mathbf{Y = A(body)^B}$, while examining the generality of the index B within and across species and higher taxonomic groups (Huxley 1924, 1932; Huxley & Teissier 1936; Voje et al. 2014).

Based on a simple physics model and scaling laws, Athreya & Singh (1989) showed that in raptors with flapping flight, like *Accipiter* hawks, mass ~ (wing-length)^3, while in raptors which habitually glide, like *Aquila* eagles and *Gyps* vultures, mass ~ (wing-length)^2. We will discuss more elaborate flight allometry models proposed in recent years (e.g. Skandallis et al 2017) later on in this chapter. Since the density of air, wind speeds and ambient temperature change from place to place (e.g with elevation) we can expect the flight dynamics, and hence wing allometries to change across (elevational) communities.

Voje et al (2014) have studied the relationship between allometries within and across species and clades in terms of their evolvability. They find limited micro-evolution in allometric indices while changes seem to be more common on scales of millions of years.

Finally, we recall here the point made by Gaston et al. (2008), that we already mentioned in Chapter 5, of the importance of explicitly distinguishing between three taxonomic levels at which spatial patterns in biological traits are investigated, i.e. intra-specific, inter-specific and assemblage (or community). The generality of any ecogeographical rule across the different levels remains a matter of debate, and we are not aware of any previous study that has tested flight allometries at all 3 levels with the same data.

6.2 Specific objectives

Using the wing measurements for individual hawkmoths and species means for birds, we have investigated the following in this chapter:

1. Allometry of wing area at the intraspecific, interspecific and assemblage levels.
2. Elevational profile of residual-wing and wing-loading of species and communities.
3. Phylogenetic conservatism in residual-wing for hawkmoths

Wing-loading is the ratio of the wing area to body mass. Residual wing is the excess of wing after subtracting the assemblage fit to the wing-area – body-mass allometry. The wing area used was the square of the wing-chord length (from literature) for birds, and for hawkmoths it is the area of the triangle defined by the 3 vertices of a wing from our calibrated images (details in Chapter 2).

6.3 Analyses and Results

In Figure 6.1 we have plotted the allometric relationship between wing area and body mass of birds and hawkmoths across all species (individuals in case of hawkmoths). The slope of the linear fit for birds and hawkmoths was very similar at 0.73 ± 0.02 and 0.71 ± 0.01, respectively

Figure 6.2 shows the allometric slopes within each genus of hawkmoths. It shows that these individual allometries are quite different from the average for the assemblage as a whole. Indeed, the values for all genera are below the community mean.

Figure 6.3 shows the plot of residual-wing for each individual moth. The means and standard deviations of all species with more than 25 individuals are marked on the plot.

Figure 6.4 shows the elevational profile of the community mean and standard deviation of residual-wing. Residual-wing was obtained by subtracting the regional assemblage allometry of wing area (Figure 6.1). The community mean residual-wing increased with elevation for hawkmoths but decreased with elevation for birds. However, the standard deviation reduced with elevation for both.

Figure 6.5 shows the elevational profile of the community mean and standard deviation of wing-loading. The community wing-loading mean and standard deviation decreased with elevation for both hawkmoths and birds. Figure 6.6 shows the elevational profile of species mean wing-loading and residual-wing. Contrary to the case of residual-wing, wing-loading decreased with elevation for both taxa.

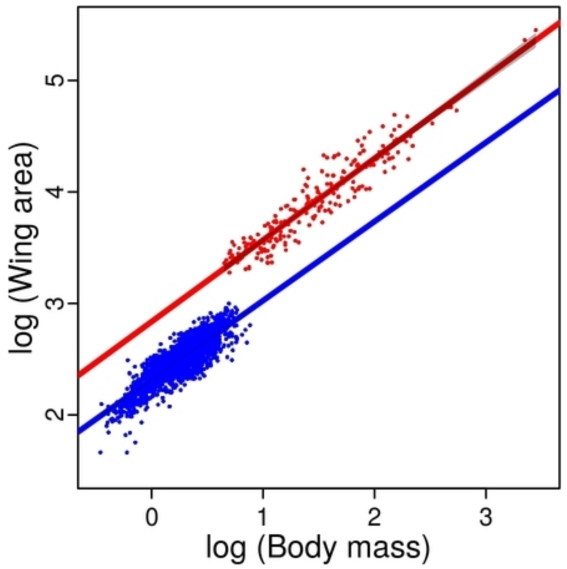
Figure 6.7 shows the intra-specific pattern in wing residuals and wing-loading by combining data from all species of hawkmoths. This was done by plotting the deviation from the species mean along both elevation and trait axis and by normalising the trait value by the species mean; i.e. $\mathbf{E' = E - \mu_{E\text{-}sp}}$ and $\mathbf{T' = (T - \mu_{T\text{-}sp})/\mu_{T\text{-}sp}}$. Both residual-wing and wing-loading exhibited a very weak (low r^2) negative relationship suggesting that intraspecific variation, at least when averaged over all the species, is insignificant.

6.4 Discussion

The close similarity in the value of the wing-area – body-mass index for birds and hawkmoths in the study region (Figure 6.1) across 4 orders of magnitude in body mass suggests very similar factors at play in the flight dynamics, essentially from biophysics requirements.

One would expect that the similarity in allometric indices of two very different taxa like birds and hawkmoths would be reflected in a similarity of indices when calculated within each genus of hawkmoths. Interestingly, we find that the allometric index varies widely among the genera. Even more, the indices for all genera except one are below the index for the hawkmoth assemblage as a whole – i.e. the average of the genera is not the average of the regional assemblage (Figure 6.2).

One scenario in which this may happen is that species from different clades slot themselves along the allometric relationship as per bio-physical requirements. On the other hand, species with a genus (or clade) will diverge from each other depending on



Fit	Intercept	Slope	p.value	r^2
Hawkmoth	2.32 ± 0.002	0.71 ± 0.01	< 0.001	0.73
Birds	2.84 ± 0.036	0.73 ± 0.02	< 0.001	0.90

Figure 6.1 *Plot of wing area (mm^2) versus body mass (g) for hawkmoths and birds (=wing length^2). Each blue dot represents a hawkmoth individual whereas each red dot is a bird species mean value. The linear fit coefficients are listed in the table below*

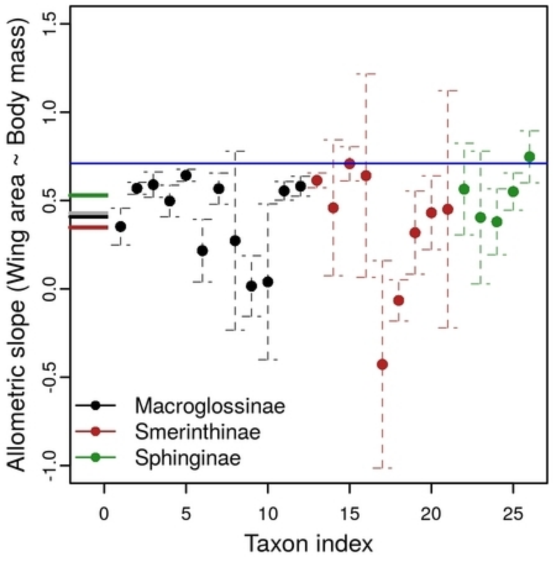


Figure 6.2 *Allometric slopes of different genera (dots) and sub-families (black: Macroglossinae, green: Smerinthinae, and red: Sphinginae) of hawkmoths. The blue line across the plot is the slope for the entire moth assemblage (from Figure 6.1). The bars against the Y-axis represent the mean values of the slopes for the genera in the 3 sub-families.*

many local biotic and abiotic factors including niche space, interspecific and intraspecific competition, phylogenetic constraints, etc. Given these multiple constraints an organism may reach some optimal position in trait space through a complex combination of (multiple) trait values; this may manifest itself in this diversity of allometric indices when the same is being viewed through the prism of just two or a few traits that are accessible to us.

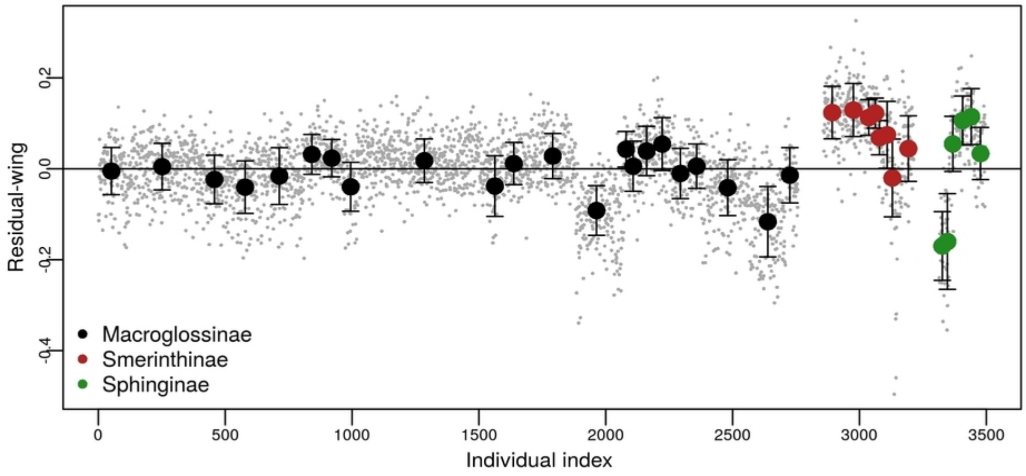


Figure 6.3 *Residual-wing from the fit in Figure 6.1 for individual hawkmoths. The symbols represent the mean and standard deviation for species with more than 25 individuals in the 3 subfamilies (black: Macroglossinae, red: Smerinthinae, and green: Sphinginae). Note: residual-wing values are logarithms.*

A similar pattern may be seen in an allometric study of hummingbirds by Skandalis et al (2017). Intraspecific allometry contrasts with the community value for most traits. Voge et al (2013) have dealt with this issue at the inter- and intra-specific level and conclude that there is no evidence for micro-evolution at the subspecific level but that there is evidence for allometric changes at the inter-specific level on scales of millions of years. Our study suggests that on an even higher evolutionary scale spanning birds and hawkmoths there is very tight bio-physical constraints which has resulted in a finely tuned allometric index. Essentially, the assemblage allometric index B = 0.71 reflects “convergent” evolution governed by very basic bio-physical constraints, while the genus-specific indices may represent local character displacement or “divergent” evolution.

Figure 6.3 shows that some species deviate significantly from the best fit allometry, i.e. in their value of residual-wing, which reflects wing area in excess of the body mass. We can understand this in two different ways. In the light of the previous discussion on evolving allometry this residual-wing is compensated by other traits which impact flight dynamics including metabolism, oxygen intake efficiency, muscle efficiency (with temperature), wing-beat amplitude, wing-beat frequency, wing-beat angle, etc. Alternatively one can view

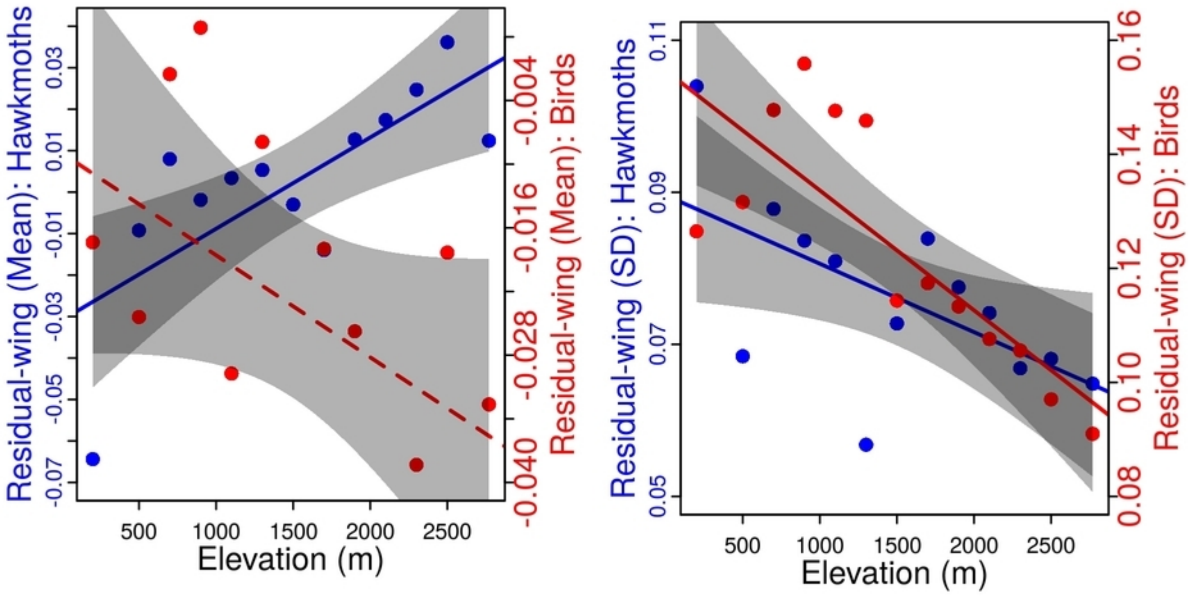


Figure 6.4 *Elevational profile of community mean and standard deviation of residual-wing (wing area minus mean fit from Figure 6.1) for hawkmoths (blue) and birds (red). Note: residual-wing values are logarithms. The linear fit coefficients are listed in the table below.*

Fits to mean	**Intercept x 10^{-2}**	**Slope x 10^{-5}**	**p.value**	**r^2**
Hawkmoths	3.08 ± 1.05	2.20 ± 0.62	< 0.001	0.49
Birds	0.02 ± 0.00	-0.96 ± 0.10	< 0.01	0.18

Fits to std devn	**Intercept x 10^{-2}**	**Slope x 10^{-6}**	**p.value**	**r^2**
Hawkmoths	8.96 ± 0.62	-8.99 ± 3.69	< 0.05	0.29
Birds	0.002 ± 0.0001	-0.021 ± 0.005	< 0.01	0.58

residual wing as reflecting differences in the ability to fly, and this may be related to life history traits including dispersal, foraging range, etc.

Athreya & Singh (1989) modelled the flight of flapping and gliding raptors using simple scaling arguments between just wing and body lengths. Skandallis et al (2017) have derived more detailed allometries between various mechanical components of a wing and the mass. The hovering of hummingbirds allows for a precise equation between the body weight and the lift generated by the wing. In our data we derived mass ~ (wing area)$^{1.03\pm0.01}$, while separating the length and the breadth components yields mass ~ (wing length)$^{1.14\pm0.04}$

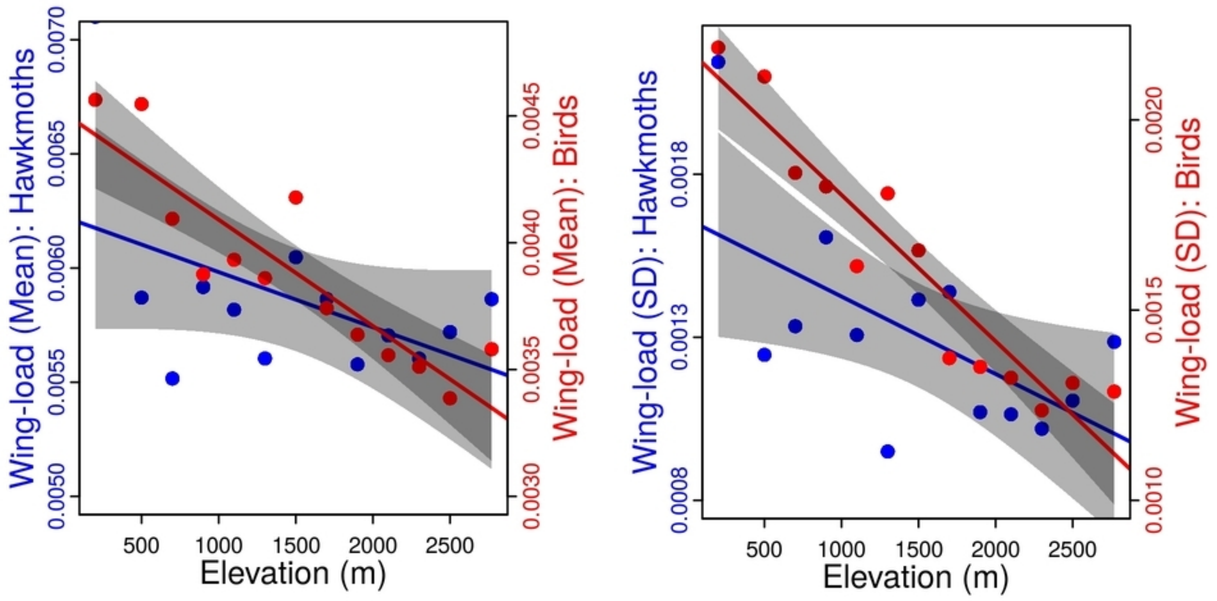


Figure 6.5 *Elevational profile of community mean and standard deviation of Wing-load for hawkmoths (blue) and birds (red).*

Fit to the mean	Intercept x 10^{-3}	Slope x 10^{-7}	p.value	r^2
Hawkmoths	6.22 ± 0.22	-2.41 ± 1.33	0.1	0.16
Birds	4.51 ± 0.11	-4.19 ± 0.64	< 0.001	0.78

Fit to the std devn	Intercept x 10^{-2}	Slope x 10^{-6}	p.value	r^2
Hawkmoths	0.17 ± 0.02	-2.38 ± 0.95	< 0.05	0.31
Birds	0.22 ± 0.001	-3.86 ± 0.39	< 0.001	0.89

(wing breadth)$^{0.91\pm0.04}$. This change in allometry between the wing length and breadth should reflect the influence of wing parameters like moment of inertia which in turn impacts wing beat frequency and manoeuvrability of the wing during the stroke. Athreya & Singh (1989) had modelled the wing as a free oscillator and therefore assumed that the wing-beat frequency would be proportional to (wing-length)$^{-0.5}$. On the other hand Greenewalt (1960) developed a theoretical model of the wing as a forced-damped oscillator and derived a scaling index of between –1 (insects) and –1.25 (hummingbirds). There is also the additional influence of temperature and oxygen level at different elevations on efficiency of wing and metabolism, as well as the dependence of mass on elevation

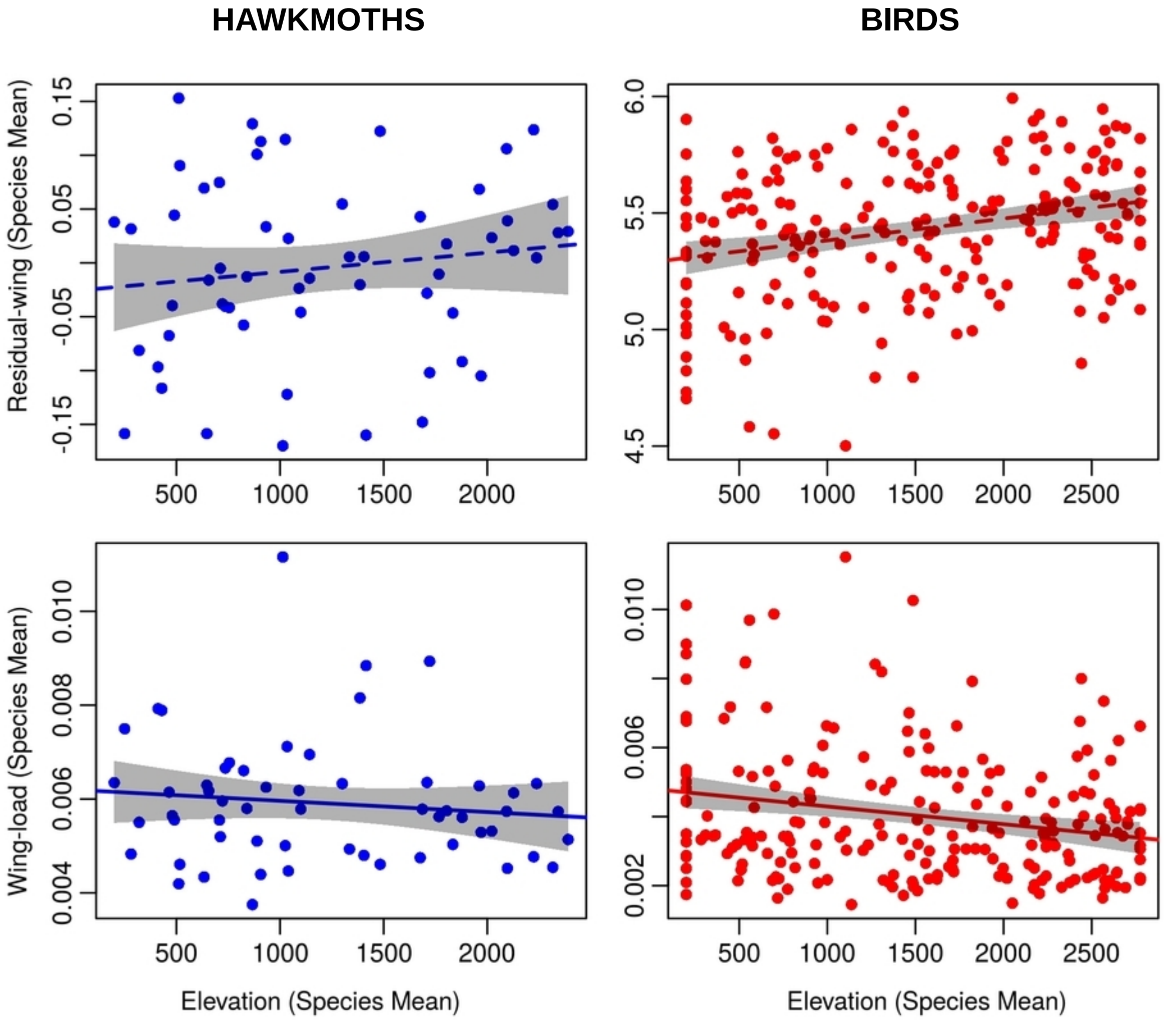


Figure 6.6 *Elevational profiles of species-mean Residual-wing (top) and Wing-load (bottom) for hawkmoths (blue) and birds (red). Note: Residual-wing values are logarithmic. The linear fit coefficients are given below*

Fit	Intercept x 10^{-3}	Slope x 10^{-5}	p.value	r^2
Hawkmoths (wing-load)	6.20 ± 0.38	–2.39 ± 2.76	0.39	-0.005
Hawkmoths (residual-wing)	-0.26 ± 0.23	1.78 ± 1.71	0.30	0.002
Birds (wing-load)	4.81 ± 0.26	-5.12 ± 1.53	< 0.001	0.04
Birds (residual-wing)	5.29 ± 0.04	9.36 ± 2.30	< 0.001	0.07

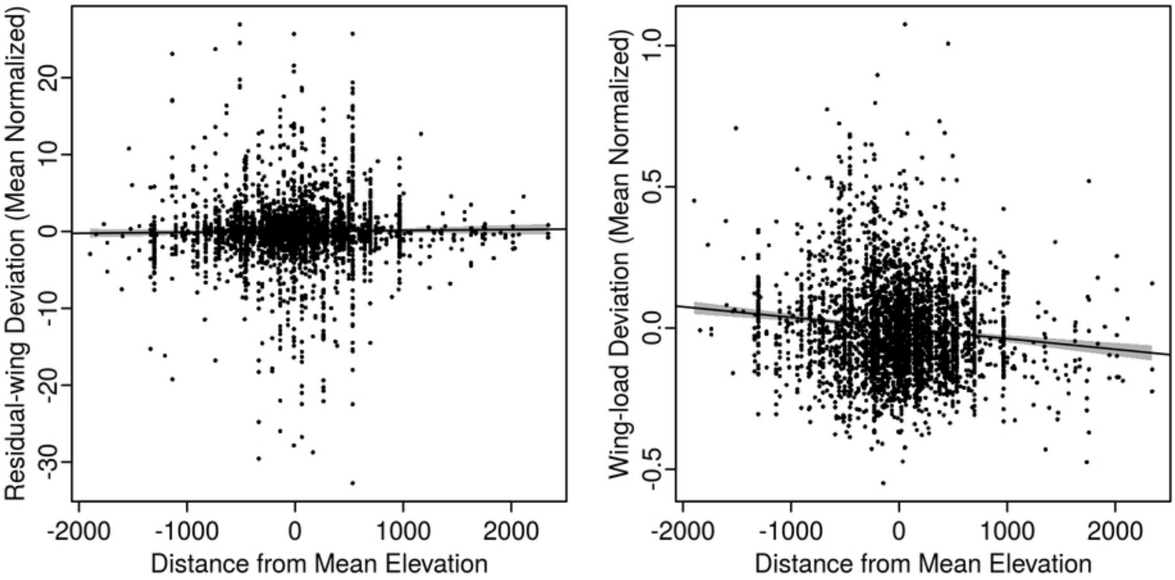


Figure 6.7 *Intraspecific variation in hawkmoth Residual-wing (left) and Wing-loading (right). The data for all species was combined by plotting the the nomalised trait deviation from the species mean, to calculate the average intraspecific variation for the entire assemblage. Note: the residual-wing values are logarithmic. Coefficients of the linear fit are presented in the table below.*

Fit	Intercept x 10^{-5}	Slope x 10^{-4}	p.value	r^2
Residual-wing	-1.52 ± 0.32	0.31 ± 0.03	< 0.001	0.03
Wing-loading	8.50 ± 1.71	-2.02 ± 0.33	< 0.001	0.01

(Chapter 5). A more comprehensive understanding of the flight of moths will require more detailed *“in-situ”* observations of the allometries of wing-beat frequency, oxygen availability, temperature, etc.

Hawkmoths exhibited a substantial increase in residual-wing and a decrease in wing-load with elevation. Both of these reflect the increase in wing area per unit body mass. Lower wing-load in cooler regions is known to reduce the temperature threshold for take-off (Gilchrist & Huey 2004; Dillon and Frazier 2006, Frazier et al. 2008) and has also been associated with higher dispersal capacity in response to the high climatic variability associated with higher latitudes or altitudes (Rohner et al. 2018).

Such correlations between dispersal capacity and latitude or altitude have been documented in several species (Hassall 2015; Kjærsgaard et al. 2015; Rohner et al. 2015; Rohner et al. 2018) at both, intra- and inter-specific levels, however seldom at the community level. Yet, greater dispersal capacity may be an essential prerequisite for colonizing habitats at high latitudes in the first place and this advantage might be best reflected in the abundance of species rather than their richness. Whether the observed reduction in wing-load at the assemblage level in our dataset is to compensate for the lower density of air at higher elevations, or lower muscle efficiency at the lower temperatures of higher elevations, or perhaps the necessity of foraging over larger areas given the larger body size and lower productivity remains to be tested by observations.

Hawkmoths are also known to compensate for decreased ambient temperatures by active “muscle-shivering” which allows them to regulate body temperatures unlike most ectotherms. This behavioural adaptation, coupled with the thermal insulation of scales on the wings, might impose a stronger selection for increased flight efficiency than thermoregulatory mechanisms (*contra* Allen’s Rule). Increased flight efficiency has been associated with reduced air density, high wind velocities and scattered and limited resources (Dillon et al. 2006; Keller et al. 2013).

Birds, on the other hand, showed a contrasting pattern between residual-wing and wing-load – the former indicated a decrease in relative wing area while the latter an increase with elevation. At the moment we are unable to suggest a possible explanation for this contradictory pattern though this can mathematically arise from the different allometric dependence of residual-wing and wing-load on body mass, and the differing dependence of the different traits on elevation. We also note that the data for hawkmoths and birds are different in that we only have species means for birds from published sources but values for individual hawkmoths from our observations. Therefore, like with almost all other studies in the past, we have had to use the same trait value of a species at all elevations. This may make a difference as we will discuss next in the context of the difference between elevational patterns at the intraspecific, interspecific and assemblage levels.

Most studies of interspecific or assemblage trait patterns along environmental gradients have tended to use species means (typically from a few individuals either measured at the study site or from museum specimens or published literature) – very few studies use large scale individual trait measurement of an entire invertebrate assemblage along the environmental gradient (but see Griffiths et al. 2016)

Figures 6.4 and 6.5 show a statistically significant and substantial change in community averaged residual-wing and wing-load with elevation with linear regression r^2 values ranging from 0.18-0.89. On the other hand, with the same data, plotting species means for both traits and elevations reduced the r^2 values to less than 0.07. Clearly, the manner of analysis play a role in the derived result and may account for the confusing welter of results in this field. The dependence of intraspecific variation with elevation – only in hawkmoths, for which we have the data – is also quite low ($r^2 < 0.03$). At first sight, this conflict between the patterns at the 3 levels is puzzling, since ultimately all processes have to operate on the individual and subsequently reflect at the level of the species and the community. Possibly, the difference that we have already discussed between allometries within and across species plays a role. Possibly, the explanation lies in community-level plots representing relative species abundance more faithfully than species mean plots do. The external/environmental filters acting at a location on an entire assemblage, even if small at the level of an individual, may yield a large signal when averaged over the whole assemblage.

We propose that more such studies which compare results across three levels of taxonomic organisation using the same data may reduce the confounding variety of patterns currently seen in published literature. Studying more than one taxon along the same gradient should also facilitate a resolution of contradictory results.

6.5 Summary

1. Hawkmoths and birds exhibited very similar allometric index between the wing-area and body-mass index across 4 orders of magnitude in body mass.
2. In hawkmoths, the allometric index varies widely among the genera and more interestingly, the average across all genera is much lower than the entire

assemblage average suggestive of a complex interplay between an overall bio-physical constraint and small scale evolutionary divergence or character displacement.

3. Assemblage mean residual-wing increased with elevation, whereas wing-load decreased with elevation for hawkmoths. Both of these reflect the increase in wing area per unit body mass and are more in line with enhanced flight efficiency rather than better thermoregulation as predicted by Allen's rule.
4. Assemblage mean residual-wing and wing-load decreased with elevation for birds which suggests a difference in the relationship between wing and body with elevation.
5. Similar to Chapter 5, the results across the three levels of investigation, assemblage, inter-specific and intra-specific are not always consistent and the lack of studies addressing trait variation across taxonomic levels requires attention.

Chapter Seven

Functional Trait Space in Hawkmoths

7.1 Introduction

Organisms interact and respond to the environment via their “functional” traits. A functional trait is any that impacts the fitness of an individual directly or indirectly via its effect on growth, reproduction and survival. Community ecologists are increasingly studying ecological communities from a “trait-based” perspective (see McGill et al. 2006 for a review).

These investigations have led to the formulation of the concept of functional diveristy (FD) or the diversity of “functional traits” within a community. FD can be defined as the number, type, and distribution of functions performed by organisms within an ecosystem (Díaz and Cabido 2001). However, it is not always clear which traits qualify as “*functional*” and how many functional traits should be measured to adequately describe community assembly patterns. In recent times, studies have progressed from quantitative descriptions of patterns of individual traits to their implication for community processes such as competition (limiting similarity) and environmental filtering

Most investigations into functional trait ecology have dealt with plants (Lavorel & Garnier 2002; Diaz et al. 2004; Diaz et al. 2007; Cornwell et al. 2008; Kraft et al. 2008; Luck et al. 2009; de Bello et al. 2010; Götzenberger et al. 2012; HilleRisLambers et al. 2012; Lavorel et al. 2013; Lamana et al. 2014; Luo et al. 2016; Kunstler et al. 2016). There have also been some studies in other taxonomic groups, including fish (Stuart-Smith et al. 2013), lichen (Ellis & Coppins 2006), fungi (Van Der Heijden et al. 2007; Cullings & Courty 2009), birds (Petchey et al. 2007; Flyn et al. 2009; Vandewalle et al. 2010; Meynard et al. 2011; Edwards et al. 2013), mammals (Flyn et al. 2009), and invertebrates (Usseglio□Polatera et al. 2000; Bady et al. 2005; Tillin et al. 2006; Hoehn et al. 2008; Vandewalle et al. 2010;

Hedde et al. 2012; Pey et al. 2014; Griffiths et al. 2016). Studies of animal taxa have been hindered by the difficulty in identifying the functionality of traits, measuring them accurately and the added complexity of quantifying behavioral traits.

Different metrics have been proposed to study functional diversity. These span the three major dimensions (indices) of functionality – richness, evenness and divergence. Furthermore, in each category metrics have been developed for different kinds of data: single versus multiple traits, species presence-absence versus abundances, and intra-specific variability versus species-mean values. Mouchet et al. (2010) suggested that all the three indices are essential for a proper understanding of community assembly. Pakeman (2011), in one of the few studies comparing the performance of multiple indices, found that the same plant communities occupying the same environmental gradient yielded different patterns for these three metrics.

Based on the principles of habitat filtering and limiting similarity, they can be classified as either metrics of ***convergence*** or metrics of ***divergence*** (Aiba et al. 2013). Convergent patterns have been attributed to environmental filtering whereas divergent distributions result from strong biotic interactions. Some of the most commonly used metrics are mean-trait-value-based indices including **FRic** (functional richness), **FEve** (functional evenness, and, **FDiv** (functional divergence) proposed by Villeger et al. (2008). More recently, Violle et al. (2012) proposed a suit of metrics (*T-statistics*) that allow incorporation of intraspecific variability for investigations into community assembly processes, although the interpretations have subtle differences. We discuss these two sets of indices below.

Metric	Value	Definition
$T_{IP/IC}$	$\sigma^2_{IP} / \sigma^2_{IC}$	Variance in trait of all individuals within a population divided by variance in trait of all individuals within the local community
$T_{IC/IR}$	$\sigma^2_{IC} / \sigma^2_{IR}$	Variance in trait of all individuals within a local community divided by variance in trait of all individuals within the regional community
$T_{PC/PR}$	$\sigma^2_{PC} / \sigma^2_{PR}$	Variance in trait of all populations within a local community divided by variance in trait of all populations within the regional community

Table 7.1 *T-statistics ratios (from Violle et al., 2012)*

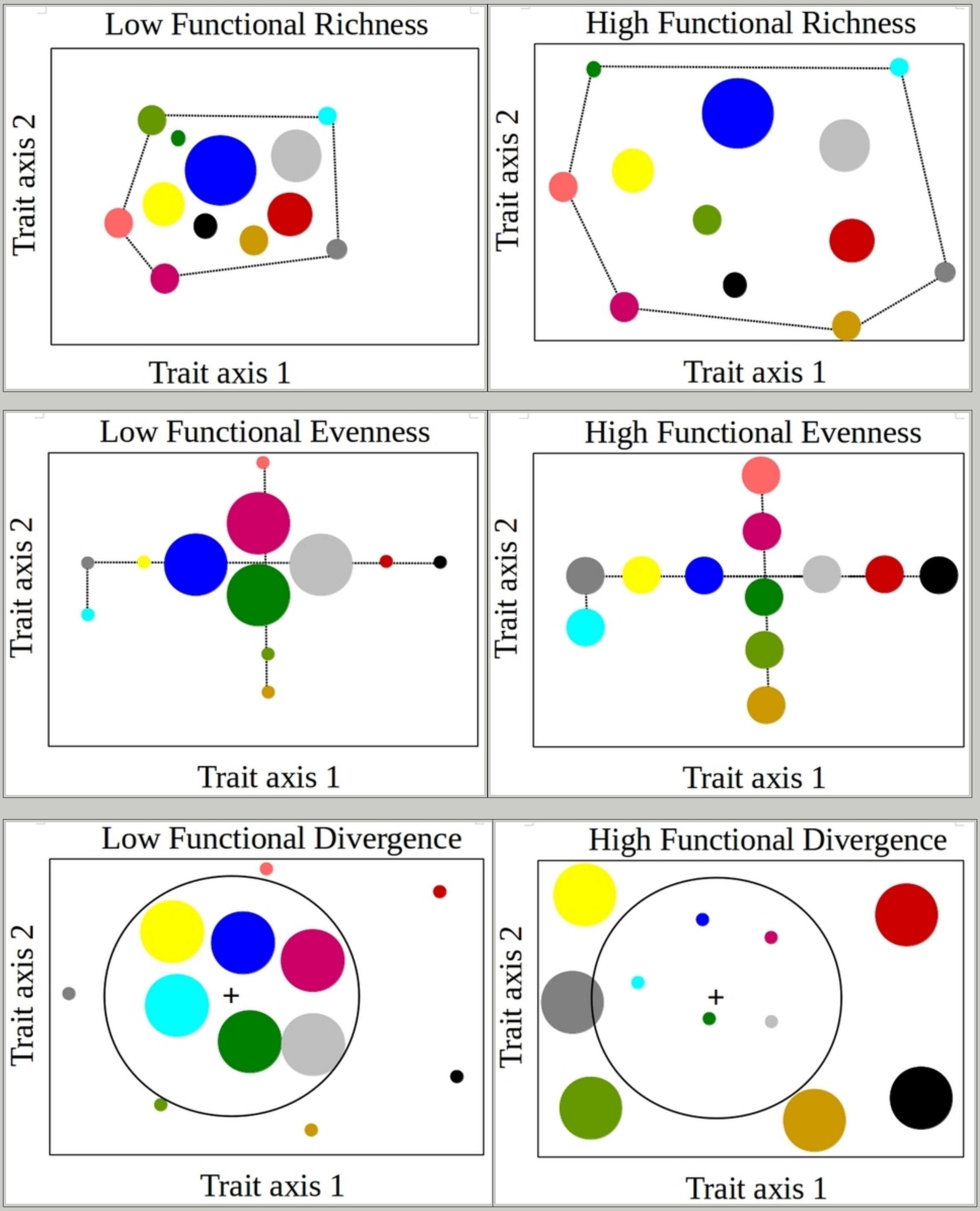
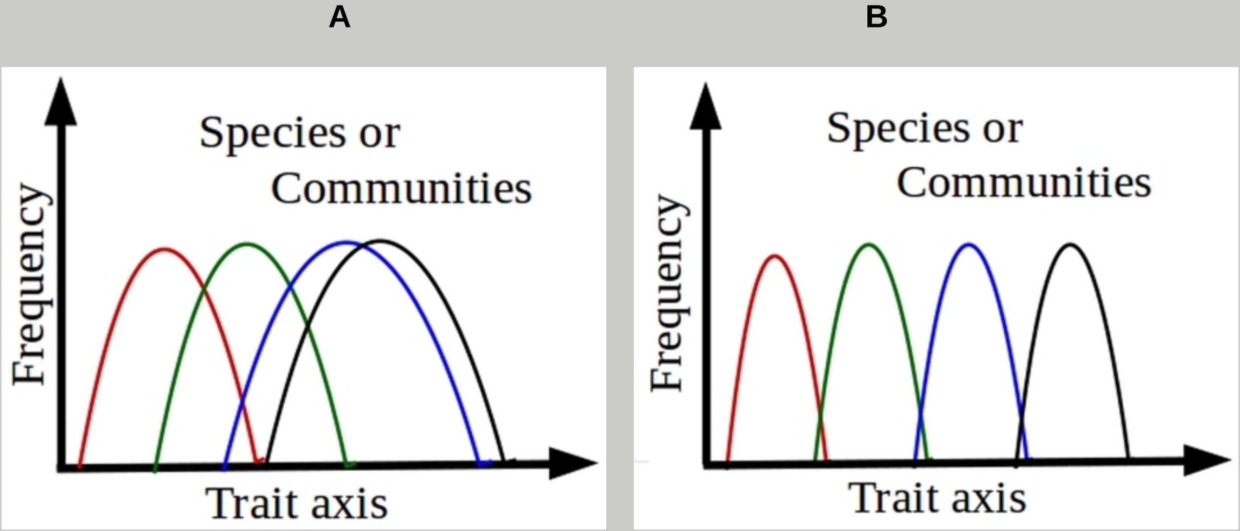


Figure 7.1 *Schematic illustration of the distribution of traits for the extremes of each metric. The location and radius of each circle represents the trait value and abundance for a species.*



When individual curve represents the trait distribution for individuals within a species

- **A:** High trait overlap = High intraspecific variability with repect to interspecific variance = Low internal filtering = High $T_{IP/IC}$
- **B:** Low trait overlap = Low intraspecific variability with respect to interspecific variation = High internal filtering = Low $T_{IP/IC}$

When individual curve represents the trait distribution for local communities within a region

- **A:** High trait overlap = High local community variance with repect to regional trait distribution = Low external filtering on individual communities = High $T_{IC/IR}$
- **B:** Low trait overlap = Low local community variance with repect to regional trait distribution = High external filtering on individual communities = Low $T_{IC/IR}$

Figure 7.2 *Schematic illustrating the distribution of traits within species (or communities) for two hypothetical extremes*

7.1.1 Functional Diversity Indices

The 3 commonest indices are described in Villeger et al. (2008) and shown in Figure 7.1.

1. **FRic** is the minimum convex hull volume of the multidimensional trait space that includes all traits of a community. For a single trait, it is simply the range of values.
2. **FEve** describes the evenness of abundance distribution in trait space. It ranges from 0 to 1 and is low when the abundance distribution is uneven.
3. **FDiv** relates to the distribution of the most abundant species within the trait space. FDiv is low when the most abundant species have functional traits that are close to the center of the functional trait range.

These metrics can be used to compare communities with different species richness without bias (Villeger et al, 2008). Moreover, the three functional diversity indices are independent of each other, and have been shown to be sensitive to the community assembly rules of limiting similarity and habitat filtering. (Mouchet et al. 2010).

7.1.2 T-statistics

A key assumption in the calculation of the FD indices is that the effects of intra-specific variability are negligible. However, this assumption has rarely been empirically validated (Albert et al. 2010; Jung et al. 2010; de Bello et al. 2011; Violle et al 2012) and almost all such attempts have been for plants (but see Griffiths et al. 2016 for a case study on dung beetles). Integrating inter- and intra-specific trait variation has provided insights into the processes of community assembly in plants (e.g Jung et al. 2010; Leps et al. 2011).

Violle et al. (2012) classify the forces structuring trait distribution within an assembly as “internal” and “external” filters, in contrast to the concepts of “niche” and “environmental” filtering used to interpret the traditional FD indices. They suggest that internal filters represent all within-community (local) processes such as micro-environmental heterogeneity, and intra- and inter-specific competition.

External filters represent large-scale environmental filters, including dispersal limitation and predator-pressure, that select specific species (traits) from a regional species pool (Taudiere & Violle 2015). Thus, external filters govern the species composition of a local community, whereas internal filters dictate their co-existence.

To investigate community assembly in terms of the relative importance of these two operational filters they proposed a suite of statistics, ***T-statistics,*** that allow the partitioning of trait variance across different hierarchical levels of taxonomic organization (populations/ species/communities).

In conjunction with appropriate null models, T-statistics can aid investigations into relative importance of external versus internal filters acting on the traits of the community.

T-statistics comprise ratios of trait-variance at 3 different scales (Figure 7.2 and Table 7.1; Taudiere & Violle 2015): variance of individual traits within a population (σ_{IP}^2), a community (σ_{IC}^2) and regional pool (σ_{IR}^2). The latter two may also be calculated using populations means – σ_{PC}^2 and σ_{PR}^2. Investigating community assembly via these variances requires large individual trait data sets which are still lacking for most , especially invertebrates.

7.2 Objectives

The specific objectives addressed in this chapter are to investigate

1. non-random assembly of traits
   using T-statistics
      - individuals within a species and within local communities
      - species within local communities,

   using Functional Diversity indices and T-statstics
      - local communities within the region
2. patterns in each metric with elevation and the relative importance of competition (or internal) and environmental (or external) filters.
3. relationship between taxonomic and functional diversity

The FD indices were calculated for the multi dimensional volume of the 3 available traits, while T-statistics were analyzed separately for each individual trait. This difference was determined by the nature of the two class of indices and the available analysis packages.

7.3 Analysis & Results

7.3.1 Trait overlap

Figure 7.3 shows the trait distribution for hawkmoth communities at different elevations as kernel density plots (Mouillot et al. 2005; Luo et al. 2016). The different elevations, classed into three groups of ***low*** (200, 500, 700 & 900 m), ***mid*** (1100, 1300, 1500 & 1700 m) and ***high*** (1900, 2100, 2300, 2500 & 2700 m) are shown in different colors. Plots are presented for body volume, wing area, wing aspect ratio (length/breadth).

Qualitatively, the separation between low and high elevations is obvious in Figure 7.3. This is demonstrated quantitatively in Figure 7.4 which shows a significant decrease in trait overlap with elevational distance, for both primary traits (body length, thorax width, wing costum length and breadth) and derived traits (body volume, wing area and aspect ratio). The overlap was defined as the integral of the intersection area of the kernel distributions.

Figure 7.5 shows the distribution of hawkmoths in trait space at different taxonomic levels. The three subfamilies – *Macroglossinae*, *Smerinthinae* and *Sphinginae* – are shown on the body-mass v/s wing-area plane at the levels of individuals and species means. While there is a higher degree of overlap at the level of individuals the species-mean plot shows that the 3 sub-families occupy distinct regions on the two dimensional morpho-plane. This is more obvious in the plot with the first two principal component vectors obtained from the 4 primary trait measurements mentioned previously. The 3 subfamilies separate out with only 4 species falling outside “their” fitted polygon. Of the 3297 individuals (57 species) which were used in the plot, the four interloper species comprise only 45 individuals (*Agrius convolvuli*: 14 individuals; *Clanis undulosa*: 14; *Dolbina inexacta*: 11; *Rhodoprasina sp*.: 6); i.e. less than 1.5% of the total community. In the figure we have also shown the same PCA analysis with the 5 most abundant genera comprising more than 75% of the individuals. The genera clearly occupy non-overlapping regions.

7.3.2 Functional Diversity indices

It has been suggested that only traits related to the function of interest should be included in the FD metric; incorporation of neutral or strongly positively correlated traits will cause artificial convergence of FD (Naeem & Wright 2003), while negatively correlated traits will inflate FD values (Cadotte et al. 2011). Therefore, given the strong correlation between wing area and body mass, we used the residual wing area (hereafter, excess wing) after eliminating its allometry with body mass (Chapter 6).

We tested for non-random assembly of traits using 1000 simulated null communities by

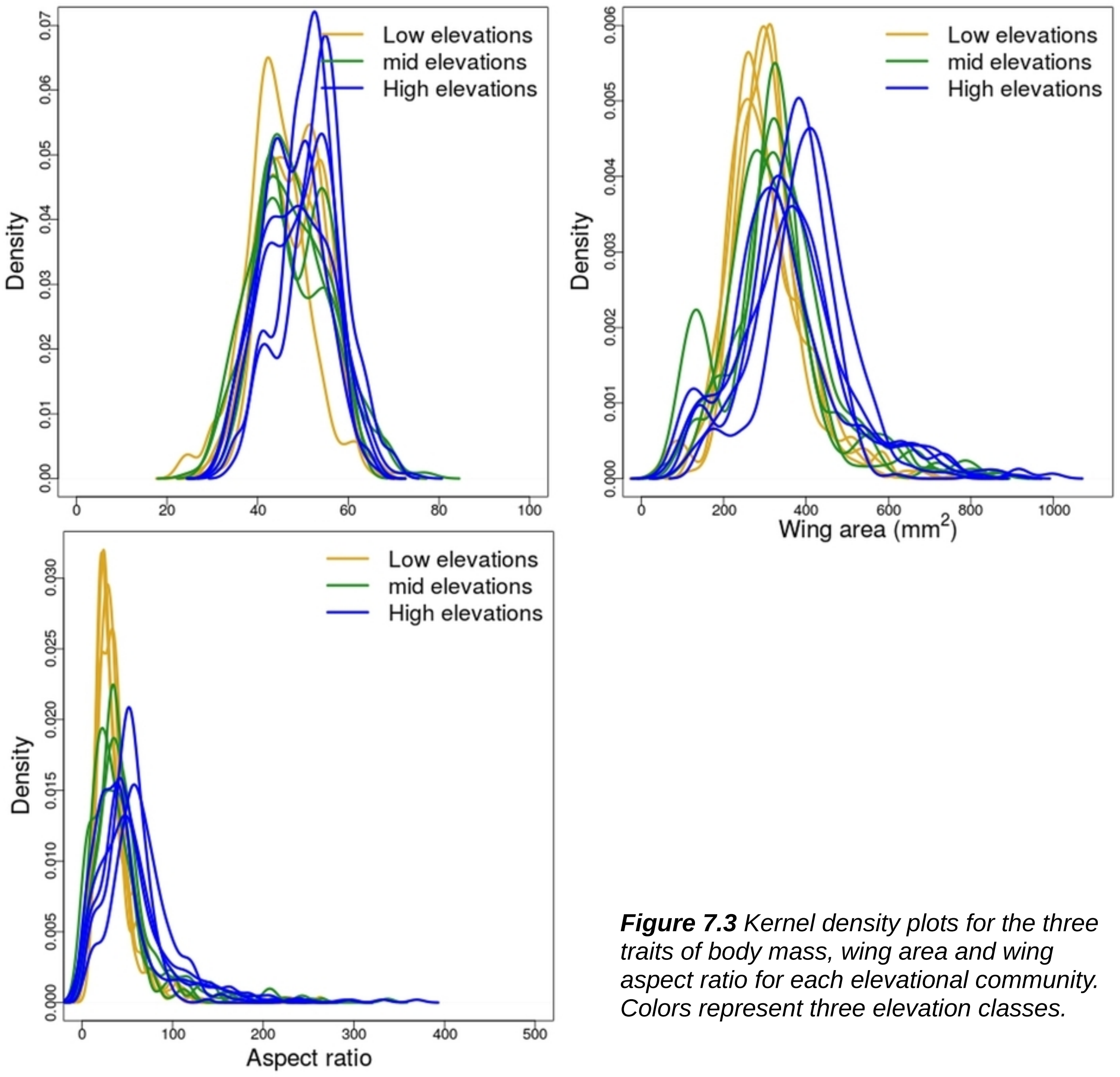


Figure 7.3 *Kernel density plots for the three traits of body mass, wing area and wing aspect ratio for each elevational community. Colors represent three elevation classes.*

randomly shuffling the mean trait values across all species, without changing the observed community-abundance matrix. The functional diversity indices – FRic, FEve and FDiv – were then calculated (FD package in *R 3.3.1: FD: dbFD* (Laliberte & Legendre 2010; Laliberte et al. 2014) for these simulated communities to get the expected frequency distribution for the null model (i.e. random trait assembly) for each community. The distribution of simulated and observed values are shown in Figure 7.6. The Wilcoxon signed rank test showed that the observed distribution of FRic and FDiv was significantly

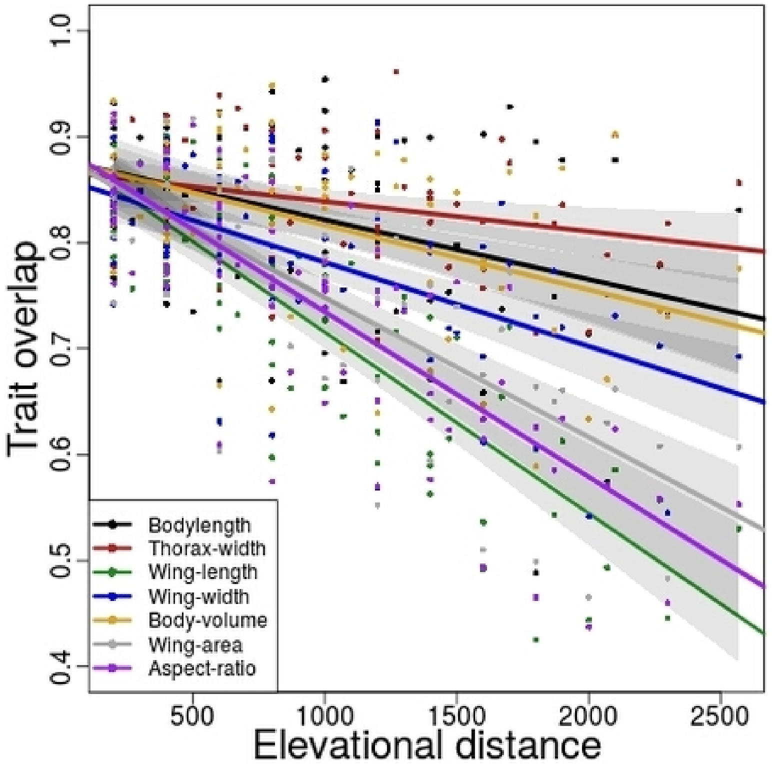


Figure 7.4 *Trait overlap, as area under intersection of kernel density plots, as a function of elevational distance. Plots are presented for the three traits of body volume, wing area, aspect ratio, as well as residual body volume. The linear regression coefficients are listed in the table below:*

Trait	Intercept	Slope x 10^{-5}	r^2	P value
Body-length	0.87 ± 0.0015	–5.62 ± 1.64	0.12	< 0.001
Thorax- width	0.87 ± 0.0011	–2.82 ± 0.97	0.09	< 0.001
Wing-length	0.89 ± 0.0014	–1.71 ± 0.13	0.70	< 0.001
Wing-width	0.86 ± 0.0015	–7.92 ± 1.31	0.32	< 0.001
Body-volume	0.88 ± 0.0015	-6.11 ± 1.33	0.21	< 0.001
Wing-area	0.88 ± 0.0016	-1.31 ± 0.14	0.53	< 0.001
Aspect-ratio	0.89 ± 0.015	-1.56 ± 1.32	0.64	< 0.001

lower than the null distribution ($p < 0.05$). FEve was not significantly different from the null communities ($p > 0.1$). FEve and FDiv decreased significantly with elevation while FRic did not show any trend. Figure 7.7 shows the linear regression of the FD indices against rarefied species richness. All three metrics increased with species richness, however the fit was significant only for FRic and Feve.

7.3.3 T-statistics

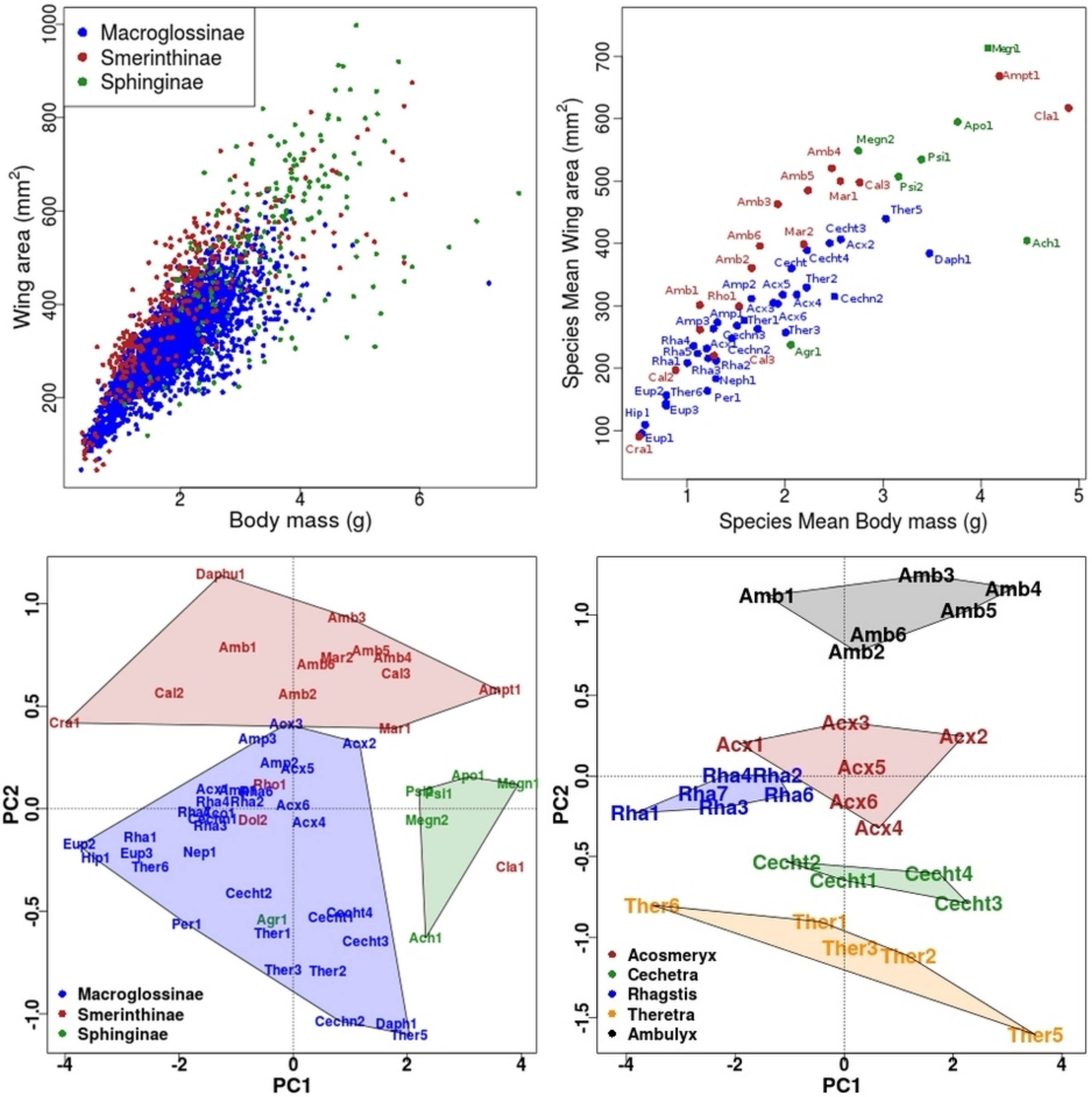
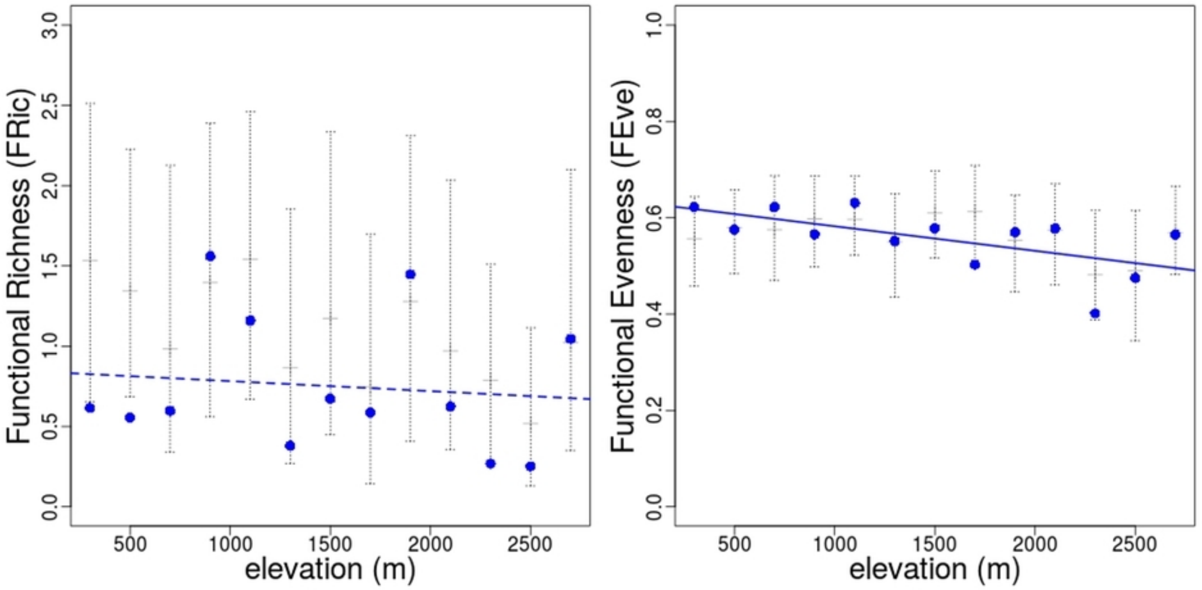
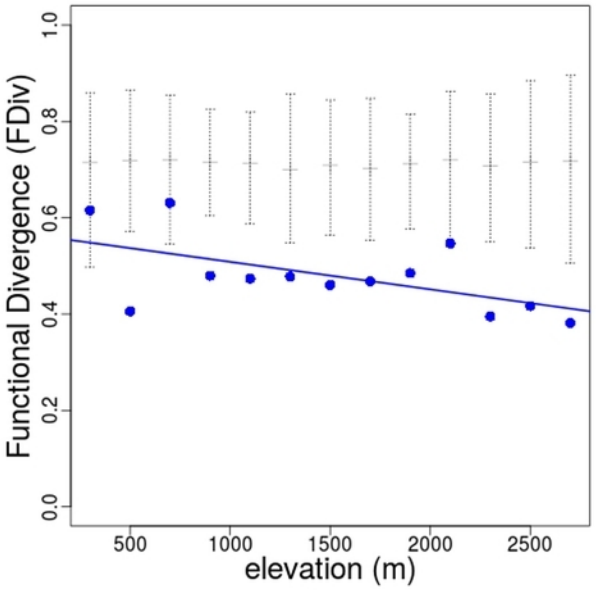


Figure 7.5 Top-left: *Scatterplot of hawkmoth wiing area versus body mass, colored by subfamily.* ***Top-right***: *Same plot with species mean values;* ***Bottom***: *PCA using thorax-width, body-length, wing-costum length and wing-breadth for all genera in the 3 subfamilies (left) and the five most abundant genera with >75% of the total number of individuals (right). Genus codes are Amb: Ambulyx; Acx: Acosmeryx; Rha: Rhagastis; Cecht: Cechetra; Ther: Theretra.*

We computed the three variance ratios – $T_{IP/IC}$, $T_{IC/IR}$ and $T_{PC/PR}$ – for each of body mass, aspect ratio and excess wing, and at each elevation, using *R 3.3.1: CATI 2.2.1: Tstats* (Taudiere & Violle 2015). Figure 7.8 shows the observed variance ratios as a function of elevation and their value relative to the null distribution of randomized traits. We generated





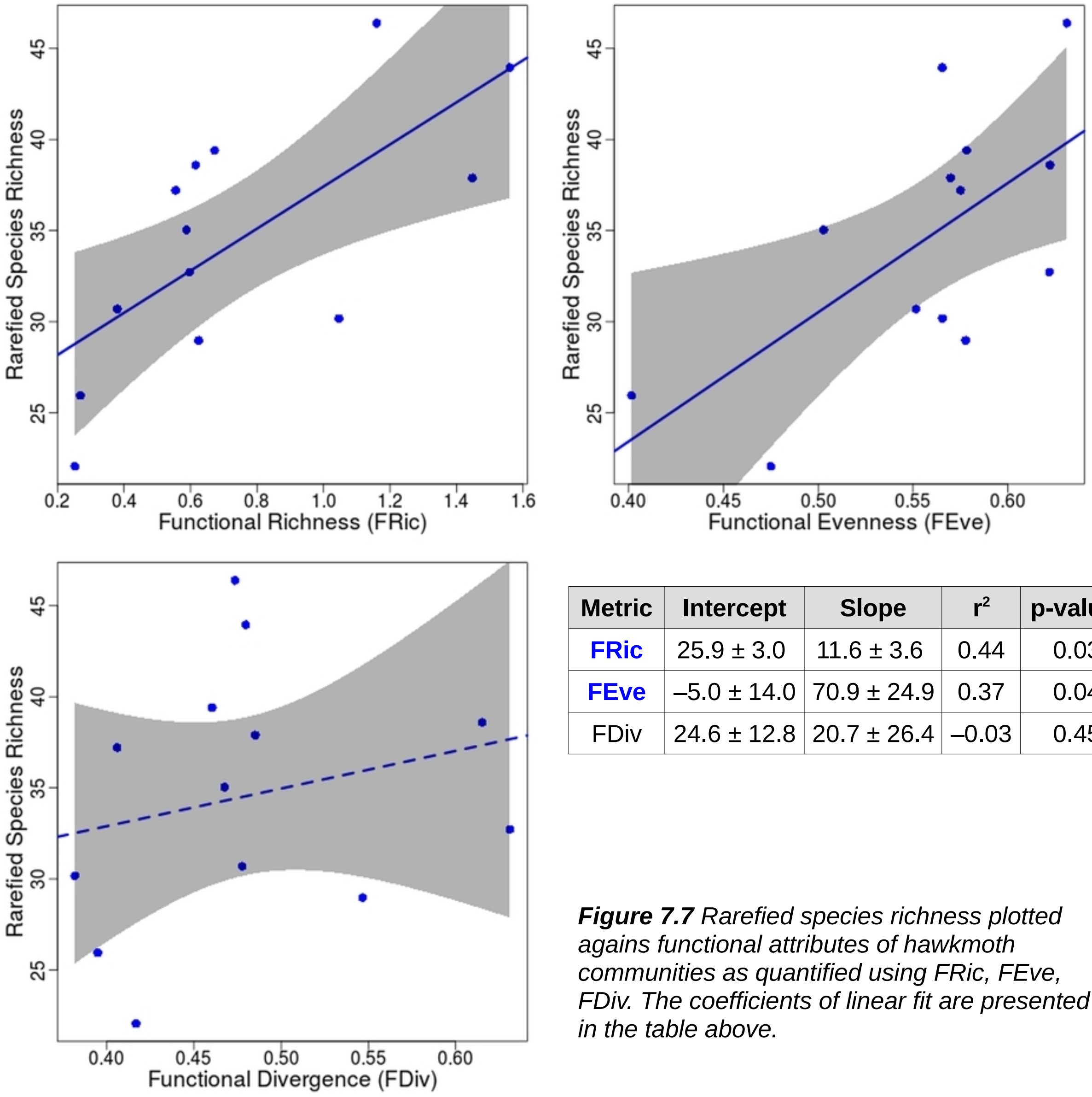
Linear Gregression Coefficients				
Metric	**Intercept**	**Slope x 10^{-5}**	**r^2**	**p-value**
FRic	1.11 ± 0.007	6.9 ± 4.1	-0.12	0.23
FEve	0.63 ± 0.003	-5.1 ± 2.0	0.33	0.03
FDiv	0.57 ± 0.004	-5.7 ± 2.5	0.27	0.01

Wilcoxon Signed Rank Test				
Metric	**Hypothesis**	**Result**	**W-stat**	**p-value**
FRic	< Null	TRUE	125	0.02
FEve	< Null	FALSE	86	0.48
FDiv	< Null	TRUE	169	< 0.001

Figure 7.6 *The observed values of functional diversity indices are plotted against the elevation (in blue). The mean±1sigma of null simulations are shown in grey. Coefficients for the linear fit versus elevation, and wilcoxon signed rank test are are shown in the table above.*

the null models using the following prescriptions:

1. $T_{IP/IC}$: randomization, without replacement, of individual trait values within each local elevational community
2. $T_{IC/IR}$: randomization, without replacement, of individual values across all elevations



Metric	Intercept	Slope	r^2	p-value
FRic	25.9 ± 3.0	11.6 ± 3.6	0.44	0.03
FEve	–5.0 ± 14.0	70.9 ± 24.9	0.37	0.04
FDiv	24.6 ± 12.8	20.7 ± 26.4	–0.03	0.45

Figure 7.7 *Rarefied species richness plotted agains functional attributes of hawkmoth communities as quantified using FRic, FEve, FDiv. The coefficients of linear fit are presented in the table above.*

3. $T_{PC/PR}$: assigned an elevation specific trait value to each individual and randomization, without replacement, of these mean trait values across all elevations

Table 7.2 shows that of the 9 linear regressions with elevations only wing aspect ratio and residual wing for $T_{IC/IR}$ showed a significant correlation. The observed $T_{IP/IC}$ was lower than the simulated μ_O–1σ at every elevation and for all traits. The other ratios are a mixed bag though they seem to show some pattern though not statistically significant.

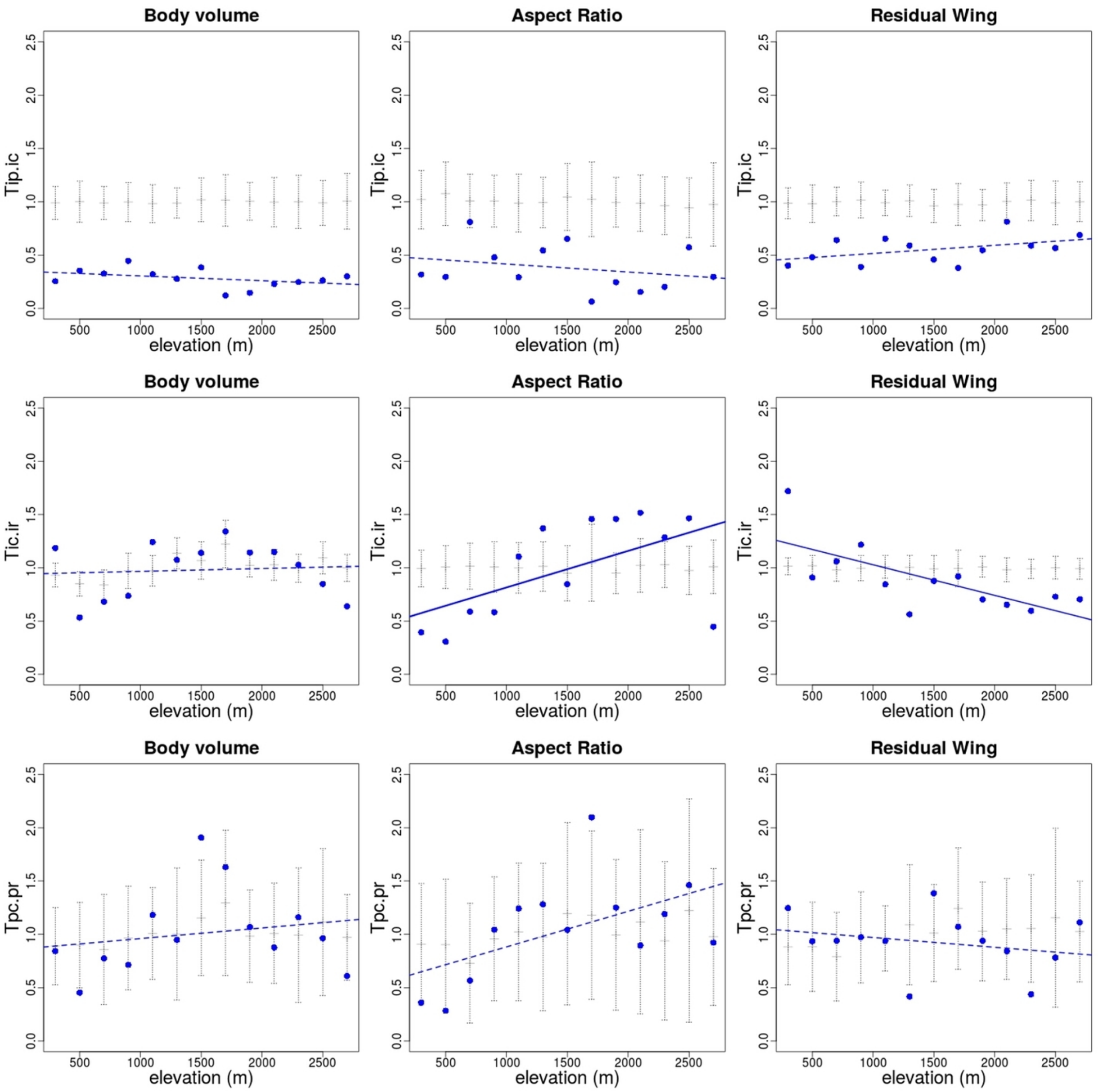
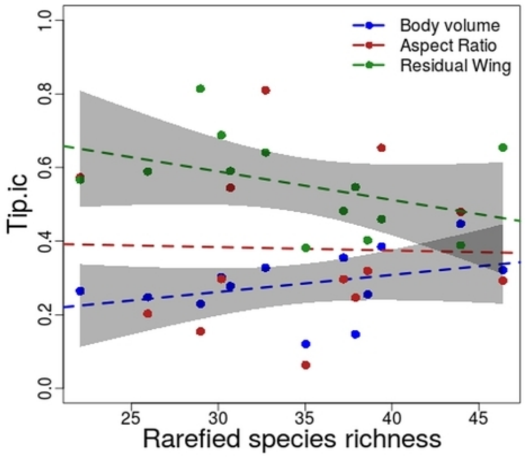


Figure 7.8 *The observed values of the three variance ratios $T_{IP.IC}$, $T_{IC.IR}$ and $T_{PC.PR}$ are plotted against the elevation (in blue). The mean + 1sigma of null simulation are shown in grey. Coefficients for the linear fit of $T_{IP.IC}$ versus elevation and wilcoxon signed rank test are shown in Table 7.2*

Figure 7.9 shows no significant relationship between $T_{IP/IC}$ and rarefied species richness.

7.4 Discussion

Species alpha and beta diversity are commonly used to investigate the response of ecological communities to environmental gradients (Bunn & Arthington 2002; Poff &



Trait	Intercept	Slope x 10^{-3}	p-value	r^2
Body volume	0.12 ± 0.13	4.6 ± 3.6	0.22	0.05
Aspect Ratio	0.41 ± 0.33	-9.1 ± 0.9	0.92	-0.09
Residual wing	0.82 ± 0.18	-7.7 ± 5.1	0.15	0.10

Figure 7.9 *The T-statistic internal filter ratio versus Rarefied species richness. The coefficients of linear fit are presented in the table above.*

Linear Regression Coefficients				
Trait	**Intercept**	**Slope x 10^{-5}**	**r^2**	**P value**
Body volume	0.35 ± 0.005	-4.52 ± 3.19	0.07	0.18
Aspect Ratio	0.49 ± 0.014	-7.49 ± 8.04	-0.01	0.37
Residual wing	0.44 ± 0.007	7.64 ± 4.43	0.14	0.11
Body volume	0.94 ± 0.017	0.26 ± 0.10	-0.08	0.80
Aspect Ratio	0.47 ± 0.250	0.34 ± 0.15	0.26	0.03
Residual wing	1.31 ± 0.014	-2.87 ± 0.84	0.47	0.03
Body volume	0.86 ± 0.025	9.96 ± 1.51	-0.05	0.52
Aspect Ratio	0.55 ± 0.261	3.33 ± 1.56	0.23	0.06
Residual wing	1.06 ± 0.017	-9.13 ± 1.02	-0.02	0.39
Wilcoxon Signed Rank Test				
Trait	**Hypothesis**	**Result**	**W-statistic**	**P value**
Body volume	Observed > Null	Reject	169	< 0.001
Aspect Ratio	Observed > Null	Reject	169	< 0.001
Residual wing	Observed > Null	Reject	169	< 0.001
Body volume	Observed < Null	FALSE	76	0.68
Aspect Ratio	Observed < Null	FALSE	78	0.68
Residual wing	Observed < Null	Reject	130	< 0.01
Body volume	Observed < Null	FALSE	76	0.20
Aspect Ratio	Observed < Null	FALSE	71	0.76
Residual wing	Observed < Null	FALSE	104	0.17

Table 7.2 *Linear regression coefficients for the observed variance ratios against elevation and wilcoxon signed rank test statistics for their deviation from the null values.*

Zimmerman 2010). However, it has been suggested that trait-based measures of diversity may be more informative in describing community responses to gradients (Walker 1995, Hoeinghaus et al. 2007, Cadotte et al. 2011). Most of the work on trait distribution across abiotic gradients has been on plants (but see Blackburn et al. 2005; Tscharntke et al. 2008; Flynn et al. 2009; Moretti et al. 2010; Barragan et al. 2011; Edwards et al. 2013; Cisneros et al. 2015). The wide range of environments along an elevational gradient is an excellent setting to assess the relative importance of habitat/environmental filtering and limiting similarity/niche partitioning (sensu Southwood 1977, 1988) that impact the trait composition of communities.

7.4.1 Trait Overlap

Functional traits may be identified as either ***effect*** or ***response*** traits (Luck et al. 2013). Response traits reflect the response of an individual to a changing environment while effect traits determine the impact of the individual on the ecosystem. A high diversity of response raits is expected to provide a greater resilience of the community against environmental perturbations. One would expect that the traits that we have selected, viz. body and wing dimensions, are examples of response traits. These traits are implicated in thermoregulation, the ability to fly, and are also dependent on the availability of food resources, and therefore may be expected to vary across the elevational gradient. The decrease in pairwise overlap of traits with increasing elevational difference suggests that the traits are indeed changing in response to the changing environment; i.e the environment is acting as a filter and selecting only certain traits for a particular elevation.

In Chapter 5, we saw that body mass increases with elevation for hawkmoths. Here, we find that the change in overlap for wing area is higher than for body mass**,** indicating that there is an additional component of change in wing area over and above that from its allometric relationship with body mass. However, it should be noted that the change of the degree of overlap does not carry any information of the direction of the change in trait.

The variation in traits across species is believed to have two non-random components: convergent adaptation to the environment and similarity between species with related ancestral history (Prinzing et al. 2001). The second component is called phylogenetic conservatism (or inertia) or historical constraint. The term, phylogenetic conservatism, was first coined by Harvey & Pagel (1991) and was subsequently popularized by Holt & Gaines (1992), Peterson *et al.* (1999), Prinzing *et al.* (2001) and many others. It has been suggested that such traits can be used for retrieving phylogeny if the convergent adaptation to environment or habitat is minimal, however this has rarely been demostrated for most taxa. Using morphological traits of body and wing attributes, we assessed overlap across different groups within the family *Sphingidae*. We found that hawkmoth subfamilies occupy distinct regions in the trait space with minimal overlap indicating high phylogenetic trait conservatism. The 5 most abundant genera in the community (>75 % individuals) exhibit no overlap in the morpho-trait space, indicating a strong phylogenetic component.

7.4.2 Functional Diversity Indices

A. Elevational profile of functional diversity indices

Low functional richness indicates a high degree of trait convergence (Webb et al. 2010; Dehling 2014). Weiher & Keddy (1995) proposed that the harsh environment and increased stress at high elevations will result in decreased functional trait diversity by limiting the range of functional groups. In “benign” or more stable environments, “competitive adversity” will cause greater functional character diversity within local communities (MacArthur & Levins 1967). However, our result show no trend with elevation.

Competition between the species of a (species rich) community should be manifested in a higher value for functional evenness (Villeger et al. 2008). Our results are consistent with this expectation in that functional evenness increases towards low elevations. This is similar to that observed in birds by Dehling et al. (2014) who attributed the pattern to the prevalence of competition in the lowlands and environmental filtering at higher elevations. We note that the relative abundance distribution of species also showed a more uneven community at higher elevation (Chapter 3). We note here that a very similar pattern has been seen from two very different data sets: species abundance and trait abundance.

Functional divergence measures the degree to which the abundance of a community is distributed toward the extremities of occupied trait space (Mouchet et al. 2010). In other words, FDiv is determined by the divergence in trait values weighted by species abundance. Thus a reduction in its value at higher elevations indicates that these elevations are dominated by species with similar trait values. We recall from Chapter 5 that dispersion in body mass of hawkmoths remained more or less the same across the elevation ... which is at odds with the result here. However, the dispersion in the body size of birds showed a strong reduction towards higher elevation.

B. Non-random assembly of traits through functional diversity indices

Functional richness was lower than the mean of null simulations. Though the shortfall was not significant at any single elevation, the consistency of the pattern at all elevations yielded a statistically significant ($p < 0.05$) shortfall. This non-random assembly of local communities indicates the influence of environmental filters in constraining the trait diversity at each elevation, relative to the regional trait diversity.

Functional evenness was not different from the mean of null simulations ($p > 0.1$). Petchey et al (2007) have discussed the null distribution for this index and concluded that the interpretation of the null model is unclear.

The functional divergence index was consistently, and considerably lower, than the null distribution. The distance below the null is significant at $p < 0.05$ indicating that the most abundant trait values are clustered closer to the mean for the elevation. This indicates that there is an “optimal” trait value at each elevation, that has outperformed other trait values in terms of species abundances.

7.4.3 Functional diversity and taxonomic diversity

We found a strong positive relationship between functional richness and functional evenness on the one hand, and rarefied species richness on the other. The form of the relationship between taxonomic and functional diversity determines the degree of functional redundancy in communities (Micheli and Halpern 2005).

A change in functional diversity is likely to affect ecosystem processes, whereas a change in species diversity may not elicit any change in an ecosystem with functional redundancy (i.e. shared traits) among species. High functional redundancy occurs when taxonomic richness is high but functional richness is low, owing to overlap in species traits (Luck et al. 2013). In such a situation the loss of a species at random from the community may not necessarily result in a loss of ecosystem functioning (Diaz & Cabido 2001; Naeem 2002; Mayfield et al. 2010).

On the other hand, species loss may have a major impact on ecosystem functioning when the two richness measures have a strong positive relationship. More functionally diverse communities are thought to offer greater resilience (Hooper et al. 2005), as has been shown for agricultural land-use gradients (Fischer et al. 2007), forest-fire disturbances (Hidasi-Neto et al. 2012), and hydrologic-alteration gradients (Pool et al. 2010).

7.4.4 T-statistics

Violle et al.’s (2012) T-statistics facilitate comparisons across communities along an elevational gradient. While other studies have attempted to interpret the assembly process in terms of interspecific competition and environmental filtering, T-statistics deals with the two categories of internal and external filters. The internal filter can be any of intra- and inter-specific competition or micro-habitat heterogeneity and is quantified by the variance ratio $T_{IP.IC}$. A higher value implies lower strength of the filter(s).

The ratios $T_{IC.IR}$ and $T_{PC.PR}$ quantify the strength of external (environmental) filters and differ only in that the former uses the data from individuals while the latter uses population means. Again, a higher value indicates a lower strength of the external filter.

We carried out a T-statistics analysis of body mass, wing aspect ratio and residual wing (wing area in excess of the body mass allometry). We analysed the elevational profiles of the absolute values of the observed ratios for each of the 3 traits, as also their relative value with respect to the null distribution corresponding to zero filters.

$T_{IP.IC}$ did not show any statistically significant dependence on elevation for any of the 3 traits. On the other hand $T_{IP.IC}$ was consistently and considerably lower than the null value at all elevations; i.e. individuals within a species in each local community are significantly more similar to each other than individuals drawn randomly from across species in that community. This is indicative of niche packing and suggests that inter-specific competition or local abiotic factors (e.g. predatory pressure, micro-environmental heterogeneity, etc) are strongly dictating the trait composition of hawkmoth communities along the entire elevational gradient. Higher niche packing has been suggested previously for tropical compared to temperate communities (Lamana et al. 2014; Neyret et al. 2016). On the other hand, $T_{IC.IR}$, values were distributed on both sides of the null distribution but showed a trend with elevation. The linear regression was statistically significant for wing aspect ratio and wing-excess but not for body mass. The plots indicate that external filters are increasing on residual wing but decreasing on aspect ratio. Generally, wing aspect ratio is more related to the mode of flight with, given the same wing area, broader wings making for better gliding ability (e.g. vultures), while shorter wings making for higher maneuverability (e.g. hawks). One can only speculate that a highly structured habitat like at low elevations may select for wing aspect ratio while the higher flight efficiency of residual wing may be of greater advantage in the rarer air and colder temperatures at high elevations. The effect weakens when population values, i.e. $T_{PC.PR}$, are used.

We have seen a similar change with Bergmann's rule in Chapter 5, where the signal was stronger when using individual trait values rather than species means. Previous studies have interpreted this in terms of the filters acting more at the level of individuals rather than at the level of species, though we are not sure what this means in terms of the ecological process responsible. In any case, this highlights the importance of using intra-specific variation in community studies, and the recent trend of using both individual and species-specific traits to investigate community assembly mechanisms ((Jung et al. 2010; Albert et al. 2010; de Bello et al. 2011; Bolnick et al. 2011; Ross et al. 2017).

Since $T_{IP.IC}$ is affected by interspecific competition one may expect a relationship between the metric and species richness. However, we did not measure any significant relationship for any of the 3 traits. If $T_{IP.IC}$ is not related to species richness, Violle et al (2012) suggest that either the communities were assembled according to Neutral theory, or the measured traits were not influential during the assembly process. We are aware of only a few published studies using T-statistics (Le Bagousse□Pinguet et al. 2014; Luo et al. 2016; Neyret et al. 2016; Peronne et al. 2017; Outreman et al. 2017), most of which deal with plants and parasites, and none of which deal with insects. We suspect that the issue lies with the lack of large datasets of intraspecific individual traits.

7.5 Summary

1. Trait-based measures of diversity may be more informative in describing community response to an environmental gradient. Most work on trait responses to abiotic gradients has been done on plants due to the complexity in identifying and measuring functionality of traits in animals for a large number of individuals.
2. We observed a decrease in trait overlap across communities with increasing elevational (environmental) distance between them using primary traits of body length, thorax width, wing length and wing breadth, as well as derived traits of body volume, wing area and wing aspect ratio. The decline was significantly stronger in wing related attributes than body mass .
3. Hawkmoth subfamilies showed very little overlap across the morpho-space and the five most abundant genera in the study region showed zero overlap, indicating strong phylogenetic conservatism of the measured traits.
4. Traits within a local community were non-randomly assembled as shown with respect to their functional richness.
5. Functional evenness and functional divergence were significantly lower at high elevations, suggesting strong environmental filtering.
6. Using T-statistics, we showed the presence of strong internal filters throughout the study gradient with species in a local community more similar than individuals across species. The case for external filters came more from correlations with elevation than departures from the null distribution.
7. The relationship between functional diversity and species richness suggests low functional redundancy in the study region.

Conclusion

We investigated elevational diversity profiles of two disparate organismal groups, hawkmoths and birds, along the same transect spanning 2600 m in the eastern Himalayas of Arunachal Pradesh, India. Since the two taxa have very different life histories – endothermic birds and ectothermic hawkmoths – the differences in their response to changing elevation along the same transect can be better interpreted along the two axes of taxon-specific and taxon-independent attributes.

We investigated two categories of diversity – species and traits – using multiple metrics for each (e.g. alpha diversity, beta diversity, evenness, etc). We found that while the patterns were similar using certain metrics (for e.g. evenness of species abundances, elevational profile of alpha diversity, beta diversity, dissimilarity with distance, allometric relationship between wing area and body mass, community mean wing-loading, etc), they were strikingly different using other metrics (e.g. elevational profile of optimum-elevation alpha diversity, community clusters based on species composition, community mean body mass and residual-wing). Even when the patterns were similar one could detect taxon-specific footprints in their details. For instance, the dissimilarity with distance increased for both hawkmoths and birds, however, the rate of increase was significantly higher for birds than hawkmoths. Even more interestingly, the same data showed different results when evaluated at the intraspecific, interspecific and assemblage levels.

There is as yet no consensus in literature on the mechanisms generating these patterns. A major reason for this are the large gaps in knowledge of the reasons behind the variation in the patterns observed across different taxa and in different mountain systems. Our study did not explicitly target the identification of the causative mechanisms responsible for the observed patterns. Instead, we focused on delineating a variety of statistically secure diversity patterns to understand the reasons for the plethora of patterns in literature and bring out the underlying complexity. Ultimately, any realistic theory will have to resolve the seemingly contradictory patterns across taxa, geography and other ecological contexts.

Moving ahead from the observed patterns we have discussed them in the light of previously published processes and hypotheses, and linked them to our knowledge of the life histories of the two taxa. The simultaneous sampling of the two taxa, along the same elevational transect, should help in identifying the taxon-specific and taxon-independent factors driving diversity patterns. Such a direct comparison between taxa at the same place will complement the meta-analyses of disparate data sets from different places and times which is currently popular. We are in the process of adding more taxa and genetic diversity to this mix at our study site. We hope that it will be a small step towards a better understanding of the process by which communities are assembled.

This work raises several important questions, particularly related to the role of life history and taxonomic scale in shaping species distribution, diversity and abundance. The role of taxonomic scale has been rarely addressed in ecological investigations along environmental gradients. Our work, particularly the discrepant patterns observed at the population, species and community level for the body size of hawkmoths warrants further investigation. An analysis of the species abundance distributions using null models may facilitate a better understanding of the processes generating these patterns. An understanding of the mechanisms leading to the observed patterns is the next step planned in this project, along with the incorporation of genetic data for a detailed evolutionary perspective on the patterns.

Glossary: R libraries

R Core Team (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

- All analysis and figures were generated using R 3.3.1 (R Core Team, 2016) on a x86_64-pc-linux-gnu platform
- All figures were produced using R 3.3.1-base graphics unless specified otherwise
- Functions from within different libraries associated with specific analysis are noted in the text.

1. ***stringi***: Gagolewski M. and others (2017). R package stringi: Character string processing facilities.
2. ***mobsim***: Felix May (2017). mobsim: Spatial Simulation and Scale-Dependent Analysis of Biodiversity Changes. R package version 0.1.0.
3. ***readODS***: Gerrit-Jan Schutten, Chung-hong Chan and Thomas J. Leeper (2016). readODS: Read and Write ODS Files. R package version 1.6.4.
4. ***boot***: Angelo Canty and Brian Ripley (2015). boot: Bootstrap R (S-Plus) Functions. R package version 1.3-17.

   Davison, A. C. & Hinkley, D. V. (1997) Bootstrap Methods and Their Applications. Cambridge University Press, Cambridge. ISBN 0-521-57391-2
5. ***SPECIES***: Ji-Ping Wang (2011). SPECIES: An R Package for Species Richness Estimation. Journal of Statistical Software, 40(9), 1-15. URL http://www.jstatsoft.org/v40/i09/.
6. ***INEXT***: T. C. Hsieh, K. H. Ma and Anne Chao. 2016 iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12
   URL: http://chao.stat.nthu.edu.tw/blog/software-download/.

   Anne Chao, Nicholas J. Gotelli, T. C. Hsieh, Elizabeth L. Sander, K. H. Ma, Robert K. Colwell, and Aaron M. Ellison 2014.

   Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84:45-67.
7. ***rangemodelR***: Aniruddha Marathe, ATREE and Bangalore (2016). rangemodelR: Mid-Domain Effect and Species Richness Patterns. R package version
   1.0.1. https://CRAN.R-project.org/package=rangemodelR
8. ***scatterplot3d***: Ligges, U. and Mächler, M. (2003). Scatterplot3d - an R Package for Visualizing Multivariate Data. Journal of Statistical Software 8(11), 1-20.
9. ***Rcpp***: Dirk Eddelbuettel and Romain Francois (2011). Rcpp: Seamless R and C++ Integration. Journal of Statistical Software, 40(8), 1-18.
   URL http://www.jstatsoft.org/v40/i08/.

   Eddelbuettel, Dirk (2013) Seamless R and C++ Integration with Rcpp. Springer, New York. ISBN 978-1-4614-6867-7.
10. ***reshape***: H. Wickham. Reshaping data with the reshape package. Journal of Statistical Software, 21(12), 2007.

11. ***lme4***: Douglas Bates, Martin Maechler, Ben Bolker, Steve Walker (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

12. ***Matrix***: Douglas Bates and Martin Maechler (2016). Matrix: Sparse and Dense Matrix Classes and Methods. R package version 1.2-7.1. https://CRAN.R-project.org/package=Matrix

13. ***varComp***: Long Qu (2015). varComp: Variance Component Models. R package version 0.1-360. https://CRAN.R-project.org/package=varComp

14. ***EcoSimR***: Nicholas J. Gotelli, Edmund M. Hart and Aaron M. Ellison (2015) EcoSimR: Null model analysis for ecological data. R package version 0.1.0. http://github.com/gotellilab/EcoSimR DOI: 10.5281/zenodo.16522

15. ***cati***: Taudiere A. & Violle C. 2015. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. Ecography.

16. ***Nlme***: Pinheiro J, Bates D, DebRoy S, Sarkar D and R Core Team (2016). _nlme: Linear and Nonlinear Mixed Effects Models_. R package version 3.1-128, <URL: http://CRAN.R-project.org/package=nlme>.

17. ***GridExtra***: Baptiste Auguie (2016). gridExtra: Miscellaneous Functions for "Grid" Graphics. R package version 2.2.1. https://CRAN.R-project.org/package=gridExtra

18. ***plyr***: Hadley Wickham (2011). The Split-Apply-Combine Strategy for Data Analysis. Journal of Statistical Software, 40(1), 1-29. URL http://www.jstatsoft.org/v40/i01/.

19. ***Astro***: Lee Kelvin (2014). astro: Astronomy Functions, Tools and Routines. R package version 1.2. https://CRAN.R-project.org/package=astro

20. ***plotrix***: Lemon, J. (2006) Plotrix: a package in the red light district of R. R-News, 6(4): 8-12.

21. ***sp***: Pebesma, E.J., R.S. Bivand, 2005. Classes and methods for spatial data in R. R News 5 (2), https://cran.r-project.org/doc/Rnews/.

    Roger S. Bivand, Edzer Pebesma, Virgilio Gomez-Rubio, 2013. Applied spatial data analysis with R, Second edition. Springer, NY. http://www.asdar-book.org/

22. ***sads***: Paulo I. Prado, Murilo Dantas Miranda and Andre Chalom (2017). sads: Maximum Likelihood Models for Species Abundance Distributions. R package version 0.4.1. https://CRAN.R-project.org/package=sads

23. ***bbmle***: Ben Bolker and R Development Core Team (2017). bbmle: Tools for General Maximum Likelihood Estimation. R package version 1.0.19. https://CRAN.R-project.org/package=bbmle

24. ***betapart***: Andres Baselga, David Orme, Sebastien Villeger, Julien De Bortoli and Fabien Leprieur (2017). betapart: Partitioning Beta

25. ***FD***: Laliberté, E., and P. Legendre (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299-305.

    Laliberté, E., Legendre, P., and B. Shipley. (2014). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0-12.

26. ***geometry***: Kai Habel, Raoul Grasman, Robert B. Gramacy, Andreas Stahel and David C. Sterratt (2015). geometry: Mesh Generation and Surface

Tesselation. R package version 0.3-6. https://CRAN.R project.org/package=geometry

27. ***magic***: R. K. S. Hankin 2005. Recreational mathematics with R: introducing the 'magic' package R News 5(1)

28. ***abind***: Tony Plate and Richard Heiberger (2016). abind: Combine Multidimensional Arrays. R package version 1.4-5. https://CRAN.R-project.org/package=abind

29. ***ape***: Paradis E., Claude J. & Strimmer K. 2004. APE: analyses of phylogenetics and evolution in R language. Bioinformatics 20: 289-290.

30. ***ade4***: Dray, S. and Dufour, A.B. (2007): The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software. 22(4): 1-20.

    Chessel, D. and Dufour, A.B. and Thioulouse, J. (2004): The ade4 package-I- One-table methods. R News. 4: 5-10.

    Dray, S. and Dufour, A.B. and Chessel, D. (2007): The ade4 package-II: Two-table and K-table methods. R News. 7(2): 47-52.

31. ***reshape2***: Hadley Wickham (2007). Reshaping Data with the reshape Package. Journal of Statistical Software, 21(12), 1-20. URL http://www.jstatsoft.org/v21/i12/.

32. data.***table***: Matt Dowle and Arun Srinivasan (2017). data.table: Extension of \`data.frame\`. R package version 1.10.4. https://CRAN.Rproject.org/package=data.table

33. ***ggfortify***: Yuan Tang, Masaaki Horikoshi, and Wenxuan Li. ggfortify: Unified Interface to Visualize Statistical Result of Popular R Packages. The R Journal, 2016.

    Masaaki Horikoshi and Yuan Tang (2016). ggfortify: Data Visualization Tools for Statistical Analysis Results. https://CRAN.R-project.org/package=ggfortify

34. ***ggplot2***: H. Wickham. ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York, 2009.

35. ***MASS***: Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

36. ***BiodiversityR***: Kindt, R. & Coe, R. (2005) Tree diversity analysis. A manual and software for common statistical methods for ecological and biodiversity studies. World Agroforestry Centre (ICRAF), Nairobi. ISBN 92-9059-179-X.

37. ***vegan***: Jari Oksanen, F. Guillaume Blanchet, Michael Friendly, Roeland Kindt, Pierre Legendre, Dan McGlinn, Peter R. Minchin, R. B. O'Hara, Gavin L. Simpson, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs and Helene Wagner (2017). vegan: Community Ecology Package. R package version 2.4-3. https://CRAN.R-project.org/package=vegan

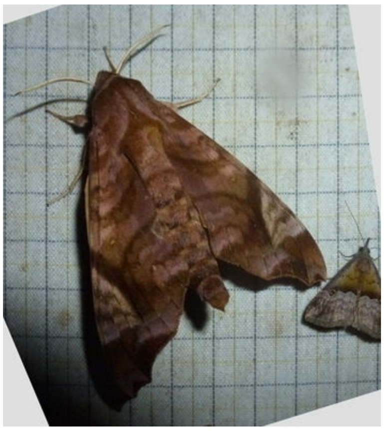
38. ***lattice***: Sarkar, Deepayan (2008) Lattice: Multivariate Data Visualization with R. Springer, New York. ISBN 978-0-387-75968-5

39. ***permute***: Gavin L. Simpson (2016). permute: Functions for Generating Restricted Permutations of Data. R package version 0.9-4. https://CRAN.R-project.org/package=permute

APPENDIX I

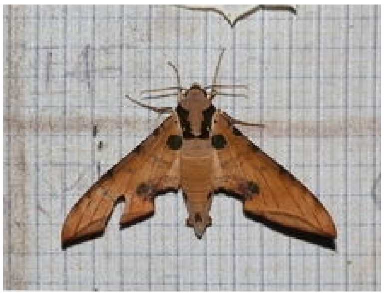
Hawkmoths species identifications and keys

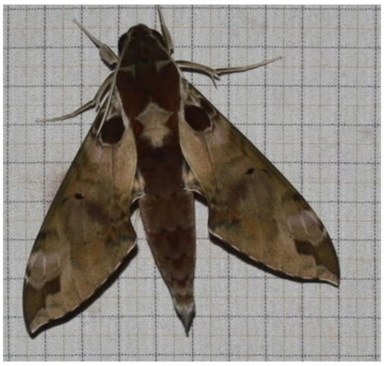
The species names assigned to our morpho-types are only meant to be name handles, and not actual species identifications, though many of them may be the correct identification. For the purpose of this thesis the actual specific identification is not essential.

Acherontia lachesis	***Acherontia styx***	***Acosmerycoides harterti***
		
Black basal patch on upper hind wing, though not always visible when sitting. See A. Styx for separation from that species. We have assumed that all others are this species and not A. atropos, which is restricted to Africa.	Differentiated from A. lachesis on the basis of upper forewing discal spot: orange and large in A. Styx, white and smaller in A. lachesis. Yellow on the abdomen extends beyond the 3rd segment, restricted to just 1 or 2 segments in A.lachesis	Monospecific genus. Distinctive colour pattern.
Acosmeryx anceus	***Acosmeryx naga***	***Acosmeryx omissa***
		
Brown with a tinge of violet. Termen slightly dentate, angulate at vein M3. Upper forewing with a diagnostic shape of inverted "tau" (τ)	Longish white band along termen. Prominent and contrasting "tau" shape. Could not separate A. naga from A. purus (newly described in 2014) but A. purus restricted to South-east China and Vietnam. The	Serrated termen like in A. sericeus. Characteristic tau at midwing with stem diffuse and dsintegrated unlike in

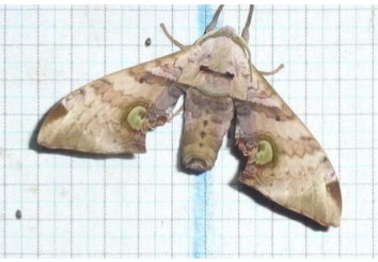
	individuals could be a mix of both.	the previous. Discal bands punctiform, unlike in A.sericeus.
Acosmeryx sericeus  Serrated termen. The midwing tau more prominent but the stem mets to upper streak close to the costum. Discal band not punctiform but continuous, unlike in A. omissa	***Acosmeryx shervillii***  Inseparable from A. pseudomissa and A. castanea but the latter two reported only from China, Thailand and Vietnam. Could not differentiate from A. Pseudonaga either. Our specimens could be a mix of all four. Light and dark forms observed for this species	***Acosmeryx sinjaevi***  Termen very smooth. Tau mark absent. or lambda shape is completely absent, only a thick band extending from mid-costa to anal angle
Agrius convolvuli  Sexually dimorphic species; closely resembling A. cingulata which is restricted to the new world. Other similar species are from Papua New Guinea and Australia.	***Ampelophaga dolichoides***  Distinctive coloration – brown with no reddish or hint of purplish. Thin discal bands	***Ampeolophaga khasiana***  Deep purplish velvety brown ground color with 4discal bands. Not distinguishable from A. nikolae (south-east China) and A. Thomasi (Nepal and W. Bengal). Latter may be in the study region.

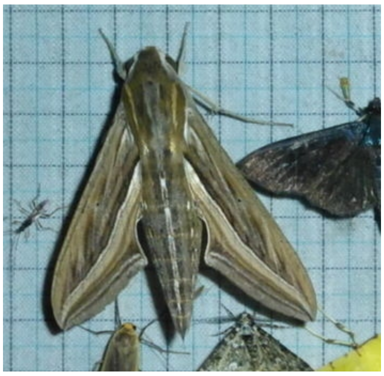
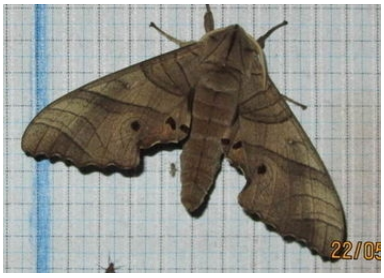
Ampelophaga rubiginosa	***Ampelophaga species4***	***Ambulyx liturata***
		
Greyish brown ground colour and rufous brown bands. 3Rd discal band is the broadest and very diffused, 4th band is very thin.	Only two individuals, from 1500m and 1900m. characteristically different from A.rubiginosa and A.khasiana. Only 3 discal bands with the 1st and 3rd thin and distinct whereas middle band broad and more diffused.	Ground color greyish, incomplete abdominal line, Basal spot along dorsum large, black and may be mildly hooked. Basal spot along the costum, if present, smaller than dorsal spot. Yellow subterminal band is broad and contrasty and ends well into dorsum. Patch on 8th abdominal tergit absen
Ambulyx tobii	***Ambulyx maculifera***	***Ambulyx moorei***
		
Ground color greyish. Abdominal line incomplete, but distinct. Basal spot along dorsum distinct but variable in size. Basal spot along costum = size dorsal spot. Subterminal yellow band ends at/just after tornus, is distinct and sometimes broad. Contrasty effect across wings. Terminal abdominal patch present.	Ground color ochraceous. Abdominal line of variable intensity, but always present. Basal spot along dorsum large, black and hooked. Subterminal yellow band ends on termen well before tornus and not prominent. Rectangular patch on 8th tergite.	Conspicuously distinguishable with its series of brown to black spots along the base of the wings.

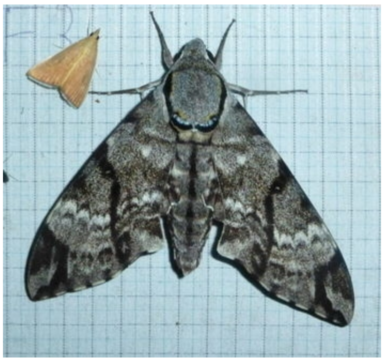
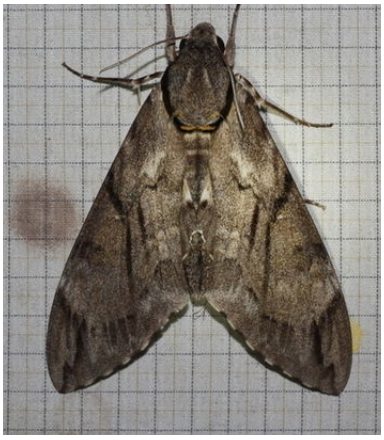
Ambulyx ochracea  Ground color ochraceous. No abdominal line. Basal spot along the dorsum large, black to dark green and sharply hooked. Subterminal yellow band ends on termen and is low contrast. Rectancular black patch on the 8th abdominal tergite. Prominent median dorsal spot.	***Ambulyx pseudoclavata***  Ground color dark rufous. Abdominal line is complete and distinct. Basal spot along the dorsum only spot on the wings. Subterminal yellow band narrow and ends just into dorsum. No patch on last tergite.	***Ambulyx sericeipennis***  Ground color grey. Abdominal line faint, partial or complete. Basal dorsal spot smallish, black, rounded. Basal spot on costum present, larger than or equal to dorsal spot. Subterminal yellow band, broad and contrasty, ends just into dorsum. Discal bands somewhat more prominent.
Ambulyx substrigilis  Ground color variable. Abdominal line may be complete or incomplete, but prominent. Basal spot along the dorsum prominent but variable. Basal spot along costum variable, may be absent. Subterminal yellow band ends at/just after tornus. Contrasty effect across wings.	***Apocalypsis velox***  Monospecific genus. Distinctive pattern.	***Amplypterus mansoni***  Distinguished from A. panopus by broader dark triangle on termen.
Amplypterus panopus  Distinguished from A. mansoni by sharperer but smaller dark triangle on termen.	***Angnonyx testacea***  Distinctive pattern of genus but indistinguishable from congenerics but only species in north-east India. A. krishna only in south India.	***Callambulyx junonia***  Conspicuous eye-spot lon upper hindwing, if open. Black marking along termen with strongly crenulate termen (contra straight in C.rubricosa).

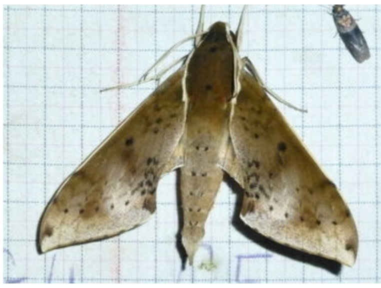
Callambulyx rubricosa	***Callambulyx poecilus***	***Cechenena aegrota***
		
Diffused dark coloration along termen. Termen less falcate, if at all, than previous.	Pale diffused green ground color. No eyespot on upper hindwing and no black marking along termen.	Distinctive except for C. Chimaera reported from Myanmar. Our species assigned to C.aegrota due to previous reports from adjacent Bhutan.
Cechenena helops	***Cechetra lineosa***	***Cechetra minor***
		
Distinctive pattern	Green in forewing and pattern disttinguishes the genus, but amount of green (versus brown) very variable. Greener specimens easily confused with C.subangustata.	Smaller than the preceeding species, the lines along the abdomen do not extend all the way into the thorax.

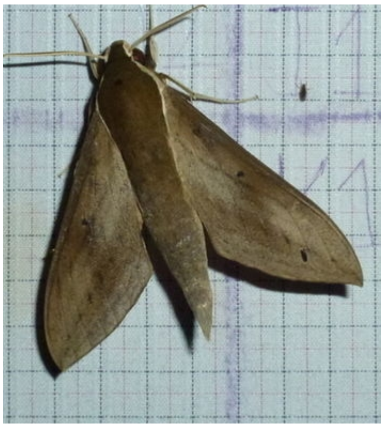
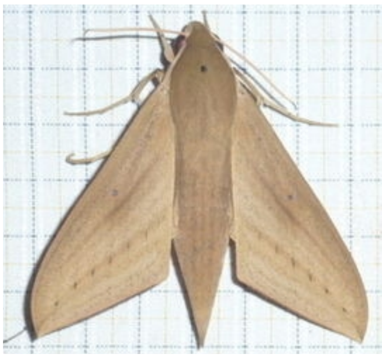
Cechetra scottii	***Cechetra subangustata***	***Clanis undulosa***
		
Either the upper forewing base pink or proximal part of antennae pinkish. 2 forms: 1. with 3rd and 4th postmedial line dark and thick (often fused into one broad band). At 2100m and above 2. all postmedial lines either equal in thickness and intensity, 3rd and 4th are thicker, darker but less contrasting than in first form. Antennae with proximal pink only in this form. More common at lower elevations.	Forewing widely flushed with green. Previously considered subspecies of C. lineosa; but Nepalese specimens may represent a separate species.	Could not differentiate between C. Undulosa, C. bilineata and C. deucalion.
Clanis scwartzi	***Clanis titan***	***Craspedortha porphyria***
		
Most similar to C. titan but has more elongate wings. Apical spot is sharper than in C.titan.	Read description of previous species.	Two species of this genus in north-east India. C. Montana has a ring-like pattern at base of forewing. Under forewing better for identification.

Daphnis hypothous  Upper forewing darker olive-green than in D. nerii with a conspicous white apical spot.	***Cypa decolor***  3 species reported from north-east India, morphologically indistinguish-able. Only a single specimen.	***Daphnusa sinocontinentalis***  D. ocellaris, D. sinocontinentalis and D. haxaire inseparable.
Dolbina inexacta  D. inexacta, D. tibetiana and D. Paraexacta could be in Arunachal, but indistinguishable.	***Eupanacra metallica***  Olive green ground color with a tinge of brown (sometimes orange). Purple-pinkish tone of forewing base and lateral sides of thorax. Separated from E. perfecta by excavated termen just below apex.	***Eupanacra busiris***  Diagnostic green of thorax and upper forewing.

Eupanacra perfecta  More reddish ground color, smaller than E. sinuata and apex of forewing not, or only faintly, dentate.	***Eupanacra variolosa***  Broad black basal patch at base of upper forewing.	***Hippotion celerio***  Smooth termen without crenulations. Conspicuous white double line along termen. Similar to H. Aporods (restricted to Africa).
Hippotion species  Could not differentiate between H. echeclus, H. rafflesi, H. boerhaviae and H. rosetta.	***Macroglossum species1***  Highly speciose genus with 32 species from north-east. Species 1 could be either M. corythus, M. glaucoptera or M. obscura.	***Macroglossum species2***  Species 2 could be either M. affictia, M. belis, M. Bombylans, M. variegatum or M. vicinum.
Marumba cristata  Tawny brown colour and 5 oblique lines diagnostic. Tornal spot size and termen crenulation variable.	***Marumba dyras***  Could not distinguish between M. dyras and M. sperchius. M. juvencus similar but only from below Myanmar.	***Marumba spectabilis***  More rufous brown and contrasty than M.dyras. Upper forewing with conspicuous tornal loop.

Marumba echephron  Our specimen is closest to Japanese species, unlike any other reported from the study region.	***Megacorma obliqua***  Distinctive pattern; only one from genus in north-east India.	***Meganoton analis***  Semicircular ring enclosing upper forewing apex distinguishes it from M. nyctiphanes.
Meganoton rubescens  Similar to M. Analis but ground color More tawny brown.	***Nephele hespera***  Distinctive morph, only one from genus in north-east India. Very similar to N. joiceyi (from South-east Islands). Our sample may have more than one species	***Pergesa acteus***  Distinctive pattern.
Psilograama increta  Discal spot faint, not present on discal lin. Discal lines thinner. Differs from P.menephron with a less contrasty grey ground color;	***Psilogramma menephron***  See previous. Apical area and mid-costal patch darker than the rest of upper forewing.	***Rhagastis acuta***  Very similar to R. hayesi. Outermost postmedial line inconspicuous, punctuated; sometimes only vein dots visible. Wing dull olive green with reddish-orange dentate suffusions along the post medial lines and at the base of upper forewing.

Rhagastis albomarginatus  Two orange spots on lateral side of thorax may be faint but always present.	***Rhagastis castor***  Outermost series of discal spots not connected by a line, inner two series connected by a sinuate line; whitish hue along termen.	***Rhagastis confusa***  Dark olive green on entire upper forewing. Pinkish white hue along termen. Very thin pink edge to costum and dorsum. Postmedial sinuate lines absent (or extremely faint).
Rhagastis gloriosa  Distinctive pattern of olive green and pink.	***Rhagastis lunata***  Crisp silvery crenulate pattern along termen. Rest variable.	***Rhagastis olivacea***  Bright olive green (sometimes ochraceous brown) ground. Reddish discal lines, sometimes broken, and white subterminal markings.
Rhagastis velata  Thick blotchy discal band. Overall maculation very dark and contrasty.	***Rhodoprasina species***  Genus distinctive with upper forewing green and termen waveform; Could be any of R. floralis, R. corrigenda or R. callantha.	***Theretra alecto***  T. suffusa has a white band along abdomen. T.mansoni has only two conspicuous postmedial lines. Postmedial continuous, unlike in T. boisduvallii.

Theretra boisduvallii  Olive to brown ground color; 4th postmedial line distinctly punctuated by dots on veins.	***Theretra clotho***  Olive to brown ground colour. 4th postmedial line strongest, not punctuate, and often the only conspicuous line. very similar to T. tibetiana.	***Theretra griseomarginata***  Distinctive pattern
Theretra lateriellii  Starightish termen is the most diagnostic character, 4th postmedial line punctuate by vein dots.	***Theretra nessus***  Distinctive pattern with green costum and golden lateral side of abdomen.	***Theretra pallicosta***  Unmistakable species with tawny red suffusions and no discrete postmedial lines.
Theretra oldenlandiae  Distinguished from T. silhetensis by two white stripes along the abdomen (versis 1). Very similar to T. lycetus.	***Theretra suffusa***  Distinguished from T. alecto by broad pale dorsal stripe running along thorax and abdomen.	

References

1. "Kitching, I.J. 2018. Sphingidae Taxonomic Inventory, http://sphingidae.myspecies.info/
2. Pittaway, A.R. & Kitching, I.J. (2018). *Sphingidae of the Eastern Palaearctic (including Siberia, the Russian Far East, Mongolia, China, Taiwan, the Korean Peninsula and Japan)*. http://tpittaway.tripod.com/china/china.htm
3. Holloway, J.D., 1987. *The moths of Borneo: superfamily Bombycoidea: families Lasiocampidae, Eupterotidae, Bombycidae, Brahmaeidae, Saturniidae, Sphingidae*. Malaysian Nature Society.
4. Inoue, H., Robert D.. Kennett and Kitching, I.J., 1997. *Moths of Thailand: Sphingidae. Vol. Two*. Chok Chai Press.

Appendix II

Bird Species Recorded during the Current Study

*The species are listed in alphabetical order

	Family	**Common Name**	***Scientific Name***
1)	*Accipitridae*	Black Eagle	*Ictinaetus malaiensis*
2)	*Accipitridae*	Crested Goshawk	*Accipiter trivirgatus*
3)	*Accipitridae*	Crested Serpent-Eagle	*Spilornis cheela*
4)	*Accipitridae*	Mountain Hawk-Eagle	*Nisaetus nipalensis*
5)	*Accipitridae*	Oriental Honey-Buzzard	*Pernis ptilorhynchus*
6)	*Aegithalidae*	Red-headed Tit	*Aegithalos concinnus*
7)	*Aegithinidae*	Common Iora	*Aegithina tiphia*
8)	*Alcedinidae*	Ruddy Kingfisher	*Halcyon coromanda*
9)	*Bucerotidae*	Great Hornbill	*Buceros bicornis*
10)	*Bucerotidae*	Oriental Pied-Hornbill	*Anthracoceros albirostris*
11)	*Bucerotidae*	Rufous-necked Hornbill	*Aceros nipalensis*
12)	*Bucerotidae*	Wreathed Hornbill	*Rhyticeros undulatus*
13)	*Campephagidae*	Black-winged Cuckooshrike	*Lalage melaschistos*
14)	*Campephagidae*	Grey-chinned Minivet	*Pericrocotus solaris*
15)	*Campephagidae*	Long-tailed Minivet	*Pericrocotus ethologus*
16)	*Campephagidae*	Scarlet Minivet	*Pericrocotus flammeus*
17)	*Campephagidae*	Short-billed Minivet	*Pericrocotus brevirostris*
18)	*Certhiidae*	Brown-throated Treecreeper	*Certhia discolor*
19)	*Chloropseidae*	Gold-fronted Leafbird	*Chloropsis aurifrons*
20)	*Chloropseidae*	Orange-bellied Leafbird	*Chloropsis hardwickii*
21)	*Cisticolidae*	Common Tailorbird	*Orthotomus sutorius*
22)	*Columbidae*	Ashy Wood-pigeon	*Columba pulchricollis*
23)	*Columbidae*	Barred Cuckoo-Dove	*Macropygia unchall*
24)	*Columbidae*	Emerald Dove	*Chalcophaps indica*
25)	*Columbidae*	Green Imperial-Pigeon	*Ducula aenea*
26)	*Columbidae*	Mountain Imperial-pigeon	*Ducula badia*
27)	*Columbidae*	Pin-tailed Green-pigeon	*Treron apicauda*
28)	*Columbidae*	Thick-billed Green-Pigeon	*Treron curvirostra*
29)	*Columbidae*	Wedge-tailed Green-pigeon	*Treron sphenurus*
30)	*Corvidae*	Collared Treepie	*Dendrocitta frontalis*
31)	*Corvidae*	Common Green-Magpie	*Cissa chinensis*
32)	*Corvidae*	Grey Treepie	*Dendrocitta formosae*
33)	*Corvidae*	Spotted Nutcracker	*Nucifraga caryocatactes*
34)	*Corvidae*	Yellow-billed Blue-Magpie	*Urocissa flavirostris*

35)	*Cuculidae*	Asian-Emerald Cuckoo	*Chrysococcyx maculatus*
36)	*Cuculidae*	Banded-Bay Cuckoo	*Cacomantis sonneratii*
37)	*Cuculidae*	Chestnut-winged Cuckoo	*Clamator coromandus*
38)	*Cuculidae*	Drongo Cuckoo	*Surniculus lugubris*
39)	*Cuculidae*	Green-billed Malkoha	*Phaenicophaeus tristis*
40)	*Cuculidae*	Indian Cuckoo	*Cuculus micropterus*
41)	*Cuculidae*	Large Hawk-Cuckoo	*Hierococcyx sparverioides*
42)	*Cuculidae*	Lesser Cuckoo	*Cuculus poliocephalus*
43)	*Cuculidae*	Oriental Cuckoo	*Cuculus saturatus*
44)	*Cuculidae*	Plaintive Cuckoo	*Cacomantis merulinus*
45)	*Cuculidae*	Whistling Hawk-Cucko	*Hierococcyx nisicolor*
46)	*Dicaeidae*	Fire-breasted Flowerpecker	*Dicaeum ignipectus*
47)	*Dicaeidae*	Scarlet-backed Flowerpecker	*Dicaeum cruentatum*
48)	*Dicaeidae*	Yellow-bellied Flowerpecker	*Dicaeum melanozanthum*
49)	*Dicruridae*	Ashy Drongo	*Dicrurus leucophaeus*
50)	*Dicruridae*	Bronzed Drongo	*Dicrurus aeneus*
51)	*Dicruridae*	Crow-billed Drongo	*Dicrurus annectens*
52)	*Dicruridae*	Greater-Racket-tailed Drongo	*Dicrurus paradiseus*
53)	*Dicruridae*	Hair-crested Drongo	*Dicrurus hottentottus*
54)	*Dicruridae*	Lesser-Racket-tailed Drongo	*Dicrurus remifer*
55)	*Elachuridae*	Spotted Wren-babbler	*Elachura formosa*
56)	*Eurylaimidae*	Long-tailed Broadbill	*Psarisomus dalhousiae*
57)	*Falconidae*	Pied Falconet	*Microhierax melanoleucos*
58)	*Fringillidae*	Brown Bullfinch	*Pyrrhula nipalensis*
59)	*Fringillidae*	Crimson-browed Finch	*Carpodacus subhimachalus*
60)	*Fringillidae*	Gold-naped Finch	*Pyrrhoplectes epauletta*
61)	*Fringillidae*	Grey-headed Bullfinch	*Pyrrhula erythaca*
62)	*Fringillidae*	Himalayan Greenfinch	*Chloris spinoides*
63)	*Fringillidae*	Plain Mountain-finch	*Leucosticte nemoricola*
64)	*Fringillidae*	Scarlet Finch	*Carpodacus sipahi*
65)	*Fringillidae*	Spot-winged Grosbeak	*Mycerobas melanozanthos*
66)	*Irenidae*	Asian Fairy-Bluebird	*Irena puella*
67)	*Leiotrichidae*	Bar-throated Minla	*Chrysominla strigula*
68)	*Leiotrichidae*	Beautiful Sibia	*Heterophasia pulchella*
69)	*Leiotrichidae*	Bhutan Laughingthrush	*Trochalopteron imbricatum*
70)	*Leiotrichidae*	Black-faced Laughingthrush	*Trochalopteron affine*
71)	*Leiotrichidae*	Blue-winged Laughingthrush	*Trochalopteron squamatum*
72)	*Leiotrichidae*	Blue-winged Minla	*Siva cyanouroptera*
73)	*Leiotrichidae*	Bugun Liocichla	*Liocichla bugunorum*

74)	*Leiotrichidae*	Greater-necklaced Laughingthrush	*Garrulax pectoralis*
75)	*Leiotrichidae*	Grey-sided Laughingthrush	*Garrulax caerulatus*
76)	*Leiotrichidae*	Himalayan Cutia	*Cutia nipalensis*
77)	*Leiotrichidae*	Lesser-necklaced Laughingthrush	*Garrulax monileger*
78)	*Leiotrichidae*	Long-tailed Sibia	*Heterophasia picaoides*
79)	*Leiotrichidae*	Nepal Fulvetta	*Alcippe nipalensis*
80)	*Leiotrichidae*	Red-faced Liocichla	*Liocichla phoenicea*
81)	*Leiotrichidae*	Red-headed Laughingthrush	*Trochalopteron*
82)	*Leiotrichidae*	Red-tailed Minla	*Minla ignotincta*
83)	*Leiotrichidae*	Rufous-backed Sibia	*Leioptila annectens*
84)	*Leiotrichidae*	Rufous-vented Laughingthrush	*Garrulax gularis*
85)	*Leiotrichidae*	Rusty-fronted Barwing	*Actinodura egertoni*
86)	*Leiotrichidae*	Scaly Laughingthrush	*Trochalopteron subunicolor*
87)	*Leiotrichidae*	Silver-eared Mesia	*Leiothrix argentauris*
88)	*Leiotrichidae*	Spotted Laughingthrush	*Garrulax ocellatus*
89)	*Leiotrichidae*	Streak-throated Barwing	*Sibia waldeni*
90)	*Leiotrichidae*	Striated Laughingthrush	*Grammatoptila striata*
91)	*Leiotrichidae*	White-crested Laughingthrush	*Garrulax leucolophus*
92)	*Leiotrichidae*	White-throated Laughingthrush	*Garrulax albogularis*
93)	*Megalaimidae*	Great Barbet	*Psilopogon virens*
94)	*Megalaimidae*	Lineated Barbet	*Psilopogon lineatus*
95)	*Meropidae*	Blue-bearded Bee-eater	*Nyctyornis athertoni*
96)	*Monarchidae*	Asian Paradise-flycatcher	*Terpsiphone paradisi*
97)	*Monarchidae*	Black-naped Monarch	*Hypothymis azurea*
98)	*Muscicapidae*	Black-backed Forktail	*Enicurus immaculatus*
99)	*Muscicapidae*	Blue Whistling-thrush	*Myophonus caeruleus*
100)	*Muscicapidae*	Blue-fronted Blue-Robin	*Cinclidium frontale*
101)	*Muscicapidae*	Blue-fronted Redstart	*Phoenicurus frontalis*
102)	*Muscicapidae*	Chestnut-bellied Rock-thrush	*Monticola rufiventris*
103)	*Muscicapidae*	Dark-sided Flycatcher	*Muscicapa sibirica*
104)	*Muscicapidae*	Ferruginous Flycatcher	*Muscicapa ferruginea*
105)	*Muscicapidae*	Hill-blue Flycatcher	*Cyornis banyumas*
106)	*Muscicapidae*	Large Niltava	*Niltava grandis*
107)	*Muscicapidae*	Lesser Shortwing	*Brachypteryx leucophris*
108)	*Muscicapidae*	Little-pied Flycatcher	*Ficedula westermanni*
109)	*Muscicapidae*	Orange-gorgeted Flycatcher	*Ficedula strophiata*
110)	*Muscicapidae*	Pale-blue Flycatcher	*Cyornis unicolor*
111)	*Muscicapidae*	Pale-chinned Flycatcher	*Cyornis poliogenys*
112)	*Muscicapidae*	Pygmy-blue Flycatcher	*Ficedula hodgsoni*

113)	*Muscicapidae*	Rufous-bellied Niltava	*Niltava sundara*
114)	*Muscicapidae*	Sapphire Flycatcher	*Ficedula sapphira*
115)	*Muscicapidae*	Slaty-backed Forktail	*Enicurus schistaceus*
116)	*Muscicapidae*	Slaty-blue Flycatcher	*Ficedula tricolor*
117)	*Muscicapidae*	Small Niltava	*Niltava macgrigoriae*
118)	*Muscicapidae*	Spotted Forktail	*Enicurus maculatus*
119)	*Muscicapidae*	Verditer Flycatcher	*Eumyias thalassinus*
120)	*Muscicapidae*	White-browed Shortwing	*Brachypteryx montana*
121)	*Muscicapidae*	White-gorgeted Flycatcher	*Anthipes monileger*
122)	*Muscicapidae*	White-rumped Shama	*Copsychus malabaricus*
123)	*Muscicapidae*	White-tailed Blue-Robin	*Myiomela leucura*
124)	*Nectariniidae*	Black-breasted Sunbird	*Aethopyga saturata*
125)	*Nectariniidae*	Crimson Sunbird	*Aethopyga siparaja*
126)	*Nectariniidae*	Gould's Sunbird	*Aethopyga gouldiae*
127)	*Nectariniidae*	Green-tailed Sunbird	*Aethopyga nipalensis*
128)	*Nectariniidae*	Streaked Spiderhunter	*Arachnothera magna*
129)	*Oriolidae*	Black-hooded Oriole	*Oriolus xanthornus*
130)	*Oriolidae*	Maroon Oriole	*Oriolus traillii*
131)	*Paridae*	Black-spotted Yellow-Tit	*Machlolophus spilonotus*
132)	*Paridae*	Sultan Tit	*Melanochlora sultanea*
133)	*Paridae*	Yellow-browed Tit	*Sylviparus modestus*
134)	*Pellorneidae*	Abbott's Babbler	*Malacocincla abbotti*
135)	*Pellorneidae*	Eyebrowed Wren-babbler	*Napothera epilepidota*
136)	*Pellorneidae*	Indian-White-hooded Babbler	*Gampsorhynchus rufulus*
137)	*Pellorneidae*	Long-billed Wren-babbler	*Rimator malacoptilus*
138)	*Pellorneidae*	Puff-throated Babbler	*Pellorneum ruficeps*
139)	*Pellorneidae*	Rufous-winged Fulvetta	*Schoeniparus castaneceps*
140)	*Pellorneidae*	Yellow-throated Fulvetta	*Schoeniparus cinereus*
141)	*Phasianidae*	Blyth's Tragopan	*Tragopan blythii*
142)	*Phasianidae*	Chestnut-breasted Hill-partridge	*Arborophila mandellii*
143)	*Phasianidae*	Common Hill-partridge	*Arborophila torqueola*
144)	*Phasianidae*	Grey Peacock-Pheasant	*Polyplectron bicalcaratum*
145)	*Phasianidae*	Kaleej Pheasant	*Lophura leucomelanos*
146)	*Phasianidae*	Red Junglefowl	*Gallus gallus*
147)	*Phasianidae*	Rufous-throated Hill-partridge	*Arborophila rufogularis*
148)	*Phasianidae*	Temminck's Tragopan	*Tragopan temminckii*
149)	*Phylloscopidae*	Blyth's Leaf-warbler	*Phylloscopus reguloides*
150)	*Phylloscopidae*	Chestnut-crowned Warbler	*Phylloscopus castaniceps*
151)	*Phylloscopidae*	Grey-cheeked Warbler	*Phylloscopus poliogenys*

152)	*Phylloscopidae*	Grey-faced Leaf-warbler	*Phylloscopus maculipennis*
153)	*Phylloscopidae*	Grey-hooded Warbler	*Phylloscopus xanthoschistos*
154)	*Phylloscopidae*	Large-billed Leaf-warbler	*Phylloscopus magnirostris*
155)	*Phylloscopidae*	Lemon-rumped Leaf-warbler	*Phylloscopus chloronotus*
156)	*Phylloscopidae*	Orange-barred Leaf-warbler	*Phylloscopus pulcher*
157)	*Phylloscopidae*	Whistler's Warbler	*Phylloscopus whistleri*
158)	*Phylloscopidae*	White-spectacled Warbler	*Phylloscopus intermedius*
159)	*Phylloscopidae*	Yellow-vented Warbler	*Phylloscopus cantator*
160)	*Picidae*	Bay Woodpecker	*Blythipicus pyrrhotis*
161)	*Picidae*	Crimson-breasted Pied-Woodpecker	*Dendrocopos cathpharius*
162)	*Picidae*	Darjeeling Pied-Woodpecker	*Dendrocopos darjellensis*
163)	*Picidae*	Fulvous-breasted Pied-Woodpecker	*Dendrocopos macei*
164)	*Picidae*	Greater Flameback	*Chrysocolaptes lucidus*
165)	*Picidae*	Greater Yellownape	*Chrysophlegma flavinucha*
166)	*Picidae*	GreatSlaty Woodpecker	*Mulleripicus pulverulentus*
167)	*Picidae*	Grey-faced Woodpecker	*Picus canus*
168)	*Picidae*	Lesser Yellownape	*Picus chlorolophus*
169)	*Picidae*	Pale-headed Woodpecker	*Gecinulus grantia*
170)	*Picidae*	Rufous Woodpecker	*Micropternus brachyurus*
171)	*Picidae*	Rufous-bellied Woodpecker	*Dendrocopos hyperythrus*
172)	*Picidae*	Speckled Piculet	*Picumnus innominatus*
173)	*Picidae*	White-browed Piculet	*Sasia ochracea*
174)	*Pittidae*	Blue-naped Pitta	*Hydrornis nipalensis*
175)	*Pittidae*	Hooded Pitta	*Pitta sordida*
176)	*Pnoepygidae*	Pygmy Wren-babbler	*Pnoepyga pusilla*
177)	*Pnoepygidae*	Scaly-breasted Wren-babbler	*Pnoepyga albiventer*
178)	*Podargidae*	Hodgson's Frogmouth	*Batrachostomus hodgsoni*
179)	*Psittacidae*	Red-breasted Parakeet	*Psittacula alexandri*
180)	*Pycnonotidae*	Ashy Bulbul	*Hemixos flavala*
181)	*Pycnonotidae*	Black-crested Bulbul	*Pycnonotus flaviventris*
182)	*Pycnonotidae*	Himalayan Black-bulbul	*Hypsipetes leucocephalus*
183)	*Pycnonotidae*	Mountain Bulbul	*Ixos mcclellandii*
184)	*Pycnonotidae*	Striated Bulbul	*Pycnonotus striatus*
185)	*Pycnonotidae*	White-throated Bulbul	*Alophoixus flaveolus*
186)	*Ramphastidae*	Blue-eared Barbet	*Megalaima australis*
187)	*Ramphastidae*	Blue-throated Barbet	*Megalaima asiatica*
188)	*Ramphastidae*	Golden-throated Barbet	*Megalaima franklinii*
189)	*Rhipiduridae*	White-throated Fantail	*Rhipidura albicollis*
190)	*Scotocercidae*	Black-faced Warbler	*Abroscopus schisticeps*

191)	*Scotocercidae*	Broad-billed Warbler	*Tickellia hodgsoni*
192)	*Scotocercidae*	Chestnut-headed Tesia	*Cettia castaneocoronata*
193)	*Scotocercidae*	Grey-sided Bush-warbler	*Cettia brunnifrons*
194)	*Scotocercidae*	Hume's Bush-warbler	*Horornis brunnescens*
195)	*Scotocercidae*	Mountain Tailorbird	*Phyllergates cucullatus*
196)	*Scotocercidae*	Rufous-faced Warbler	*Abroscopus albogularis*
197)	*Scotocercidae*	Slaty-bellied Tesia	*Tesia olivea*
198)	*Scotocercidae*	Strong-footed Bush-warbler	*Horornis fortipes*
199)	*Scotocercidae*	Yellow-bellied Warbler	*Abroscopus superciliaris*
200)	*Scotocercidae*	Yellow-browed Tesia	*Tesia cyaniventer*
201)	*Sittidae*	Beautiful Nuthatch	*Sitta formosa*
202)	*Sittidae*	Chestnut-bellied Nuthatch	*Sitta cinnamoventris*
203)	*Sittidae*	White-tailed Nuthatch	*Sitta himalayensis*
204)	*Stenostiridae*	Grey-headed Canary-flycatcher	*Culicicapa ceylonensis*
205)	*Stenostiridae*	Yellow-bellied Fantail	*Chelidorhynx hypoxanthus*
206)	*Strigidae*	Asian-Barred Owlet	*Glaucidium cuculoides*
207)	*Strigidae*	Collared Owlet	*Glaucidium brodiei*
208)	*Sturnidae*	Common Hill-Myna	*Gracula religiosa*
209)	*Sturnidae*	Common Myna	*Acridotheres tristis*
210)	*Sylviidae*	Black-throated Parrotbill	*Suthora nipalensis*
211)	*Sylviidae*	Brown Parrotbill	*Cholornis unicolor*
212)	*Sylviidae*	Brown-throated Fulvetta	*Fulvetta ludlowi*
213)	*Sylviidae*	Fire-tailed Myzornis	*Myzornis pyrrhoura*
214)	*Sylviidae*	Golden-breasted Fulvetta	*Lioparus chrysotis*
215)	*Sylviidae*	Greater-Rufous-headed Parrotbill	*Psittiparus ruficeps*
216)	*Sylviidae*	Grey-headed Parrotbill	*Paradoxornis gularis*
217)	*Sylviidae*	Lesser-Rufous-headed Parrotbill	*Chleuasicus atrosuperciliaris*
218)	*Timaliidae*	Bar-winged Wren-babbler	*Spelaeornis troglodytoides*
219)	*Timaliidae*	Coral-billed Scimitar-babbler	*Pomatorhinus ferruginosus*
220)	*Timaliidae*	Golden Babbler	*Cyanoderma chrysaeum*
221)	*Timaliidae*	Grey-throated Babbler	*Stachyris nigriceps*
222)	*Timaliidae*	Rufous-capped Babbler	*Cyanoderma ruficeps*
223)	*Timaliidae*	Rufous-throated Wren-babbler	*Spelaeornis caudatus*
224)	*Timaliidae*	Sikkim-Wedge-billed Babbler	*Sphenocichla humei*
225)	*Timaliidae*	Slender-billed Scimitar-babbler	*Pomatorhinus superciliaris*
226)	*Timaliidae*	Streak-breasted Scimitar-babbler	*Pomatorhinus ruficollis*
227)	*Timaliidae*	Striped Tit-babbler	*Macronous gularis*
228)	*Timaliidae*	White-browed Scimitar-babbler	*Pomatorhinus schisticeps*
229)	*Trogonidae*	Red-headed Trogon	*Harpactes erythrocephalus*

230)	*Trogonidae*	Ward's Trogon	*Harpactes wardi*
231)	*Turdidae*	Green Cochoa	*Cochoa viridis*
232)	*Turdidae*	Purple Cochoa	*Cochoa purpurea*
233)	*Vangidae*	Large Woodshrike	*Tephrodornis virgatus*
234)	*Vangidae*	Pied Flycatcher-shrike	*Hemipus picatus*
235)	*Vireonidae*	Black-eared Shrike-babbler	*Pteruthius melanotis*
236)	*Vireonidae*	Black-headed Shrike-babbler	*Pteruthius rufiventer*
237)	*Vireonidae*	Green Shrike-babbler	*Pteruthius xanthochlorus*
238)	*Vireonidae*	White-bellied Erpornis	*Erpornis zantholeuca*
239)	*Vireonidae*	White-browed Shrike-babbler	*Pteruthius flaviscapis*
240)	*Zosteropidae*	Black-chinned Yuhina	*Yuhina nigrimenta*
241)	*Zosteropidae*	Rufous-vented Yuhina	*Yuhina occipitalis*
242)	*Zosteropidae*	Striated Yuhina	*Yuhina castaniceps*
243)	*Zosteropidae*	Stripe-throated Yuhina	*Yuhina gularis*
244)	*Zosteropidae*	Whiskered Yuhina	*Yuhina flavicollis*
245)	*Zosteropidae*	White-naped Yuhina	*Yuhina bakeri*

References

1. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A. & de Juana, E. (eds.) (2011). *Handbook of the Birds of the World Alive*. Lynx Edicions, Barcelona. (retrieved from http://www.hbw.com/ in August 2011).

2. Rasmussen, P.C. and Anderton, J.C., 2005. Birds of south Asia: the Ripley guide. *Washington, DC*.

BIBLIOGRAPHY

1. Able, K.P. & Noon, B.R. 1976. Avian Community Structure along Elevational Gradients in the Northeastern United States. Oecologia 26 (3): 275 – 294.
2. Acharya, B.K. and Vijayan, L., 2015. Butterflies of Sikkim with reference to elevational gradient in species, abundance, composition, similarity and range size distribution. Biodiversity of Sikkim: Exploring and Conserving A Global Hotspot. Information and Public Relations Department, Government of Sikkim, xxviii+ 542pp, pp.207-220.
3. Acharya, B.K., Sanders, N.J., Vijayan, L. and Chettri, B., 2011. Elevational gradients in bird diversity in the Eastern Himalaya: an evaluation of distribution patterns *and* their underlying mechanisms. *PLoS One*, *6*(12), p.e29097.
4. Acharya, K.P., Vetaas, O.R. and Birks, H.J.B., 2011. Orchid species richness along Himalayan elevational gradients. *Journal of Biogeography*, *38*(9), pp.1821-1833.
5. Addicott, J.F., Aho, J.M., Antolin, M.F., Padilla, D.K., Richardson, J.S. and Soluk, D.A., 1987. Ecological neighborhoods: scaling environmental patterns. *Oikos*, pp.340-346.
6. Agarwal, I., Mistry, V.K. and Athreya, R., 2010. A preliminary checklist of the reptiles of Eaglenest Wildlife Sanctuary, West Kameng District, Arunachal Pradesh, India. Russian Journal of Herpetology, 17(2), pp.81-93.
7. Aiba, M., Katabuchi, M., Takafumi, H., Matsuzaki, S.I.S., Sasaki, T. and Hiura, T., 2013. Robustness of trait distribution metrics for community assembly studies under the uncertainties of assembly processes. *Ecology*, *94*(12), pp.2873-2885.
8. Alahuhta, J., Kosten, S., Akasaka, M., Auderset, D., Azzella, M.M., Bolpagni, R., Bove, C.P., Chambers, P.A., Chappuis, E., Clayton, J. and de Winton, M., 2017. Global variation in the beta diversity of lake macrophytes is driven by environmental heterogeneity rather than latitude. *Journal of Biogeography*, *44*(8), pp.1758-1769.
9. Albert, C.H., Thuiller, W., Yoccoz, N.G., Douzet, R., Aubert, S. and Lavorel, S., 2010. A multi‐trait approach reveals the structure and the relative importance of intra‐vs. interspecific variability in plant traits. *Functional Ecology*, *24*(6), pp.1192-1201.
10. Alerstam, T., Rosén, M., Bäckman, J., Ericson, P.G. and Hellgren, O., 2007. Flight speeds among bird species: allometric and phylogenetic effects. *PLoS biology*, *5*(8), p.e197.
11. Alhajeri, B.H. and Steppan, S.J., 2016. Association between climate and body size in rodents: A phylogenetic test of Bergmann's rule. *Mammalian Biology-Zeitschrift für Säugetierkunde*, *81*(2), pp.219-225.
12. Alho, J.S., Herczeg, G., Laugen, A.T., Räsänen, K., Laurila, A. and Merilä, J., 2011. Allen’s rule revisited: quantitative genetics of extremity length in the common frog along a latitudinal gradient. *Journal of evolutionary biology*, *24*(1), pp.59-70.
13. Allen, A. P., Brown, J. H., Gillooly, J. F. 2002. Global Biodiversity, Biochemical Kinetics, and the Energetic-Equivalence Rule, Science 297 : 1545.
14. Allen, J.A., 1877. The influence of physical conditions in the genesis of species. *Radical review*, *1*, pp.108-140.
15. Altshuler, D.L. and Dudley, R., 2002. The ecological and evolutionary interface of hummingbird flight physiology. *Journal of Experimental Biology*, *205*(16), pp.2325-2336.
16. Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F. and Harrison, S.P., 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology letters*, *14*(1), pp.19-28.
17. Angermeier, P. L., Schlosser , I. J. 1989. Species-Area Relationship for Stream Fishes. Ecology. 70 (5): 1450 – 1462.
18. Angilletta Jr, M.J., Steury, T.D. and Sears, M.W., 2004b. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and comparative biology*, *44*(6), pp.498-509.
19. Aravind, N. A., and K. V. Gururaja. 2001. Amphibians of the Western Ghats. A report submitted to Western Ghats Ecology Expert Panel
20. Arellano, G., Umaña, M.N., Macía, M.J., Loza, M.I., Fuentes, A., Cala, V. and Jørgensen, P.M., 2017. The role of niche overlap, environmental heterogeneity, landscape roughness and productivity in shaping species abundance distributions along the Amazon–Andes gradient. *Global Ecology and Biogeography*, *26*(2), pp.191-202.
21. Arnett, A.E. and Gotelli, N.J., 2003. Bergmann's rule in larval ant lions: testing the starvation resistance hypothesis. *Ecological Entomology*, *28*(6), pp.645-650.

22. Ashton, K.G. and Feldman, C.R., 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution*, *57*(5), pp.1151-1163.
23. Ashton, K.G., 2001. Are ecological and evolutionary rules being dismissed prematurely?. *Diversity and Distributions*, *7*(6), pp.289-295.
24. Ashton, K.G., 2002. Do amphibians follow Bergmann's rule?. *canadian Journal of Zoology*, *80*(4), pp.708-716.
25. Ashton, K.G., 2002. Patterns of within‐species body size variation of birds: strong evidence for Bergmann's rule. *Global Ecology and Biogeography*, *11*(6), pp.505-523.
26. Ashton, L.A., Nakamura, A., Basset, Y., Burwell, C.J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E.G., Hurley, K., Katabuchi, M. and Maunsell, S., 2016. Vertical stratification of moths across elevation and latitude. *Journal of biogeography*, *43*(1), pp.59-69.
27. Ashton, P.S., 2003. Floristic zonation of tree communities on wet tropical mountains revisited. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*(1), pp.87-104.
28. Astorga, A., Oksanen, J., Luoto, M., Soininen, J., Virtanen, R. and Muotka, T., 2012. Distance decay of similarity in freshwater communities: do macro‐and microorganisms follow the same rules?. *Global Ecology and Biogeography*, *21*(3), pp.365-375.
29. Athreya, R. 2006b A new species of liocichla (Aves:Timaliidae) from Eaglenest wildlife sanctuary, Arunachal Pradesh, India. Indian Birds. 2(4): 82-95.
30. Athreya, R. M. & Singh, V. A. 1990 Scaling models for flight patterns and sexual dimorphism in raptors. J. Bombay Nat. Hist. Soc. 87(2), 210
31. Athreya, R., 2006a. Eaglenest Biodiversity Project (2003–2006): Conservation Resources for Eaglenest Wildlife Sanctuary. *Kaati Trust, Pune*.
32. Atkinson, D., 1994. Temperature and organism size: a biological law for ectotherms?. *Adv Ecol Res*, *25*, pp.1-58.
33. Axmacher, J.C., Holtmann, G., Scheuermann, L., Brehm, G., Müller‐Hohenstein, K. and Fiedler, K., 2004. Diversity of geometrid moths (Lepidoptera: Geometridae) along an Afrotropical elevational rainforest transect. *Diversity and Distributions*, *10*(4), pp.293-302.
34. Ayyappan, N. and Parthasarathy, N., 1999. Biodiversity inventory of trees in a large-scale permanent plot of tropical evergreen forest at Varagalaiar, Anamalais, Western Ghats, India. Biodiversity & Conservation, 8(11), pp.1533-1554.
35. Azevedo, R.B., James, A.C., McCabe, J. and Partridge, L., 1998. Latitudinal variation of wing: thorax size ratio and wing-aspect ratio in Drosophila melanogaster. *Evolution*, *52*(5), pp.1353-1362.
36. Bachman, S., et. al. 2004. Elevational Gradients, Area and Tropical Island Diversity: An Example from the Palms of New Guinea. Ecography. 27 (3) : 299 – 310.
37. Bady, P., Dolédec, S., Fesl, C., Gayraud, S., Bacchi, M. and Schöll, F., 2005. Use of invertebrate traits for the biomonitoring of European large rivers: the effects of sampling effort on genus richness and functional diversity. *Freshwater Biology*, *50*(1), pp.159-173.
38. Bai, Y., Dong, J.J., Guan, D.L., Xie, J.Y. and Xu, S.Q., 2016. Geographic variation in wing size and shape of the grasshopper Trilophidia annulata (Orthoptera: Oedipodidae): morphological trait variations follow an ecogeographical rule. *Scientific Reports*, *6*, p.32680.
39. Barlow, H.S., Woidwod, I. P. 1989. Moth Diversity of a Tropical Forest in Peninsular Malaysia. Journal of Tropical Ecology. 5 (1) : 37 – 50.
40. Barragán, F., Moreno, C.E., Escobar, F., Halffter, G. and Navarrete, D., 2011. Negative impacts of human land use on dung beetle functional diversity. *PloS one*, *6*(3), p.e17976.
41. Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), pp.134-143.
42. Baselga, A., 2013. Multiple site dissimilarity quantifies compositional heterogeneity among several sites, while average pairwise dissimilarity may be misleading. *Ecography*, *36*(2), pp.124-128.
43. Basset, Y. ed., 2003. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy. Cambridge University Press.

44. Basset, Y., Cizek, L., Cuénoud, P., Didham, R.K., Guilhaumon, F., Missa, O., Novotny, V., Ødegaard, F., Roslin, T., Schmidl, J. and Tishechkin, A.K., 2012. Arthropod diversity in a tropical forest. Science, 338(6113), pp.1481-1484.
45. Bazzaz, F. A. 1975. Plant Species Diversity in Old-Field Successional Ecosystems in Southern Illinois. Ecology. 56 (2) : 485 – 488.
46. Beck, J. and Kitching, I.J., 2007. Correlates of range size and dispersal ability: a comparative analysis of sphingid moths from the Indo‐Australian tropics. *Global Ecology and Biogeography*, *16*(3), pp.341-349.
47. Beck, J. and Kitching, I.J., 2009. Drivers of moth species richness on tropical altitudinal gradients: a cross regional comparison. *Global Ecology and Biogeography*, *18*(3), pp.361-371.
48. Beck, J., 2005. The macroecology of Southeast-Asian hawkmoths (Lepidoptera: Sphingidae).
49. Beck, J., Kitching, I.J. and Eduard Linsenmair, K., 2006. Determinants of regional species richness: an empirical analysis of the number of hawkmoth species (Lepidoptera: Sphingidae) on the Malesian archipelago. *Journal of Biogeography*, *33*(4), pp.694-706.
50. Beck, J., Kitching, I.J. and Linsenmair, K.E., 2006. Wallace's line revisited: has vicariance or dispersal shaped the distribution of Malesian hawkmoths (Lepidoptera: Sphingidae)?. *Biological Journal of the Linnean Society*, *89*(3), pp.455-468.
51. Beck, J., Liedtke, H.C., Widler, S., Altermatt, F., Loader, S.P., Hagmann, R., Lang, S. and Fiedler, K., 2016. Patterns or mechanisms? Bergmann's and Rapoport's rule in moths along an elevational gradient. *Community Ecology*, *17*(2), pp.137-148.
52. Beck, J., McCain, C.M., Axmacher, J.C., Ashton, L.A., Bärtschi, F., Brehm, G., Choi, S.W., Cizek, O., Colwell, R.K., Fiedler, K. and Francois, C.L., 2017. Elevational species richness gradients in a hyperdiverse insect taxon: a global meta‐study on geometrid moths. Global Ecology and Biogeography, 26(4), pp.412-424.
53. Beck, J., Rudlinger, M. C., McCain, M. C. 2017. Is the ecological belt zonation of the Swiss Alps relevant for moth diversity and turnover?, Acta Oecologica 80 : 1-7.
54. Bergmann, C. 1847 Uber die Verhaltnisse der Warmeokonomie deThiere zu ihrer Gross. Gottinger Studien1, 595^708.
55. Bibby, C.J., 2000. Bird census techniques. Elsevier.
56. Birand, A.Y.S.E.G.U.L. and Pawar, S.A.M.R.A.A.T., 2004. An ornithological survey in north-east India. Forktail, 20, pp.15-24.
57. Blackburn, T.M. and Ruggiero, A., 2001. Latitude, elevation and body mass variation in Andean passerine birds. *Global Ecology and Biogeography*, *10*(3), pp.245-259.
58. Blackburn, T.M., Gaston, K.J. and Loder, N., 1999. Geographic gradients in body size: a clarification of Bergmann's rule. *Diversity and distributions*, *5*(4), pp.165-174.
59. Blackburn, T.M., Petchey, O.L., Cassey, P. and Gaston, K.J., 2005. Functional diversity of mammalian predators and extinction in island birds. *Ecology*, *86*(11), pp.2916-2923.
60. Blake, J.G. and Loiselle, B.A., 2000. Diversity of birds along an elevational gradient in the Cordillera Central, Costa Rica. *The Auk*, pp.663-686.
61. Blake, J.G., 2007. Neotropical forest bird communities: a comparison of species richness and composition at local and regional scales. *Condor*, pp.237-255.
62. Blanckenhorn, W.U. and Demont, M., 2004. Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum?. *Integrative and Comparative Biology*, *44*(6), pp.413-424.
63. Blem, C.R., 1975. Geographic variation in wing-loading of the house sparrow. *The Wilson Bulletin*, pp.543-549.
64. Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H., Schreiber, S.J., Urban, M.C. and Vasseur, D.A., 2011. Why intraspecific trait variation matters in community ecology. *Trends in ecology & evolution*, *26*(4), pp.183-192.
65. Borowitzka, M. A. 1972. Intertidal algal species diversity and the effect of pollution. Australian Journal of Marine and Freshwater Research. 23 (2): 73 – 84.
66. Boucher, D.H., James, S. and Keeler, K.H., 1982. The ecology of mutualism. *Annual Review of Ecology and Systematics*, *13*(1), pp.315-347.

67. Bowden, J., 1982. An analysis of factors affecting catches of insects in light-traps. Bulletin of Entomological Research, 72(4), pp.535-556.

68. Bray, J.R. and Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological monographs*, *27*(4), pp.325-349.

69. Brehm, G. and Fiedler, K., 2004. Bergmann's rule does not apply to geometrid moths along an elevational gradient in an Andean montane rain forest. *Global Ecology and Biogeography*, *13*(1), pp.7-14.

70. Brehm, G., Colwell, R.K. and Kluge, J., 2007. The role of environment and mid-domain effect on moth species richness along a tropical elevational gradient. *Global Ecology and biogeography*, *16*(2), pp.205-219.

71. Brehm, G., Hebert, P. D. N., Colwell, R. K., Adams, M., Bodner, F., Friedemann, K., Mockel, L., Fiedler, K. 2016. Turning Up the Heat on a Hotspot: DNA Barcodes Reveal 80% More Species of Geometrid Moths along an Andean Elevational Gradient, PloS ONE 11(3): e0150327.

72. Brehm, G., Homeier, J. and Fiedler, K., 2003. Beta diversity of geometrid moths (Lepidoptera: Geometridae) in an Andean montane rainforest. *Diversity and Distributions*, *9*(5), pp.351-366.

73. Brehm, G., Süssenbach, D., Fiedler, K. 2003. Unique Elevational Diversity Patterns of Geometrid Moths in an Andean Montane Rainforest. Ecography 26 (4): 456 – 466.

74. Brose, U., Martinez, N.D. and Williams, R.J., 2003. Estimating species richness: sensitivity to sample coverage and insensitivity to spatial patterns. *Ecology*, *84*(9), pp.2364-2377.

75. Brown, H.E., Paladini, M., Cook, R.A., Kline, D., Barnard, D. and Fish, D., 2014. Effectiveness of mosquito traps in measuring species abundance and composition. *Journal of medical entomology*, *45*(3), pp.517-521.

76. Brown, J.H. and Maurer, B.A., 1989. Macroecology: the division of food and space among species on continents. *Science*, *243*(4895), pp.1145-1150.

77. Bryant, J.A., Lamanna, C., Morlon, H., Kerkhoff, A.J., Enquist, B.J. and Green, J.L., 2008. Microbes on mountainsides: contrasting elevational patterns of bacterial and plant diversity. *Proceedings of the National Academy of Sciences*.

78. Bull, L. S. 2006. Geographical variation in the morphology of the wedge-tailed shearwater (Puffinus pacificus). Emu 106:233–243.

79. Bunn, S.E. and Arthington, A.H., 2002. Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental management*, *30*(4), pp.492-507.

80. Burnham, K.P. and Anderson, D.R., 1976. Mathematical models for nonparametric inferences from line transect data. *Biometrics*, pp.325-336.

81. Burnham, K.P. and Overton, W.S., 1978. Estimation of the size of a closed population when capture probabilities vary among animals. *Biometrika*, *65*(3), pp.625-633.

82. Burnham, K.P. and Overton, W.S., 1979. Robust estimation of population size when capture probabilities vary among animals. *Ecology*, *60*(5), pp.927-936.

83. Cadotte, M.W., Carscadden, K. and Mirotchnick, N., 2011. Beyond species: functional diversity and the maintenance of ecological processes and services. *Journal of applied ecology*, *48*(5), pp.1079-1087.

84. Caliman, A., Carneiro, L.S., Bozelli, R.L., Farjalla, V.F. and Esteves, F.A., 2011. Bioturbating space enhances the effects of non-additive interactions among benthic ecosystem engineers on cross-habitat nutrient regeneration. *Oikos*, *120*(11), pp.1639-1648.

85. Carothers, J.H., Fox, S.F., Marquet, P.A. and Jaksic, F.M., 1997. Thermal characteristics of ten Andean lizards of the genus Liolaemus in central Chile. *Revista Chilena de Historia Natural*, *70*, pp.297-309.

86. Cartar, R.V. and Guy Morrison, R.I., 2005. Metabolic correlates of leg length in breeding arctic shorebirds: the cost of getting high. *Journal of Biogeography*, *32*(3), pp.377-382.

87. Caswell, H., 1976. Community structure: a neutral model analysis. *Ecological monographs*, *46*(3), pp.327-354.

88. Catano, C.P., Dickson, T.L. and Myers, J.A., 2017. Dispersal and neutral sampling mediate contingent effects of disturbance on plant beta-diversity: a meta-analysis. *Ecology letters*, *20*(3), pp.347-356.

89. Chai, Z. and Wang, D., 2016. Environmental influences on the successful regeneration of pine-oak mixed forests in the Qinling Mountains, China. *Scandinavian journal of forest research*, *31*(4), pp.368-381.

90. Champion, S.H. and Seth, S.K., 1968. A revised survey of the forest types of India. A revised survey of the forest types of India.

91. Chan, F.T., Bradie, J., Briski, E., Bailey, S.A., Simard, N. and MacIsaac, H.J., 2015. Assessing introduction risk using species' rank-abundance distributions. *Proceedings of the Royal Society of London B: Biological Sciences*, *282*(1799), p.20141517.

92. Chao, A. and Lee, S.M., 1992. Estimating the number of classes via sample coverage. *Journal of the American statistical Association*, *87*(417), pp.210-217.

93. Chao, A., 1984. Nonparametric estimation of the number of classes in a population. *Scandinavian Journal of statistics*, pp.265-270.

94. Chao, A., 1987. Estimating the population size for capture-recapture data with unequal catchability. *Biometrics*, pp.783-791.

95. Chao, A., Chazdon, R.L., Colwell, R.K. and Shen, T.J., 2005. A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology letters*, *8*(2), pp.148-159.

96. Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. and Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*(1), pp.45-67.

97. Chao, A., Hsieh, T.C., Chazdon, R.L., Colwell, R.K. and Gotelli, N.J., 2015. Unveiling the species-rank abundance distribution by generalizing the Good-Turing sample coverage theory. *Ecology*, *96*(5), pp.1189-1201.

98. Chapin Iii, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E. and Mack, M.C., 2000. Consequences of changing biodiversity. *Nature*, *405*(6783), p.234.

99. Chapman, R.F., Douglas, A.E. and Siva-Jothy, M.T., 2013. Circulatory system, blood and the immune system. *The insects: structure and function*, pp.107-131.

100. Chase, J.M., 2010. Stochastic community assembly causes higher biodiversity in more productive environments. *science*, p.1187820.

101. Chave, J., Muller-Landau, H.C. and Levin, S.A., 2002. Comparing classical community models: theoretical consequences for patterns of diversity. *The American Naturalist*, *159*(1), pp.1-23.

102. Chen, J., Bittinger, K., Charlson, E.S., Hoffmann, C., Lewis, J., Wu, G.D., Collman, R.G., Bushman, F.D. and Li, H., 2012. Associating microbiome composition with environmental covariates using generalized UniFrac distances. *Bioinformatics*, *28*(16), pp.2106-2113.

103. Cheng, J., Mi, X., Nadrowski, K., Ren, H., Zhang, J. and Ma, K., 2012. Separating the effect of mechanisms shaping species-abundance distributions at multiple scales in a subtropical forest. *Oikos*, *121*(2), pp.236-244.

104. Choudhury, A., 2003. Birds of Eaglenest Wildlife Sanctuary and Sessa Orchid Sanctuary, Arunachal Pradesh, India. Forktail, pp.1-14.

105. Chown, S.L. and Gaston, K.J., 2010. Body size variation in insects: a macroecological perspective. *Biological Reviews*, *85*(1), pp.139-169.

106. Cisneros, L.M., Burgio, K.R., Dreiss, L.M., Klingbeil, B.T., Patterson, B.D., Presley, S.J. and Willig, M.R., 2014. Multiple dimensions of bat biodiversity along an extensive tropical elevational gradient. *Journal of Animal Ecology*, *83*(5), pp.1124-1136.

107. Cisneros, L.M., Fagan, M.E. and Willig, M.R., 2015. Effects of human-modified landscapes on taxonomic, functional and phylogenetic dimensions of bat biodiversity. *Diversity and Distributions*, *21*(5), pp.523-533.

108. Clark, J.S., 2012. The coherence problem with the Unified Neutral Theory of Biodiversity. *Trends in ecology & evolution*, *27*(4), pp.198-202.

109. Clarke, K.R. and Warwick, R.M., 2001. A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Marine ecology Progress series*, *216*, pp.265-278.

110. Clay, K., Holah, J. 1999. Fungal Endophyte Symbiosis and Plant Diversity in Successional Fields. Science. 285 (5434) : 1742 – 1744.

111. Colwell, R. K., Rahbeck, C., Gotelli, N. J. 2004. The Mid-Domain Effect and Species Richness Patterns: What Have We Learned So Far? The American Naturalist 163 (3) 1 – 23.

112. Colwell, R.K. & Hurtt, G.C. 1994. Nonbiological gradients in species richness and a spurious Rapoport effect. The American Naturalist. 144, 570–595.

113. Colwell, R.K. and Coddington, J.A., 1994. Estimating terrestrial biodiversity through extrapolation. *Phil. Trans. R. Soc. Lond. B*, *345*(1311), pp.101-118.

114. Colwell, R.K. and Rangel, T.F., 2010. A stochastic, evolutionary model for range shifts and richness on tropical elevational gradients under Quaternary glacial cycles. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*(1558), pp.3695-3707.

115. Colwell, R.K., Gotelli, N.J., Ashton, L.A., Beck, J., Brehm, G., Fayle, T.M., Fiedler, K., Forister, M.L., Kessler, M., Kitching, R.L. and Klimes, P., 2016. Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. *Ecology letters*, *19*(9), pp.1009-1022.

116. Connor, E. F. et. al. 1979. The Statistics and Biology of the Species-Area Relationship. The American Naturalist. 113 (6) : 791 – 833.

117. Cornwell, W.K., Cornelissen, J.H., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N. and Quested, H.M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecology letters*, *11*(10), pp.1065-1071.

118. Cullings, K. and Courty, P.E., 2009. Saprotrophic capabilities as functional traits to study functional diversity and resilience of ectomycorrhizal community. *Oecologia*, *161*(4), pp.661-664.

119. Cushman, J.H., Lawton, J.H. and Manly, B.F., 1993. Latitudinal patterns in European ant assemblages: variation in species richness and body size. *Oecologia*, *95*(1), pp.30-37.

120. Dahanukar, N., R. Raut, and A. Bhat. 2004. Distribution, endemism and threat status of freshwater fishes in the Western Ghats of India. J. Biogeogr. 31:123–136.

121. Daniels, R.R., 1992. Geographical distribution patterns of amphibians in the Western Ghats, India. Journal of Biogeography, pp.521-529.

122. Datta, A., 1998. Hornbill abundance in unlogged forest, selectively logged forest and a forest plantation in Arunachal Pradesh, India. Oryx, 32(4), pp.285-294.

123. Davidson RS, Armstrong DP 2002. Estimating impacts of poison operations on non-target species using mark– recapture analysis and simulation modelling: an example

124. de Bello, F., Lavorel, S., Albert, C.H., Thuiller, W., Grigulis, K., Dolezal, J., Janeček, Š. and Lepš, J., 2011. Quantifying the relevance of intraspecific trait variability for functional diversity. *Methods in Ecology and Evolution*, *2*(2), pp.163-174.

125. Death, R.G., 1996. The effect of patch disturbance on stream invertebrate community structure: the influence of disturbance history. *Oecologia*, *108*(3), pp.567-576.

126. Dehling, D.M., Fritz, S.A., Töpfer, T., Päckert, M., Estler, P., Böhning-Gaese, K. and Schleuning, M., 2014. Functional and phylogenetic diversity and assemblage structure of frugivorous birds along an elevational gradient in the tropical Andes. Ecography, 37(11), pp.1047-1055.

127. Derroire, G. et. al. 2016. Resilience of tropical dry forests – a meta-analysis of changes in species diversity and composition during secondary succession. Oikos. 125 (10) : 1386 – 1397.

128. DeVries, P.J., Murray, D. and Lande, R., 1997. Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological journal of the Linnean Society*, *62*(3), pp.343-364.

129. Diaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.3., Jalili, A., Montserrat-Marti, G., Grime, J.P., Zarrinkamar, F., Asri, Y. and Band, S.R., 2004. The plant traits that drive ecosystems: evidence from three continents. *Journal of vegetation science*, *15*(3), pp.295-304.

130. Díaz, S., Lavorel, S., de Bello, F., Quétier, F., Grigulis, K. and Robson, T.M., 2007. Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, *104*(52), pp.20684-20689.

131. Dillon, M.E., Frazier, M.R. and Dudley, R., 2006. Into thin air: physiology and evolution of alpine insects. *Integrative and Comparative Biology*, *46*(1), pp.49-61.

132. Ding, T.S., Yuan, H.W., Geng, S., Lin, Y.S. and Lee, P.F., 2005. Energy flux, body size and density in relation to bird species richness along an elevational gradient in Taiwan. *Global Ecology and Biogeography*, *14*(4), pp.299-306.

133. Díaz, S. and Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends in ecology & evolution*, *16*(11), pp.646-655.

134. Dong, K., Moroenyane, I., Tripathi, B., Kerfahi, D., Takahashi, K., Yamamoto, N., An, C., Cho, H. and Adams, J., 2017. Soil nematodes show a mid-elevation diversity maximum and elevational zonation on Mt. Norikura, Japan. *Scientific reports*, *7*(1), p.3028.

135. Drake, D.A.R., Chan, F.T., Briski, E., Bailey, S.A. and MacIsaac, H.J., 2014. Assemblage structure: an overlooked component of human-mediated species movements among freshwater ecosystems. *Journal of Limnology*, *73*(s1).

136. Duan, M., Liu, Y., Yu, Z., Baudry, J., Li, L., Wang, C. and Axmacher, J.C., 2016. Disentangling effects of abiotic factors and biotic interactions on cross-taxon congruence in species turnover patterns of plants, moths and beetles. *Scientific Reports*, *6*, p.23511.

137. Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C. and Fitter, A.H., 2010. Relative roles of niche and neutral processes in structuring a soil microbial community. *The ISME journal*, *4*(3), p.337.

138. Dumbrell, A.J., Nelson, M., Helgason, T., Dytham, C. and Fitter, A.H., 2010b. Idiosyncrasy and overdominance in the structure of natural communities of arbuscular mycorrhizal fungi: is there a role for stochastic processes?. *Journal of Ecology*, *98*(2), pp.419-428.

139. Dunning Jr, J.B., 2008. CRC handbook of avian body masses. CRC press.

140. Edwards, F.A., Edwards, D.P., Hamer, K.C. and Davies, R.G., 2013. Impacts of logging and conversion of rainforest to oil palm on the functional diversity of birds in Sundaland. *Ibis*, *155*(2), pp.313-326.

141. Ellers, J. and Jervis, M., 2003. Body size and the timing of egg production in parasitoid wasps. *Oikos*, *102*(1), pp.164-172.

142. Ellis, C.J. and Coppins, B.J., 2006. Contrasting functional traits maintain lichen epiphyte diversity in response to climate and autogenic succession. *Journal of Biogeography*, *33*(9), pp.1643-1656.

143. Ellis, T.M. and Betts, M.G., 2011. Bird abundance and diversity across a hardwood gradient within early seral plantation forest. *Forest Ecology and Management*, *261*(8), pp.1372-1381.

144. Elsen, P.R. and Tingley, M.W., 2015. Global mountain topography and the fate of montane species under climate change. *Nature Climate Change*, *5*(8), p.772.

145. Empson RA, Miskelly CM 1999. The risks, costs and benefits of using brodifacoum to eradicate rats from Kapiti Island, New Zealand. New Zealand Journal of Ecology 23: 241 – 254.

146. Ensslin, A., Rutten, G., Pommer, U., Zimmermann, R., Hemp, A. and Fischer, M., 2015. Effects of elevation and land use on the biomass of trees, shrubs and herbs at Mount Kilimanjaro. *Ecosphere*, *6*(3), pp.1-15.

147. Erwin, T.L., 1982. Tropical forests: their richness in Coleoptera and other arthropod species. Coleopterists Bulletin, 36(1), pp.74-75.

148. Escobar, F., 2004. Diversity and composition of dung beetle (Scarabaeinae) assemblages in a heterogeneous Andean landscape. *Tropical Zoology*, *17*(1), pp.123-136.

149. Fattorini, S., 2005. A simple method to fit geometric series and broken stick models in community ecology and island biogeography. *Acta Oecologica*, *28*(3), pp.199-205.

150. Fattorini, S., 2007. To fit or not to fit? A poorly fitting procedure produces inconsistent results when the species–area relationship is used to locate hotspots. *Biodiversity and Conservation*, *16*(9), pp.2531-2538.

151. Fattorini, S., et. al. 2016. What can the parameters of the species–area relationship (SAR) tell us? Insights from Mediterranean islands. Journal of Biogeography. 44 (5) : 1018 - 1028

152. Fauth, J.E., Crother, B.I. and Slowinski, J.B., 1989. Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica*, pp.178-185.

153. Feinsinger, P. and Chaplin, S.B., 1975. On the relationship between wing disc loading and foraging strategy in hummingbirds. *The American Naturalist*, *109*(966), pp.217-224.

154. Feldman, A. and Meiri, S., 2014. Australian snakes do not follow Bergmann's rule. *Evolutionary Biology*, *41*(2), pp.327-335.

155. Fiedler, K., Schulze, C. 2004. Forest Modification Affects Diversity (But Not Dynamics) of Speciose Tropical Pyraloid Moth Communities. Biotropica 36 (4) : 615 – 627.

156. Fischer, J. and Lindenmayer, D.B., 2007. Landscape modification and habitat fragmentation: a synthesis. *Global ecology and biogeography*, *16*(3), pp.265-280.

157. Fisher, R.A., Corbet, A.S. and Williams, C.B., 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *The Journal of Animal Ecology*, pp.42-58.

158. Flynn, D.F., Gogol‐Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., Simpson, N., Mayfield, M.M. and DeClerck, F., 2009. Loss of functional diversity under land use intensification across multiple taxa. *Ecology letters*, *12*(1), pp.22-33.

159. Fooden, J. & Albretch ,G.H (1999) Tail-length evolution in Fascicularis-group macaques (Ceropithecidae: Macaca) .International Journal of Primatology, 20, 431-440.

160. Foster, J.B., 1964. Evolution of mammals on islands. *Nature*, *202*(4929), p.234.

161. Foster, S.D. and Dunstan, P.K., 2010. The analysis of biodiversity using rank abundance distributions. *Biometrics*, *66*(1), pp.186-195.

162. Frazier, M.R., Harrison, J.F., Kirkton, S.D. and Roberts, S.P., 2008. Cold rearing improves cold-flight performance in Drosophila via changes in wing morphology. *Journal of Experimental Biology*, *211*(13), pp.2116-2122.

163. Freeman, B.G., 2017. Little evidence for Bergmann's rule body size clines in passerines along tropical elevational gradients. *Journal of biogeography*, *44*(3), pp.502-510.

164. Fristoe, T.S., Burger, J.R., Balk, M.A., Khaliq, I., Hof, C. and Brown, J.H., 2015. Metabolic heat production and thermal conductance are mass-independent adaptations to thermal environment in birds and mammals. *Proceedings of the National Academy of Sciences*, *112*(52), pp.15934-15939.

165. Fu, C., Wang, J., Pu, Z., Zhang, S. Chen, H., Zhao, B., Chen, J., Wu, J. 2007. Elevational gradients of diversity for lizards and snakes in the Hengduan Mountains, China, Biodiversity and Conservation 16 : 707 – 726.

166. G. Vazquez, J. A., Givnish, T. J. 1998. Altitudinal gradients in tropical forest composition, structure, and diversity in the Sierra de Manantlan. Journal of Ecology. 86 : 999 – 1020.

167. Gallou, A., Baillet, Y., Ficetola, G.F. and Després, L., 2017. Elevational gradient and human effects on butterfly species richness in the French Alps. *Ecology and evolution*, *7*(11), pp.3672-3681.

168. Gaston, K. J. 2000. Global patterns in biodiversity. Nature. 405 : 220 – 227.

169. Gaston, K. J. 2007. Latitudinal gradient in species richness. Current Biology. 17 (15) : 574.

170. Gaston, K.J. and Blackburn, T.M., 1995. Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proc. R. Soc. Lond. B*, *262*(1365), pp.335-341.

171. Gaston, K.J. and Chown, S.L., 2013. Macroecological patterns in insect body size. *Body size: Linking pattern and process across space, time and taxonomic group*, pp.13-61.

172. Gaston, K.J. and Kunin, W.E., 1997. Rare—common differences: an overview. In *The biology of rarity* (pp. 12-29). Springer, Dordrecht.

173. Gaston, K.J., Blackburn, T.M., Greenwood, J.J., Gregory, R.D., Quinn, R.M. and Lawton, J.H., 2000. Abundance–occupancy relationships. *Journal of Applied Ecology*, *37*, pp.39-59.

174. Gaston, K.J., Chown, S.L. and Evans, K.L., 2008. Ecogeographical rules: elements of a synthesis. *Journal of Biogeography*, *35*(3), pp.483-500.

175. Gilbert, B. and Lechowicz, M.J., 2004. Neutrality, niches, and dispersal in a temperate forest understory. *Proceedings of the National Academy of Sciences*, *101*(20), pp.7651-7656.

176. Gilchrist, G.W. and Huey, R.B., 2004. Plastic and genetic variation in wing loading as a function of temperature within and among parallel clines in Drosophila subobscura. *Integrative and Comparative Biology*, *44*(6), pp.461-470.

177. Gillooly, J.F., Charnov, E.L., West, G.B., Savage, V.M. and Brown, J.H., 2002. Effects of size and temperature on developmental time. *Nature*, *417*(6884), p.70.

178. Gini, C., 1912. Variabilità e mutabilità. *Reprinted in Memorie di metodologica statistica (Ed. Pizetti E, Salvemini, T). Rome: Libreria Eredi Virgilio Veschi.*

179. Girardin, C.A., Farfan-Rios, W., Garcia, K., Feeley, K.J., Jørgensen, P.M., Murakami, A.A., Cayola Pérez, L., Seidel, R., Paniagua, N., Fuentes Claros, A.F. and Maldonado, C., 2014. Spatial patterns of above-ground structure, biomass and composition in a network of six Andean elevation transects. *Plant Ecology & Diversity*, *7*(1-2), pp.161-171.

180. Gloger, C.L. (1883) Das Abandern der Vogel durch Einfluss des Klimas. A. Schulz, Breslau

181. Godbold, J.A., Bulling, M.T. and Solan, M., 2011. Habitat structure mediates biodiversity effects on ecosystem properties. *Proceedings of the Royal Society of London B: Biological Sciences*, *278*(1717), pp.2510-2518.

182. Götzenberger, L., de Bello, F., Bråthen, K.A., Davison, J., Dubuis, A., Guisan, A., Lepš, J., Lindborg, R., Moora, M., Pärtel, M. and Pellissier, L., 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. *Biological reviews*, *87*(1), pp.111-127.

183. Graham, G.L., 1983. Changes in bat species diversity along an elevational gradient up the Peruvian Andes. *Journal of mammalogy*, *64*(4), pp.559-571.

184. Grau, O., Grytnes, J.A. and Birks, H.J.B., 2007. A comparison of altitudinal species richness patterns of bryophytes with other plant groups in Nepal, Central Himalaya. *Journal of Biogeography*, *34*(11), pp.1907-1915.

185. Gravel, D., Canham, C.D., Beaudet, M. and Messier, C., 2006. Reconciling niche and neutrality: the continuum hypothesis. *Ecology letters*, *9*(4), pp.399-409.

186. Gray, B.R., 2005. Selecting a distributional assumption for modelling relative densities of benthic macroinvertebrates. *Ecological Modelling*, *185*(1), pp.1-12.

187. Gray, J.S., 1979. Pollution-induced changes in populations. *Phil. Trans. R. Soc. Lond. B*, *286*(1015), pp.545-561.

188. Greenewalt, C.H., 1960. The wings of insects and birds as mechanical oscillators. *Proceedings of the American Philosophical Society*, *104*(6), pp.605-611.

189. Griffiths, H.M., Louzada, J., Bardgett, R.D. and Barlow, J., 2016. Assessing the importance of intraspecific variability in dung beetle functional traits. *PloS one*, *11*(3), p.e0145598.

190. Grinell, J., Storer, T. I. 1924. Animal life in the Yosemite. University of California Press, Berkeley, California.

191. Grytnes, J. A., Beaman, J. H. 2006. Elevational species richness patterns for vascular plants on Mount Kinabalu, Borneo. Journal of Biogeography. 33 : 1838 – 1849.

192. Grytnes, J.A. and Vetaas, O.R., 2002. Species richness and altitude: a comparison between null models and interpolated plant species richness along the Himalayan altitudinal gradient, Nepal. *The American Naturalist*, *159*(3), pp.294-304.

193. Gutiérrez-Pinto, N., McCracken, K.G., Alza, L., Tubaro, P., Kopuchian, C., Astie, A. and Cadena, C.D., 2014. The validity of ecogeographical rules is context-dependent: testing for Bergmann's and Allen's rules by latitude and elevation in a widespread Andean duck. *Biological Journal of the Linnean Society*, *111*(4), pp.850-862.

194. Haber, W. A., Frankie, G. W. 1989. A Tropical Hawkmoth Community: Costa Rican Dry Forest Sphingidae. Biotropica 21 (2) : 155 – 172.

195. Hainsworth, F.R., 1981. *Animal physiology: adaptations in function*. Addison-Wesley.

196. Hamilton, T.H., 1961. The adaptive significances of intraspecific trends of variation in wing length and body size among bird species. *Evolution*, *15*(2), pp.180-195.

197. Haripriya, G.S., 2000. Estimates of biomass in Indian forests. *Biomass and bioenergy*, *19*(4), pp.245-258.

198. Harpole, W. and Tilman, D., 2006. Non-neutral patterns of species abundance in grassland communities. *Ecology letters*, *9*(1), pp.15-23.

199. Harvey, P.H. and Pagel, M.D., 1991. *The comparative method in evolutionary biology* (Vol. 239). Oxford: Oxford university press.

200. Hassall, C., 2015. Strong geographical variation in wing aspect ratio of a damselfly, Calopteryx maculata (Odonata: Zygoptera). *PeerJ*, *3*, p.e1219.

201. Hawkins, B. A., et al. 2003. Energy, water, and broad-scale geographic patterns of species richness. Ecology 84 : 3105–3117.

202. Hawkins, B.A. and Diniz-Filho, J.A.F., 2002. The mid-domain effect cannot explain the diversity gradient of Nearctic birds. *Global Ecology and Biogeography*, *11*(5), pp.419-426.

203. Hawkins, B.A., 2001. Ecology's oldest pattern?. *Trends in Ecology & Evolution*, *16*(8), p.470.

204. Hayek, L.A.C. and Buzas, M.A., 2010. *Surveying natural populations: quantitative tools for assessing biodiversity*. Columbia University Press.

205. He, J., et. al. 2017. Drivers of coastal bacterioplankton community diversity and structure along a nutrient gradient in the East China Sea. Chinese Journal of Oceanology and Limnology. 35 (150) : 1- 12.

206. Heaney, L.R., 2001. Small mammal diversity along elevational gradients in the Philippines: an assessment of patterns and hypotheses. *Global ecology and Biogeography*, *10*(1), pp.15-39.

207. Hedde, M., Van Oort, F. and Lamy, I., 2012. Functional traits of soil invertebrates as indicators for exposure to soil disturbance. *Environmental Pollution*, *164*, pp.59-65.

208. Heinrich, B., 1974. Thermoregulation in endothermic insects. *Science*, *185*(4153), pp.747-756.

209. Heinrich, B., 1993. The hot-blooded insects: mechanisms and evolution of thermoregulation.

210. Hidasi-Neto, J., Barlow, J. and Cianciaruso, M.V., 2012. Bird functional diversity and wildfires in the Amazon: the role of forest structure. *Animal Conservation*, *15*(4), pp.407-415.

211. Hillebrand, H., Bennett, D.M. and Cadotte, M.W., 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology*, *89*(6), pp.1510-1520.

212. HilleRisLambers, J., Adler, P.B., Harpole, W.S., Levine, J.M. and Mayfield, M.M., 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics*, *43*.

213. Hoehn, P., Tscharntke, T., Tylianakis, J.M. and Steffan-Dewenter, I., 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London B: Biological Sciences*, *275*(1648), pp.2283-2291.

214. Hoeinghaus, D.J., Winemiller, K.O. and Birnbaum, J.S., 2007. Local and regional determinants of stream fish assemblage structure: inferences based on taxonomic vs. functional groups. *Journal of Biogeography*, *34*(2), pp.324-338.

215. Holloway, J.D., Kibby, G. and Peggie, D., 2001. The families of Malesian moths and butterflies (Vol. 3). Brill.

216. Holt, B.G., Lessard, J.P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.H., Graham, C.H., Graves, G.R., Jønsson, K.A. and Nogués-Bravo, D., 2013. Response to comment on “An update of Wallace’s zoogeographic regions of the world”. science, 341(6144), pp.343-343.

217. Holt, R.D. and Gaines, M.S., 1992. Analysis of adaptation in heterogeneous landscapes: implications for the evolution of fundamental niches. *Evolutionary Ecology*, *6*(5), pp.433-447.

218. Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S. and Schmid, B., 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological monographs*, *75*(1), pp.3-35.

219. Hopkins, G.W. and Freckleton, R.P., 2002, August. Declines in the numbers of amateur and professional taxonomists: implications for conservation. In Animal Conservation forum (Vol. 5, No. 3, pp. 245-249). Cambridge University Press.

220. Hu, J., Xie, F., Li, C. and Jiang, J., 2011. Elevational patterns of species richness, range and body size for spiny frogs. *PLoS One*, *6*(5), p.e19817.

221. Huang, Y. et. al. 2017. Positive effects of tree species diversity on litterfall quantity and quality along a secondary successional chronosequence in a subtropical forest. Journal of Plant Ecology. 10 (1) : 28 – 35.

222. Hubbell, S.P., 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science*, *203*(4387), pp.1299-1309.

223. Hubbell, S.P., 2001. The unified neutral theory of species abundance and diversity. *Princeton University Press, Princeton, NJ. Hubbell, SP (2004) Quarterly Review of Biology*, *79*, pp.96-97.

224. Hubbell, S.P., 2005. Neutral theory in community ecology and the hypothesis of functional equivalence. *Functional ecology*, *19*(1), pp.166-172.

225. Huey, R.B., 1978. Latitudinal pattern of between-altitude faunal similarity: mountains might be" higher" in the tropics. *The American Naturalist*, *112*(983), pp.225-229.

226. Hurlbert SH (1971) The nonconcept of species diversity:a critique and alternative parameters. *Ecology*, 52, 577–586.

227. Hurlbert, A.H., 2004. Species–energy relationships and habitat complexity in bird communities. *Ecology Letters*, *7*(8), pp.714-720.

228. Hutchinson, G.E. (1957). Concluding remarks. Cold Spring Harb. Symp. Quant. Biol., 22, 415–427.

229. Hutchinson, G.E., 1959. Homage to Santa Rosalia or why are there so many kinds of animals?. *The American Naturalist*, *93*(870), pp.145-159.

230. Huxley, J., 1942. *Evolution the modern synthesis*. George Allen and Unwin.

231. Huxley, J.S. and Teissier, G., 1936. Terminology of relative growth. *Nature*, *137*(3471), p.780.

232. Huxley, J.S., 1924. Constant differential growth-ratios and their significance. *Nature*, *114*(2877), p.895.

233. Innes J, Nugent G, Prime K, Spurr EB 2004. Responses of kukupa (Hemiphaga novaeseelandiae) and other birds to mammal pest control at Motatau, Northland. New Zealand Journal of Ecology 28: 73–81.

234. Izsák, J. and Pavoine, S., 2012. Links between the species abundance distribution and the shape of the corresponding rank abundance curve. *Ecological indicators*, *14*(1), pp.1-6.

235. James, F.C. and Rathbun, S., 1981. Rarefaction, relative abundance, and diversity of avian communities. *The Auk*, pp.785-800.

236. Jankowski, J. E., Ciecka, A. L., Meyer, N. Y., Rabenold, K. N. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes, Journal of Animal Ecology. 78 : 315 – 327.

237. Janzen, D.H., 1967. Why mountain passes are higher in the tropics. *The American Naturalist*, *101*(919), pp.233-249.

238. Jha, C.S., Dutt, C.B.S. and Bawa, K.S., 2000. Deforestation and land use changes in Western Ghats, India. Current Science, pp.231-238.

239. Jin, Y., Liu, N. and Li, J., 2007. Elevational variation in body size of Phrynocephalus vlangalii in the North Qinghai-Xizang (Tibetan) Plateau. *Belgian Journal of Zoology*, *137*(2), p.197.

240. Johnston, R.F. and Selander, R.K., 1964. House sparrows: rapid evolution of races in North America. *Science*, *144*(3618), pp.548-550.

241. Johnston, R.F. and Selander, R.K., 1973. Evolution in the house sparrow. III. Variation in size and sexual dimorphism in Europe and North and South America. *The American Naturalist*, *107*(955), pp.373-390.

242. Johnston, R.F., 1969. Character variation and adaptation in European sparrows. *Systematic Zoology*, *18*(2), pp.206-231.

243. Jordan, D.S. (1892) Temperature and vertebrae: a study in evolution. Wilder-Quarter Century Books, New York

244. Joshi, J. and Karanth, K.P., 2012. Coalescent method in conjunction with niche modeling reveals cryptic diversity among centipedes in the Western Ghats of South India. PloS one, 7(8), p.e42225.

245. Jost, L., 2010. The relation between evenness and diversity. *Diversity*, *2*(2), pp.207-232.

246. Jung, V., Violle, C., Mondy, C., Hoffmann, L. and Muller, S., 2010. Intraspecific variability and trait-based community assembly. *Journal of ecology*, *98*(5), pp.1134-1140.

247. Jurasinski, G., Retzer, V. and Beierkuhnlein, C., 2009. Inventory, differentiation, and proportional diversity: a consistent terminology for quantifying species diversity. *Oecologia*, *159*(1), pp.15-26.

248. Kattan, G. H., Franco, P. 2004. Bird Diversity along Elevational Gradients in the Andes of Colombia: Area and Mass Effects. Global Ecology and Biogeography. 13 (5) : 451 – 458.

249. Kawahara, A.Y., Mignault, A.A., Regier, J.C., Kitching, I.J. and Mitter, C., 2009. Phylogeny and biogeography of hawkmoths (Lepidoptera: Sphingidae): evidence from five nuclear genes. *PLoS One*, *4*(5), p.e5719.

250. Keller, I., Alexander, J.M., Holderegger, R. and Edwards, P.J., 2013. Widespread phenotypic and genetic divergence along altitudinal gradients in animals. *Journal of evolutionary biology*, *26*(12), pp.2527-2543.

251. Kendall, D.G., 1948a. On some modes of population growth leading to RA Fisher's logarithmic series distribution. *Biometrika*, *35*(1/2), pp.6-15.

252. Kessler, M., Kluge, J., Hemp, A. and Ohlemüller, R., 2011. A global comparative analysis of elevational species richness patterns of ferns. *Global Ecology and Biogeography*, *20*(6), pp.868-880.

253. Kitching, I.J. 2017. Sphingidae Taxonomic Inventory, http://sphingidae.myspecies.info/, accessed on 23 August 2017

254. Kitching, I.J. and Cadiou, J.M., 2000. Hawkmoths of the world: an annotated and illustrated revisionary checklist (Lepidoptera: Sphingidae) (No. C/595.781 K5). Ithaca: Cornell university press.

255. Kjærsgaard, A., Blanckenhorn, W.U., Pertoldi, C., Loeschcke, V., Kaufmann, C., Hald, B., Pagès, N. and Bahrndorff, S., 2015. Plasticity in behavioural responses and resistance to temperature stress in Musca domestica. *Animal Behaviour*, *99*, pp.123-130.

256. Koleff, P. and Gaston, K.J., 2001. Latitudinal gradients in diversity: real patterns and random models. *Ecography*, *24*(3), pp.341-351.

257. Koleff, P., Gaston, K.J. and Lennon, J.J., 2003. Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, *72*(3), pp.367-382.

258. Kotliar, N.B. and Wiens, J.A., 1990. Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, pp.253-260.

259. Kraft, N.J., Comita, L.S., Chase, J.M., Sanders, N.J., Swenson, N.G., Crist, T.O., Stegen, J.C., Vellend, M., Boyle, B., Anderson, M.J. and Cornell, H.V., 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. *Science*, *333*(6050), pp.1755-1758.

260. Kraft, N.J., Valencia, R. and Ackerly, D.D., 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science*, *322*(5901), pp.580-582.

261. Krell, F.T., 2003. Parataxonomy vs. taxonomy in biodiversity studies–pitfalls and applicability of 'morphospecies' sorting. Biodiversity and Conservation, 13(4), pp.795-812.

262. Kromer, T., Kessler, M., Gradstein, R.S., Acebey, A. 2005. Diversity patterns of vascular epiphytes along an elevational gradient in the Andes, J. Biogeogr. 32 : 1799 – 1809.

263. Kumar, R.S. and Singh, P., 2003. A new subspecies of Sclater's Monal Lophophorus sclateri from western Arunachal Pradesh, India. Bulletin of the British Ornithologist'Club, 124, pp.16-27.

264. Kunstler, G., Falster, D., Coomes, D.A., Hui, F., Kooyman, R.M., Laughlin, D.C., Poorter, L., Vanderwel, M., Vieilledent, G., Wright, S.J. and Aiba, M., 2016. Plant functional traits have globally consistent effects on competition. *Nature*, *529*(7585), p.204.

265. LAIOLO, P. and ROLANDO, A., 2001. Ecogeographic correlates of morphometric variation in the red-billed chough Pyrrhocorax pyrrhocorax and the alpine chough Pyrrhocorax graculus. *Ibis*, *143*(3), pp.602-616.

266. Laliberté, E. and Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, *91*(1), pp.299-305.

267. Laliberté, E., Legendre, P., Shipley, B. and Laliberté, M.E., 2014. Package 'FD'. *Version*, *1*, p.12.

268. Lamanna, C. et. al. 2014. Functional trait space and the latitudinal diversity gradient. PNAS. 111 (38) : 13745 – 13750.

269. Langenheder, S., Bulling, M.T., Prosser, J.I. and Solan, M., 2012. Role of functionally dominant species in varying environmental regimes: evidence for the performance-enhancing effect of biodiversity. *BMC ecology*, *12*(1), p.14.

270. Laurie, H. and Silander Jr, J.A., 2002. Geometric constraints and spatial pattern of species richness: critique of range-based null models. *Diversity and Distributions*, *8*(6), pp.351-364.

271. Lavorel, S. and Garnier, É., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional ecology*, *16*(5), pp.545-556.

272. Lavorel, S., Storkey, J., Bardgett, R.D., de Bello, F., Berg, M.P., Le Roux, X., Moretti, M., Mulder, C., Pakeman, R.J., Díaz, S. and Harrington, R., 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. *Journal of Vegetation Science*, *24*(5), pp.942-948.

273. Lawton, J.H., 1999. Are there general laws in ecology?. *Oikos*, pp.177-192.

274. Le Bagousse-Pinguet, Y., de Bello, F., Vandewalle, M., Leps, J. and Sykes, M.T., 2014. Species richness of limestone grasslands increases with trait overlap: evidence from within-and between-species functional diversity partitioning. *Journal of ecology*, *102*(2), pp.466-474.

275. Legendre, P. and Anderson, M.J., 1999. Distance-based redundancy analysis: testing multispecies responses in multifactorial ecological experiments. *Ecological monographs*, *69*(1), pp.1-24.

276. Legendre, P. and De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecology letters*, *16*(8), pp.951-963.

277. Legendre, P. and Legendre, L., 1998. Numerical Ecology, Volume 24, (Developments in Environmental Modelling).

278. Legendre, P., 2014. Interpreting the replacement and richness difference components of beta diversity. *Global Ecology and Biogeography*, *23*(11), pp.1324-1334.

279. Legendre, P., Borcard, D. and Peres-Neto, P.R., 2005. Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, *75*(4), pp.435-450.

280. Lepš, J., de Bello, F., Šmilauer, P. and Doležal, J., 2011. Community trait response to environment: disentangling species turnover vs intraspecific trait variability effects. *Ecography*, *34*(5), pp.856-863.

281. Li, J.S., Song, Y.L. and Zeng, Z.G., 2003. Elevational gradients of small mammal diversity on the northern slopes of Mt. Qilian, China. *Global Ecology and Biogeography*, *12*(6), pp.449-460.

282. Lindstroem, J., L. Kaila and P. Niemelä. 1994. Polyphagy and adult body size in geometrid moths. Oecologia 98: 130–132.

283. Liu, C., Dudley, K.L., Xu, Z.H. and Economo, E.P., 2017. Mountain metacommunities: climate and spatial connectivity shape ant diversity in a complex landscape. *Ecography*, *41*(1), pp.101-112.

284. Lomolino, M. V. 2000. Ecology's Most General, Yet Protean Pattern: The Species-Area Relationship. Journal of Biogeography. 27 (1) : 17 – 26.

285. Lomolino, M.V., 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography*, *32*(10), pp.1683-1699.

286. Luck, G.W., Carter, A. and Smallbone, L., 2013. Changes in bird functional diversity across multiple land uses: interpretations of functional redundancy depend on functional group identity. *PloS one*, *8*(5), p.e63671.

287. Luck, G.W., Harrington, R., Harrison, P.A., Kremen, C., Berry, P.M., Bugter, R., Dawson, T.P., De Bello, F., Díaz, S., Feld, C.K. and Haslett, J.R., 2009. Quantifying the contribution of organisms to the provision of ecosystem services. *Bioscience*, *59*(3), pp.223-235.

288. Luo, Y., Liu, J., Tan, S., Cadotte, M.W., Xu, K., Gao, L. and Li, D., 2016. Trait variation and functional diversity maintenance of understory herbaceous species coexisting along an elevational gradient in Yulong Mountain, Southwest China. *Plant Diversity*, *38*(6), pp.303-311.

289. Mac Nally, R., Fleishman, E., Bulluck, L.P. and Betrus, C.J., 2004. Comparative influence of spatial scale on beta diversity within regional assemblages of birds and butterflies. *Journal of biogeography*, *31*(6), pp.917-929.

290. MacArthur, R. and Levins, R., 1967. The limiting similarity, convergence, and divergence of coexisting species. *The american naturalist*, *101*(921), pp.377-385.

291. MacArthur, R.H. and MacArthur, J.W., 1961. On bird species diversity. *Ecology*, *42*(3), pp.594-598.

292. MacArthur, R.H. and Wilson, E.O., 2001. *The theory of island biogeography* (Vol. 1). Princeton university press.

293. MacArthur, R.H., 1957. On the relative abundance of bird species. *Proceedings of the National Academy of Sciences*, *43*(3), pp.293-295.

294. Magurran, A.E. (2004). Measuring Biological Diversity. Blackwell, Oxford.

295. Magurran, A.E. and Henderson, P.A., 2003. Explaining the excess of rare species in natural species abundance distributions. *Nature*, *422*(6933), p.714.

296. Magurran, A.E. and McGill, B.J., 2011. Biological diversity. *Frontiers in*.

297. Magurran, A.E. and Queiroz, H., 2010. Evaluating tropical biodiversity: do we need a more refined approach?. *Biotropica*, *42*(5), pp.537-539.

298. Magurran, A.E., 2013. *Measuring biological diversity*. John Wiley & Sons.

299. Maire, V., Gross, N., Börger, L., Proulx, R., Wirth, C., Pontes, L.D.S., Soussana, J.F. and Louault, F., 2012. Habitat filtering and niche differentiation jointly explain species relative abundance within grassland communities along fertility and disturbance gradients. *New Phytologist*, *196*(2), pp.497-509.

300. Mantel, N., 1967. Ranking procedures for arbitrarily restricted observation. *Biometrics*, pp.65-78.

301. Marquet, P.A., Keymer, J.E. and Cofre, H., 2003. Breaking the stick in space: of niche models, metacommunities and patterns in the relative abundance of species. *Macroecology: concepts and consequences*, pp.64-84.

302. Martinez, P.A., Marti, D.A., Molina, W.F. and Bidau, C.J., 2013. Bergmann's rule across the equator: a case study in Cerdocyon thous (Canidae). *Journal of Animal Ecology*, *82*(5), pp.997-1008.

303. Matthews, T.J. and Whittaker, R.J., 2014. Fitting and comparing competing models of the species abundance distribution: assessment and prospect. *Frontiers of Biogeography*, *6*(2).

304. Mayfield, M.M., Bonser, S.P., Morgan, J.W., Aubin, I., McNamara, S. and Vesk, P.A., 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, *19*(4), pp.423-431.

305. Mayr, E. 1963. Animal species and evolution. Cambridge: Harvard University Press.

306. Mayr, E., 1970. *Populations, species, and evolution: an abridgment of animal species and evolution* (Vol. 19). Harvard University Press.

307. McCain, C. M. 2007b. Could temperature and water availability drive elevational species richness? A global case study for bats. Global Ecology and Biogeography 16: 1–13.

308. McCain, C.M. 2007a Area and mammalian elevational diversity. Ecology 88: 76–86.

309. McCain, C.M. 2009. Global analysis of bird elevational diversity. Global Ecology and Biogeography. 18: 346–360.

310. McCain, C.M. 2010. Global analysis of reptile elevational diversity. Global Ecology and Biogeography. 19: 541–553.

311. McCain, C.M. and Grytnes, J.A., 2010. Elevational gradients in species richness. *Encyclopedia of life sciences (ELS)*, pp.1-10.

312. McCain, C.M., 2004. The mid-domain effect applied to elevational gradients: species richness of small mammals in Costa Rica. *Journal of Biogeography*, *31*(1), pp.19-31.

313. McGill, B.J., 2003. A test of the unified neutral theory of biodiversity. *Nature*, *422*(6934), p.881.

314. McGill, B.J., Enquist, B.J., Weiher, E. and Westoby, M., 2006. Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, *21*(4), pp.178-185.

315. McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J., Benecha, H.K., Dornelas, M., Enquist, B.J., Green, J.L., He, F. and Hurlbert, A.H., 2007. Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology letters*, *10*(10), pp.995-1015.

316. McKnight, M.W., White, P.S., McDonald, R.I., Lamoreux, J.F., Sechrest, W., Ridgely, R.S. and Stuart, S.N., 2007. Putting beta-diversity on the map: broad-scale congruence and coincidence in the extremes. *PLoS biology*, *5*(10), p.e272.

317. McNab, B.K., 1971. On the ecological significance of Bergmann's rule. *Ecology*, *52*(5), pp.845-854.

318. McNab, B.K., 2010. Geographic and temporal correlations of mammalian size reconsidered: a resource rule. *Oecologia*, *164*(1), pp.13-23.

319. Meiri, S. and Dayan, T., 2003. On the validity of Bergmann's rule. *Journal of biogeography*, *30*(3), pp.331-351.

320. Meiri, S., 2011. Bergmann's Rule–what's in a name?. *Global Ecology and Biogeography*, *20*(1), pp.203-207.

321. Melo, A.S., Rangel, T.F.L. and Diniz‐Filho, J.A.F., 2009. Environmental drivers of beta‐diversity patterns in New‐World birds and mammals. *Ecography*, *32*(2), pp.226-236.

322. Meynard, C.N., Devictor, V., Mouillot, D., Thuiller, W., Jiguet, F. and Mouquet, N., 2011. Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France?. *Global Ecology and Biogeography*, *20*(6), pp.893-903.

323. Micheli, F. and Halpern, B.S., 2005. Low functional redundancy in coastal marine assemblages. *Ecology Letters*, *8*(4), pp.391-400.

324. Miller CJ, Anderson S 1992. Impacts of aerial 1080 poisoning on the birds of Rangitoto Island, Hauraki Gulf, New Zealand. New Zealand Journal of Ecology 16: 103 – 107.

325. Mishra, C., Madhusudan, M.D. and Datta, A., 2006. Mammals of the high altitudes of western Arunachal Pradesh, eastern Himalaya: an assessment of threats and conservation needs. Oryx, 40(1), pp.29-35.

326. Mittelbach, G.G., Schemske, D.W., Cornell, H.V., Allen, A.P., Brown, J.M., Bush, M.B., Harrison, S.P., Hurlbert, A.H., Knowlton, N., Lessios, H.A. and McCain, C.M., 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology letters*, *10*(4), pp.315-331.

327. Moore, R.P., Robinson, W.D., Lovette, I.J. and Robinson, T.R., 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology letters*, *11*(9), pp.960-968.

328. Mora, C., Tittensor, D.P., Adl, S., Simpson, A.G. and Worm, B., 2011. How many species are there on Earth and in the ocean?. *PLoS biology*, *9*(8), p.e1001127.

329. Moretti, M., De Bello, F., Roberts, S.P. and Potts, S.G., 2010. Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology*, *78*(1), pp.98-108.

330. Moretti, M., Dias, A.T., De Bello, F., Altermatt, F., Chown, S.L., Azcárate, F.M., Bell, J.R., Fournier, B., Hedde, M., Hortal, J. and Ibanez, S., 2016. Handbook of protocols for standardized measurement of terrestrial invertebrate functional traits. *Functional Ecology*, *31*(3), pp.558-567.

331. Mori, A.S., Shiono, T., Koide, D., Kitagawa, R., Ota, A.T. and Mizumachi, E., 2013. Community assembly processes shape an altitudinal gradient of forest biodiversity. *Global Ecology and Biogeography*, *22*(7), pp.878-888.

332. Morin, X. and Chuine, I., 2006. Niche breadth, competitive strength and range size of tree species: a trade-off based framework to understand species distribution. *Ecology Letters*, *9*(2), pp.185-195.

333. Morin, X. and Lechowicz, M.J., 2013. Niche breadth and range area in North American trees. *Ecography*, *36*(3), pp.300-312.

334. Moser, G., Leuschner, C., Hertel, D., Graefe, S., Soethe, N. and Iost, S., 2011. Elevation effects on the carbon budget of tropical mountain forests (S Ecuador): the role of the belowground compartment. *Global Change Biology*, *17*(6), pp.2211-2226.

335. Motomura, I., 1932. A statistical treatment of ecological communities. *Zoological Magazine*, *44*, pp.379-383.

336. Mouchet, M.A., Villéger, S., Mason, N.W. and Mouillot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, *24*(4), pp.867-876.

337. Mouillot, D., Stubbs, W., Faure, M., Dumay, O., Tomasini, J.A., Wilson, J.B. and Do Chi, T., 2005. Niche overlap estimates based on quantitative functional traits: a new family of non-parametric indices. *Oecologia*, *145*(3), pp.345-353.

338. Moulds, M.S., 1981. Larval food plants of hawk moths (Lepidoptera: Sphingidae) affecting commercial crops in Australia. General and Applied Entomology: The Journal of the Entomological Society of New South Wales, 13, p.69.

339. Moulds, M.S., 1984. Larval food plants of hawk moths (Lepidoptera: Sphingidae) affecting garden ornamentals in Australia. General and Applied Entomology: The Journal of the Entomological Society of New South Wales, 16, p.57.

340. Muirhead-Thomson, R.C. 1991. Light traps. Trap responses of flying insects. Academic Press, London, pp.1-39.

341. Mukherjee, S., Krishnan, A., Tamma, K., Home, C., Navya, R., Joseph, S., Das, A. and Ramakrishnan, U., 2010. Ecology driving genetic variation: a comparative phylogeography of jungle cat (Felis chaus) and leopard cat (Prionailurus bengalensis) in India. PLoS One, 5(10), p.e13724.

342. Müller, H., Liedtke, H.C., Menegon, M., Beck, J., Ballesteros-Mejia, L., Nagel, P. and Loader, S.P., 2013. Forests as promoters of terrestrial life-history strategies in East African amphibians. *Biology letters*, *9*(3), p.20121146.

343. Myers, J.A., Chase, J.M., Jiménez, I., Jørgensen, P.M., Araujo-Murakami, A., Paniagua-Zambrana, N. and Seidel, R., 2013. Beta-diversity in temperate and tropical forests reflects dissimilar mechanisms of community assembly. *Ecology letters*, *16*(2), pp.151-157.

344. Myers, N. et al. 1992. Biodiversity hotspots for conservation priorities. Nature. 403 : 853 – 858.

345. Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. and Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature, 403(6772), pp.853-858.

346. Nachtigall, W., 1985. Calliphora as a model system for analysing insect flight. *Comprehensive insect physiology, biochemistry and pharmacology*, *5*(15), pp.501-605.

347. Naeem, S. and Wright, J.P., 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology letters*, *6*(6), pp.567-579.

348. Naeem, S., Loreau, M. and Inchausti, P., 2002. Biodiversity and ecosystem functioning: the emergence of a synthetic ecological framework. *Biodiversity and ecosystem functioning: synthesis and perspectives*, pp.3-11.

349. Nally, R.M., Fleishman, E. and Murphy, D.D., 2004. Influence of temporal scale of sampling on detection of relationships between invasive plants and the diversity patterns of plants and butterflies. *Conservation Biology*, *18*(6), pp.1525-1532.

350. Nee, S. and May, R.M., 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *Journal of Animal Ecology*, pp.37-40.

351. Nekola, J.C. and Brown, J.H., 2007. The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecology letters*, *10*(3), pp.188-196.

352. Nekola, J.C. and White, P.S., 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, *26*(4), pp.867-878.

353. Neyret, M., Bentley, L.P., Oliveras, I., Marimon, B.S., Marimon-Junior, B.H., Almeida de Oliveira, E., Barbosa Passos, F., Castro Ccoscco, R., dos Santos, J., Matias Reis, S. and Morandi, P.S., 2016. Examining variation in the leaf mass per area of dominant species across two contrasting tropical gradients in light of community assembly. *Ecology and evolution*, *6*(16), pp.5674-5689.

354. Norberg, U.M., 1985. Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *The American Naturalist*, *126*(3), pp.303-327.

355. Nudds, R.L. and Oswald, S.A., 2007. An interspecific test of Allen's rule: evolutionary implications for endothermic species. *Evolution: International Journal of Organic Evolution*, *61*(12), pp.2839-2848.

356. Olalla-Tárraga M. Á. 2011. "Nullius in Bergmann" or the pluralistic approach to ecogeographical rules: a reply to Watt et al. (2010). Oikos 120: 1441–1444.

357. Oliver, I. and Beattie, A.J., 1993. A possible method for the rapid assessment of biodiversity. Conservation biology, 7(3), pp.562-568.

358. Oliver, I. and Beattie, A.J., 1996. Invertebrate morphospecies as surrogates for species: a case study. Conservation Biology, 10(1), pp.99-109.

359. Olsgard, F. and Somerfield, P.J., 2000. Surrogates in marine benthic investigations-which taxonomic unit to target?. *Journal of Aquatic Ecosystem Stress and Recovery*, *7*(1), pp.25-42.

360. Olsgard, F., Somerfield, P.J. and Carr, M.R., 1998. Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine ecology progress series*, *172*, pp.25-36.

361. Orme, C.D.L., Davies, R.G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V.A., Webster, A.J., Ding, T.S., Rasmussen, P.C., Ridgely, R.S. and Stattersfield, A.J., 2005. Global hotspots of species richness are not congruent with endemism or threat. Nature, 436(7053), p.1016.

362. Osuri, A.M., Kumar, V.S. and Sankaran, M., 2014. Altered stand structure and tree allometry reduce carbon storage in evergreen forest fragments in India's Western Ghats. Forest ecology and management, 329, pp.375-383.

363. Outreman, Y., Andrade, T.O., Louâpre, P., Krespi, L., Violle, C. and Baaren, J., 2017. Multi-scale and antagonist selection on life-history traits in parasitoids: A community ecology perspective. *Functional Ecology*, *32*(3), pp.736-751.

364. Pagel, M., 1997. Inferring evolutionary processes from phylogenies. *Zoologica Scripta*, *26*(4), pp.331-348.

365. Pakeman, R.J., 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology*, *92*(6), pp.1353-1365.

366. Palmer, M.W., 1990. Spatial scale and patterns of species-environment relationships in hardwood forest of the North Carolina piedmont. *Coenoses*, pp.79-87.

367. Parmesan, C., 2006. Ecological and evolutionary responses to recent climate change. *Annu. Rev. Ecol. Evol. Syst.*, *37*, pp.637-669.

368. Partridge, L. and Pring-Mill, F., 1977. Canary Island blue tits and English coal tits: convergent evolution?. *Evolution*, *31*(3), pp.657-665.

369. Patterson, B.D., Stotz, D.F., Solari, S., Fitzpatrick, J.W. and Pacheco, V., 1998. Contrasting patterns of elevational zonation for birds and mammals in the Andes of southeastern Peru. *Journal of Biogeography*, *25*(3), pp.593-607.

370. Paul, A., Khan, M.L., Arunachalam, A. and Arunachalam, K., 2005. Biodiversity and conservation of rhododendrons in Arunachal Pradesh in the Indo-Burma biodiversity hotspot. Current Science, 89(4), pp.623-634.

371. Peixoto, F.P., Villalobos, F., Melo, A.S., Diniz-Filho, J.A.F., Loyola, R., Rangel, T.F. and Cianciaruso, M.V., 2017. Geographical patterns of phylogenetic beta-diversity components in terrestrial mammals. *Global Ecology and Biogeography*, *26*(5), pp.573-583.

372. Pennycuick, C., 1975. Actual and'optimum'flight speeds: field data reassessed. *Journal of Experimental Biology*, *200*(17), pp.2355-2361.

373. Pennycuick, C.J., 1971. Gliding flight of the white-backed vulture Gyps africanus. *Journal of Experimental Biology*, *55*(1), pp.13-38.

374. Peris, S.J., 1997. Distribution of birds on eastern and western slopes of The Sierra Aconquija in the northwestern Argentine Andes. Studies on Neotropical Fauna and Environment, 32(3), pp.135-141.

375. Petchey, O.L., Evans, K.L., Fishburn, I.S. and Gaston, K.J., 2007. Low functional diversity and no redundancy in British avian assemblages. *Journal of Animal Ecology*, *76*(5), pp.977-985.

376. Peterson, A.T., Soberón, J. and Sánchez-Cordero, V., 1999. Conservatism of ecological niches in evolutionary time. *Science*, *285*(5431), pp.1265-1267.

377. Pey, B., Nahmani, J., Auclerc, A., Capowiez, Y., Cluzeau, D., Cortet, J., Decaens, T., Deharveng, L., Dubs, F., Joimel, S. and Briard, C., 2014. Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic and Applied Ecology*, *15*(3), pp.194-206.

378. Pielou, E. C. 1966. Species-diversity and pattern-diversity in the study of ecological succession. Journal of Theoretical Biology. 10 (2) : 370 – 383.

379. Pielou, E.C., 1975. Ecology diversity. *New York: John*.

380. Pincheira-Donoso, D. and Meiri, S., 2013. An intercontinental analysis of climate-driven body size clines in reptiles: no support for patterns, no signals of processes. *Evolutionary Biology*, *40*(4), pp.562-578.

381. Poff, N.L. and Zimmerman, J.K., 2010. Ecological responses to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology*, *55*(1), pp.194-205.

382. Pool, T.K., Olden, J.D., Whittier, J.B. and Paukert, C.P., 2010. Environmental drivers of fish functional diversity and composition in the Lower Colorado River Basin. *Canadian Journal of Fisheries and Aquatic Sciences*, *67*(11), pp.1791-1807.

383. Powlesland R, Knegtmans J, Marshall I 1998. Evaluating the impacts of 1080 possum control operations on North Island robins, North Island tomtits and more porks at Pureora – preliminary results. Science for Conservation Wellington, Department of Conservation. 23 p.

384. Powlesland RG, Knegtmans JW, Marshall ISJ 1999. Costs and benefits of aerial 1080 possum control operations using carrot baits to North Island robins (Petroica australis

385. Powlesland RG, Knegtmans JW, Styche A 2000. Mortality of North Island tomtits (Petroica macrocephala toitoi) caused by aerial 1080 possum control operations, 1997–98,

386. Prado, P.I., Miranda, M.D. and Chalom, A., 2014. Package 'sads': Maximum likelihood models for species abundance distributions. *Available at cran. r-project. org/web/packages/sads/index. html*.

387. Preston, F.W., 1948. The commonness, and rarity, of species. *Ecology*, *29*(3), pp.254-283.

388. Price, J., 2003. Climate change, birds, and ecosystems—Why should we care?. In *Managing for Healthy Ecosystems* (Vol. 471, No. 475, pp. 471-475). ROUTLEDGE in association with GSE Research.

389. Price, T.D., 2012. Eaglenest Wildlife Sanctuary: Pressures on Biodiversity: (EO Wilson Award Address).

390. Price, T.D., Hooper, D.M., Buchanan, C.D., Johansson, U.S., Tietze, D.T., Alström, P., Olsson, U., Ghosh-Harihar, M., Ishtiaq, F., Gupta, S.K. and Martens, J., 2014. Niche filling slows the diversification of Himalayan songbirds. Nature, 509(7499), p.222.

391. Price, Trevor D. "The seasonality and occurrence of birds in the Eastern Ghats of Andhra Pradesh." J. Bombay Nat. Hist. Soc 76, no. 3 (1979): 379-422.

392. Prinzing, A., 2001. The niche of higher plants: evidence for phylogenetic conservatism. *Proceedings of the Royal Society of London B: Biological Sciences*, *268*(1483), pp.2383-2389.

393. Purvis, A. and Orme, C.D.L., 2005. Evolutionary trends in body size. In *Deciphering growth* (pp. 1-18). Springer, Berlin, Heidelberg.

394. Qian, H., 2009. Global comparisons of beta diversity among mammals, birds, reptiles, and amphibians across spatial scales and taxonomic ranks. *Journal of Systematics and Evolution*, *47*(5), pp.509-514.

395. Quimbayo, N., Serna, F., Olivares, T.S. and Angulo, A.O., 2010. Noctuids (Lepidoptera) in Colombian flower crops. Revista Colombiana de Entomología, 36(1), pp.38-46.

396. Rabinowitz, D., 1981. Buried viable seeds in a North American tall-grass prairie: the resemblance of their abundance and composition to dispersing seeds. *Oikos*, pp.191-195.

397. Rahbeck, C. 1995. The Elevational Gradient of Species Richness : A Uniform Pattern? Ecograhy 18(2) : 200 – 205.

398. Rahbek, C., 2005. The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology letters*, *8*(2), pp.224-239.

399. Rahbek, C., Gotelli, N.J., Colwell, R.K., Entsminger, G.L., Rangel, T.F.L. and Graves, G.R., 2007. Predicting continental-scale patterns of bird species richness with spatially explicit models. *Proceedings of the Royal Society of London B: Biological Sciences*, *274*(1607), pp.165-174.

400. Raman, T.R., Joshi, N.V. and Sukumar, R., 2005. Tropical rainforest bird community structure in relation to altitude, tree species composition, and null models in the Western Ghats, India. arXiv preprint q-bio/0510033.

401. Rana, B.S., Singh, S.P. and Singh, R.P., 1989. Biomass and net primary productivity in Central Himalayan forests along an altitudinal gradient. *Forest ecology and management*, *27*(3-4), pp.199-218.

402. Rand, A. L. 1936. Altitudinal variation in New Guinea birds. Amer. Mus. Novit., 890:1-14

403. Rand, A.L., 1961. Wing length as an indicator of weight: a contribution. *Bird-banding*, *32*(2), pp.71-79.

404. Rapoport, E.H., 1994. Remarks on marine and continental biogeography: an areographical viewpoint. *Phil. Trans. R. Soc. Lond. B*, *343*(1303), pp.71-78.

405. Rasmussen, P.C. and Anderton, J.C., 2005. Birds of south Asia: the Ripley guide. Washington, DC.

406. Ray, C., 1960. The application of Bergmann's and Allen's rules to the poikilotherms. *Journal of morphology*, *106*(1), pp.85-108.

407. Reimchen, T.E. and Cox, K.D., 2015. Differential temperature preferences of vertebral phenotypes in Gasterosteus. *Canadian Journal of Zoology*, *94*(1), pp.1-5.

408. Rensch, B., 1938, December. Some problems of geographical variation and species-formation. In *Proceedings of the Linnean Society of London* (Vol. 150, No. 4, pp. 275-285). Oxford, UK: Blackwell Publishing Ltd.

409. Reynolds, C.S., 2006. *The ecology of phytoplankton*. Cambridge University Press.

410. Ricklefs, R.E., 2006. The unified neutral theory of biodiversity: do the numbers add up?. *Ecology*, *87*(6), pp.1424-1431.

411. Riemer, K., Guralnick, R.P. and White, E.P., 2017. No general relationship between mass and temperature in endothermic species. *eLife*, *7*, p.e27166.

412. Ritchie, M.E. and Olff, H., 1999. Spatial scaling laws yield a synthetic theory of biodiversity. *Nature*, *400*(6744), p.557.

413. Robin, V. V., A. Sinha, and U. Ramakrishnan. 2010. Ancient geographical gaps and paleo-climate shape the phylogeography of an endemic bird in the sky islands of southern India. PLoS ONE 5:e13321

414. Rohde, K., 1992. Latitudinal gradients in species diversity: the search for the primary cause. *Oikos*, pp.514-527.

415. Rohner, P.T., Bächli, G., Pollini Paltrinieri, L., Duelli, P., Obrist, M.K., Jochmann, R. and Blanckenhorn, W.U., 2015. Distribution, diversity gradients and Rapoport's elevational rule in the black scavenger flies of the Swiss Alps (Diptera: Sepsidae). *Insect Conservation and Diversity*, *8*(4), pp.367-376.

416. Rohner, P.T., Pitnick, S., Blanckenhorn, W.U., Snook, R.R., Bächli, G. and Lüpold, S., 2018. Interrelations of global macroecological patterns in wing and thorax size, sexual size dimorphism, and range size of the Drosophilidae. *Ecography*.

417. Romdal, T.S. and Grytnes, J.A., 2007. An indirect area effect on elevational species richness patterns. *Ecography*, *30*(3), pp.440-448.

418. Rominger, A.J., Miller, T.E. and Collins, S.L., 2009. Relative contributions of neutral and niche-based processes to the structure of a desert grassland grasshopper community. *Oecologia*, *161*(4), pp.791-800.

419. Rosenberg, G.H., 2005. Magurran, A. 2004. Measuring Biological Diversity. Oxford, RU: Blackwell Publishing. Schemske, DW y N. Brokaw. 1981."Treefalls and the distribution of. *ica de Costa Rica*, *9*(1), p.17.

420. Rosenberg, R. et. al. 2004. Marine quality assessment by use of benthic species-abundance distributions: a proposed new protocol within the European Union Water Framework Directive. Marine Pollution Bulletin. 49 (9-10) : 728 – 739.

421. Rosenzweig, M.L., 1995. *Species diversity in space and time*. Cambridge University Press.

422. Ross, S.R.J., Hassall, C., Hoppitt, W.J., Edwards, F.A., Edwards, D.P. and Hamer, K.C., 2017. Incorporating intraspecific trait variation into functional diversity: Impacts of selective logging on birds in Borneo. *Methods in Ecology and Evolution*, *8*(11), pp.1499-1505.
423. Rydell, J. and Lancaster, W.C., 2000. Flight and thermoregulation in moths were shaped by predation from bats. *Oikos*, *88*(1), pp.13-18.
424. Rygg, B. 1985. Distribution of species along pollution-induced diversity gradients in benthic communities in Norwegian fjords. Marine Pollution Bulletin. 16 (12) : 469 – 474.
425. Ryland, J.S. and Hayward, P.J. eds., 2017. *Handbook of the marine fauna of North-West Europe*. Oxford University Press.
426. Saeedghalati, M., Farahpour, F., Budeus, B., Lange, A., Westendorf, A.M., Seifert, M., Küppers, R. and Hoffmann, D., 2017. Quantitative Comparison of Abundance Structures of Generalized Communities: From B-Cell Receptor Repertoires to Microbiomes. *PLoS computational biology*, *13*(1), p.e1005362.
427. Salewski, V. and Watt, C., 2017. Bergmann's rule: a biophysiological rule examined in birds. *Oikos*, *126*(2).
428. Sanchez-Cordero, V. 2001. Elevation Gradients of Diversity for Rodents and Bats in Oaxaca, Mexico. Global Ecology and Biogeography. 10 (1) : 63 – 76.
429. Sanders, N. J, Carsten, R. 2012. The patterns and causes of elevational diversity gradients. Ecography. 35: 1 -3.
430. Sanders, N.J. 2002. Elevational gradients in ant species richness: area, geometry, and Rapoport's rule. Ecography. 25: 25–32.
431. Sanders, N.J., Lessard, J.P., Fitzpatrick, M.C. and Dunn, R.R., 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. *Global Ecology and Biogeography*, *16*(5), pp.640-649.
432. Schmidt & Nielsen, K., 1972. Locomotion: energy cost of swimming, flying, and running. *Science*, *177*(4045), pp.222-228.
433. Schrama, M., Plas, F., Berg, M.P. and Olff, H., 2017. Decoupled diversity dynamics in green and brown webs during primary succession in a saltmarsh. *Journal of animal ecology*, *86*(1), pp.158-169.
434. Schulze, C.H. and Fiedler, K., 2002. Vertical and temporal diversity of a species-rich moth taxon in Borneo. Arthropods of tropical forests: spatio-temporal dynamics and resource use in the canopy, pp.69-85.
435. Scoble, M.J. and Hausmann, A., 2007. Online list of valid and available names of the Geometridae of the World. Lepidoptera Barcode of Life, iBOL.
436. Shelomi, M. and Zeuss, D., 2017. Bergmann's and Allen's Rules in Native European and Mediterranean Phasmatodea. *Frontiers in Ecology and Evolution*, *5*, p.25.
437. Shelomi, M., 2012. Where are we now? Bergmann's rule sensu lato in insects. *The American Naturalist*, *180*(4), pp.511-519.
438. Shoemaker, L.G. and Melbourne, B.A., 2016. Linking metacommunity paradigms to spatial coexistence mechanisms. *Ecology*, *97*(9), pp.2436-2446.
439. Silva, I.A., Cianciaruso, M.V. and Batalha, M.A., 2010. Abundance distribution of common and rare plant species of Brazilian savannas along a seasonality gradient. *Acta Botanica Brasilica*, *24*(2), pp.407-413.
440. Simpson, E.H., 1949. Measurement of diversity. *nature*.
441. Singh, I.J. and Kitching, I.J., 2014. A first record of Clanis hyperion Cadiou and Kitching, 1990 (Lepidoptera: Sphingidae) in Bhutan, and a preliminary checklist of the hawkmoths of Mendrelgang, Bhutan. *Journal of Threatened Taxa*, *6*(1), pp.5386-5388.
442. Singh, N., 1986. On the duration of the rainy season over different parts of India. Theoretical and applied climatology, 37(1-2), pp.51-62.
443. Singh, S.P., Adhikari, B.S. and Zobel, D.B., 1994. Biomass, productivity, leaf longevity, and forest structure in the central Himalaya. *Ecological Monographs*, *64*(4), pp.401-421.
444. Sinha, A., Datta, A., Madhusudan, M.D. and Mishra, C., 2005. Macaca munzala: a new species from western Arunachal Pradesh, northeastern India. International Journal of Primatology, 26(4), pp.977-989.
445. Šizling, A.L., Storch, D., Šizlingová, E., Reif, J. and Gaston, K.J., 2009. Species abundance distribution results from a spatial analogy of central limit theorem. *Proceedings of the National Academy of Sciences*, *106*(16), pp.6691-6695.

446. Skandalis, D.A., Segre, P.S., Bahlman, J.W., Groom, D.J., Welch Jr, K.C., Witt, C.C., McGuire, J.A., Dudley, R., Lentink, D. and Altshuler, D.L., 2017. The biomechanical origin of extreme wing allometry in hummingbirds. *Nature communications*, *8*(1), p.1047.
447. Smith, B. and Wilson, J.B., 1996. A consumer's guide to evenness indices. *Oikos*, pp.70-82.
448. Smith, R.J., Hines, A., Richmond, S., Merrick, M., Drew, A. and Fargo, R., 2000. Altitudinal variation in body size and population density of Nicrophorus investigator (Coleoptera: Silphidae). *Environmental Entomology*, *29*(2), pp.290-298.
449. Snow, D.W., 1954. Trends in geographical variation in Palaearctic members of the genus Parus. *Evolution*, *8*(1), pp.19-28.
450. Snow, D.W., 1958. *A study of blackbirds*. British Museum of Natural.
451. Soininen, J., McDonald, R. and Hillebrand, H., 2007. The distance decay of similarity in ecological communities. *Ecography*, *30*(1), pp.3-12.
452. Soininen, J., Passy, S. and Hillebrand, H., 2012. The relationship between species richness and evenness: a meta-analysis of studies across aquatic ecosystems. *Oecologia*, *169*(3), pp.803-809.
453. Somerfield, P.J. and Clarke, K.R., 1995. Taxonomic levels, in marine community studies, revisited. *Marine Ecology Progress Series*, *127*, pp.113-119.
454. Sondhi, S. and Kunte, K., 2014. Butterflies and Moths of Pakke Tiger Reserve. Samrakshan Trust.
455. Sondhi, S. and Kunte, K., 2016. Butterflies (Lepidoptera) of the Kameng Protected Area Complex, western Arunachal Pradesh, India. Journal of Threatened Taxa, 8(8), pp.9053-9124.
456. Sondhi, S. and Ohler, A., 2011. A blue-eyed Leptobrachium (Anura: Megophryidae) from Arunachal Pradesh, India. Zootaxa, 2912, pp.28-36.
457. Southwood, T.R., 1977. Habitat, the templet for ecological strategies?. *Journal of animal ecology*, *46*(2), pp.337-365.
458. Southwood, T.R.E. and Henderson, P.A., 2000. Ecological Methods–Blackwell Science.
459. Southwood, T.R.E., 1988. Tactics, strategies and templets. *Oikos*, pp.3-18.
460. Spurr EB 2000. Impacts of possum control on non-target species. In: Montague TL ed The brushtail possum – biology, impact and management of an introduced marsupial. Lincoln, Manaaki Whenua Press. Pp. 175–186.
461. Spurr, E.B. and Warburton, B., 1991. Methods of measuring the proportions of plant species present in forest and their effect on estimates of bird preferences for plant species. New Zealand journal of ecology, pp.171-175.
462. Srinivasan, U., Dalvi, S., Naniwadekar, R., Anand, M.O. and Datta, A.., 2010. The birds of Namdapha National Park and surrounding areas: recent significant records and a checklist of the species. Forktail, 26, pp.92-116.
463. Stark, J.S., Riddle, M.J. and Simpson, R.D., 2003. Human impacts in soft‐sediment assemblages at Casey Station, East Antarctica: Spatial variation, taxonomic resolution and data transformation. *Austral Ecology*, *28*(3), pp.287-304.
464. STARMER, W.T. and WOLF, L.L., 1988. Causes of variation in wing loading among Drosophila species. *Biological Journal of the Linnean Society*, *37*(3), pp.247-261.
465. Stephens, P.R. and Wiens, J.J., 2003. Ecological diversification and phylogeny of emydid turtles. *Biological Journal of the Linnean Society*, *79*(4), pp.577-610.
466. Stevens, G. C. 1989. The Latitudinal Gradient in Geographical Range: How so Many Species Coexist in the Tropics. The American Naturalist. 133 (2) : 240 – 256.
467. Stevens, G.C., 1992. The elevational gradient in altitudinal range: an extension of Rapoport's latitudinal rule to altitude. *The American Naturalist*, *140*(6), pp.893-911.
468. Stevenson, R.D., 1985a. The relative importance of behavioral and physiological adjustments controlling body temperature in terrestrial ectotherms. *The American Naturalist*, *126*(3), pp.362-386.
469. Stevenson, R.D., 1985b. Body size and limits to the daily range of body temperature in terrestrial ectotherms. *The American Naturalist*, *125*(1), pp.102-117.
470. Stirling, G. and Wilsey, B., 2001. Empirical relationships between species richness, evenness, and proportional diversity. *The American Naturalist*, *158*(3), pp.286-299.
471. Storch, D. 2016. The theory of the nested species - area relationship: geometric foundations of biodiversity scaling. Journal of Vegetation Science. 27 : 880 – 891.

472. Stuart-Smith, R.D., Bates, A.E., Lefcheck, J.S., Duffy, J.E., Baker, S.C., Thomson, R.J., Stuart-Smith, J.F., Hill, N.A., Kininmonth, S.J., Airoldi, L. and Becerro, M.A., 2013. Integrating abundance and functional traits reveals new global hotspots of fish diversity. *Nature*, *501*(7468), p.539.

473. Sugihara, G., Bersier, L.F., Southwood, T.R.E., Pimm, S.L. and May, R.M., 2003. Predicted correspondence between species abundances and dendrograms of niche similarities. *Proceedings of the National Academy of Sciences*, *100*(9), pp.5246-5251.

474. Sun, Y., Li, M., Song, G., Lei, F., Li, D. and Wu, Y., 2017. The role of climate factors in geographic variation in body mass and wing length in a passerine bird. *Avian Research*, *8*(1), p.1.

475. Sun, Y.F., Ren, Z.P., Wu, Y.F., Lei, F.M., Dudley, R. and Li, D.M., 2016. Flying high: limits to flight performance by sparrows on the Qinghai-Tibet Plateau. *Journal of Experimental Biology*, pp.jeb-142216.

476. Symonds, M.R. and Tattersall, G.J., 2010. Geographical variation in bill size across bird species provides evidence for Allen's rule. *The American Naturalist*, *176*(2), pp.188-197.

477. Szewczyk, T. and McCain, C.M., 2016. A systematic review of global drivers of ant elevational diversity. *PloS one*, *11*(5), p.e0155404.

478. Taudiere, A. and Violle, C., 2016. cati: an R package using functional traits to detect and quantify multi-level community assembly processes. *Ecography*, *39*(7), pp.699-708.

479. Teplitsky, C. and Millien, V., 2014. Climate warming and Bergmann's rule through time: is there any evidence?. *Evolutionary applications*, *7*(1), pp.156-168.

480. Terborgh, J. 1977. Bird species diversity on an Andean elevational gradient. Ecology. 58: 1007–1019.

481. Terborgh, J. and Weske, J.S., 1975. The role of competition in the distribution of Andean birds. *Ecology*, *56*(3), pp.562-576.

482. Terborgh, J., 1973. On the notion of favorableness in plant ecology. *The American Naturalist*, *107*(956), pp.481-501.

483. Terborgh, J., 1985. The vertical component of plant species diversity in temperate and tropical forests. *The American Naturalist*, *126*(6), pp.760-776.

484. Tillin, H.M., Hiddink, J.G., Jennings, S. and Kaiser, M.J., 2006. Chronic bottom trawling alters the functional composition of benthic invertebrate communities on a sea-basin scale. *Marine Ecology Progress Series*, *318*, pp.31-45.

485. Tilman, D., 1982. *Resource competition and community structure* (No. 17). Princeton university press.

486. Tissot, C., Chikhi, H. and Nayar, T.S., 1994. Pollen of wet evergreen forests of the Western Ghats, India (pp. 133-p). Institut français de Pondichéry.

487. Tokeshi, M., 1993. Species abundance patterns and community structure. In *Advances in ecological research* (Vol. 24, pp. 111-186). Academic Press.

488. Tokeshi, M., 1996. Power fraction: a new explanation of relative abundance patterns in species-rich assemblages. *Oikos*, pp.543-550.

489. Tscharntke, T., Sekercioglu, C.H., Dietsch, T.V., Sodhi, N.S., Hoehn, P. and Tylianakis, J.M., 2008. Landscape constraints on functional diversity of birds and insects in tropical agroecosystems. *Ecology*, *89*(4), pp.944-951.

490. Tuomisto, H. and Ruokolainen, K., 1994. Distribution of Pteridophyta and Melastomataceae along an edaphic gradient in an Amazonian rain forest. *Journal of vegetation Science*, *5*(1), pp.25-34.

491. Tuomisto, H., 2010. A diversity of beta diversities: straightening up a concept gone awry

492. Tuomisto, H., Ruokolainen, K. and Yli-Halla, M., 2003. Dispersal, environment, and floristic variation of western Amazonian forests. *Science*, *299*(5604), pp.241-244.

493. Uetz, G.W., 1976. Gradient analysis of spider communities in a streamside forest. *Oecologia*, *22*(4), pp.373-385.

494. Ugland, K.I., Lambshead, P.J.D., McGill, B., Gray, J.S., O'Dea, N., Ladle, R.J. and Whittaker, R.J., 2007. Modelling dimensionality in species abundance distributions: description and evaluation of the Gambin model. *Evolutionary Ecology Research*, *9*(2), pp.313-324.

495. Ulrich, W., Kusumoto, B., Shiono, T. and Kubota, Y., 2016. Climatic and geographic correlates of global forest tree species–abundance distributions and community evenness. *Journal of vegetation science*, *27*(2), pp.295-305.

496. Ulrich, W., Ollik, M. and Ugland, K.I., 2010. A meta-analysis of species–abundance distributions. *Oikos*, *119*(7), pp.1149-1155.

497. Unger, M., Homeier, J. and Leuschner, C., 2012. Effects of soil chemistry on tropical forest biomass and productivity at different elevations in the equatorial Andes. *Oecologia*, *170*(1), pp.263-274.

498. Unwin, D.M. and Corbet, S.A., 1984. Wingbeat frequency, temperature and body size in bees and flies. *Physiological Entomology*, *9*(1), pp.115-121.

499. Van Der Heijden, M.G. and Scheublin, T.R., 2007. Functional traits in mycorrhizal ecology: their use for predicting the impact of arbuscular mycorrhizal fungal communities on plant growth and ecosystem functioning. *New Phytologist*, *174*(2), pp.244-250.

500. Veech, J.A., Crist, T.O. and Summerville, K.S., 2003. Intraspecific aggregation decreases local species diversity of arthropods. *Ecology*, *84*(12), pp.3376-3383.

501. Velho, N. and Laurance, W.F., 2013. Hunting practices of an Indo-Tibetan Buddhist tribe in Arunachal Pradesh, north-east India. Oryx, 47(3), pp.389-392.

502. Vellend, M., 2001. Do commonly used indices of β-diversity measure species turnover?. *Journal of Vegetation Science*, *12*(4), pp.545-552.

503. Villéger, S., Mason, N.W. and Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), pp.2290-2301.

504. Vinarski, M.V., 2014. On the applicability of Bergmann’s rule to ectotherms: the state of the art. *Biology Bulletin Reviews*, *4*(3), pp.232-242.

505. Violle, C., Enquist, B.J., McGill, B.J., Jiang, L.I.N., Albert, C.H., Hulshof, C., Jung, V. and Messier, J., 2012. The return of the variance: intraspecific variability in community ecology. *Trends in ecology & evolution*, *27*(4), pp.244-252.

506. Voje, K.L., Hansen, T.F., Egset, C.K., Bolstad, G.H. and Pelabon, C., 2014. Allometric constraints and the evolution of allometry. *Evolution*, *68*(3), pp.866-885.

507. Volkov, I., Banavar, J.R., He, F., Hubbell, S.P. and Maritan, A., 2005. Density dependence explains tree species abundance and diversity in tropical forests. *Nature*, *438*(7068), p.658.

508. Volkov, I., Banavar, J.R., Hubbell, S.P. and Maritan, A., 2007. Patterns of relative species abundance in rainforests and coral reefs. *Nature*, *450*(7166), p.45.

509. Walker, B., 1995. Conserving biological diversity through ecosystem resilience. *Conservation biology*, *9*(4), pp.747-752.

510. Walker, M.D., Wahren, C.H., Hollister, R.D., Henry, G.H., Ahlquist, L.E., Alatalo, J.M., Bret-Harte, M.S., Calef, M.P., Callaghan, T.V., Carroll, A.B. and Epstein, H.E., 2006. Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences*, *103*(5), pp.1342-1346.

511. Wang, J., Meier, S., Soininen, J., Casamayor, E.O., Pan, F., Tang, X., Yang, X., Zhang, Y., Wu, Q., Zhou, J. and Shen, J., 2017. Regional and global elevational patterns of microbial species richness and evenness. *Ecography*, *40*(3), pp.393-402.

512. Wang, X., Wiegand, T., Wolf, A., Howe, R., Davies, S.J. and Hao, Z., 2011. Spatial patterns of tree species richness in two temperate forests. *Journal of Ecology*, *99*(6), pp.1382-1393.

513. Warwick, R.M., 1988a. The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin*, *19*(6), pp.259-268.

514. Watt, C., Mitchell, S. and Salewski, V., 2010. Bergmann's rule; a concept cluster?. *Oikos*, *119*(1), pp.89-100.

515. Webb, C.T., Hoeting, J.A., Ames, G.M., Pyne, M.I. and LeRoy Poff, N., 2010. A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecology letters*, *13*(3), pp.267-283.

516. Wehn, S. et. al. 2017. Effects of abandonment on plant diversity in semi-natural grasslands along soil and climate gradients. Journal of Vegetative Science. 28 (4) : 838 – 847.

517. Weiher, E. and Keddy, P.A., 1995. Assembly rules, null models, and trait dispersion: new questions from old patterns. *Oikos*, pp.159-164.

518. Weinstein, B.A., 2015. Muscle Mass, Wing Morphology, and Related Flight Mechanics in Passeriforme Birds.

519. Westbrooke IM, Etheridge ND, Powlesland RG 2003. Comparing methods for assessing mortality impacts of an aerial 1080 pest control operation on tomtits (Petroica macrocephala toitoi) in Tongariro Forest. New Zealand

520. Westbrooke IM, Powlesland RG 2005. Comparison of impact between carrot and cereal 1080 baits on tomtits (Petroica macrocephala). New Zealand Journal of Ecology 29: with saddlebacks. Biological Conservation 105: 375–381.

521. Whittaker, R.H., 1965. Dominance and diversity in land plant communities: numerical relations of species express the importance of competition in community function and evolution. *Science*, *147*(3655), pp.250-260.

522. Whittaker, R.H., 1972. Evolution and measurement of species diversity. *Taxon*, pp.213-251.

523. Whittaker, R.J., 2010. Meta-analyses and mega-mistakes: calling time on meta-analysis of the species richness–productivity relationship. *Ecology*, *91*(9), pp.2522-2533.

524. Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P. and Hawkins, B.A., 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology letters*, *13*(10), pp.1310-1324.

525. Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. and Reeder, T.W., 2006. Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist*, *168*(5), pp.579-596.

526. Wilsey, B.J. and Potvin, C., 2000. Biodiversity and ecosystem functioning: importance of species evenness in an old field. *Ecology*, *81*(4), pp.887-892.

527. Wittebolle, L., Marzorati, M., Clement, L., Balloi, A., Daffonchio, D., Heylen, K., De Vos, P., Verstraete, W. and Boon, N., 2009. Initial community evenness favours functionality under selective stress. *Nature*, *458*(7238), p.623.

528. Wohlgemuth, D., Solan, M. and Godbold, J.A., 2016. Specific arrangements of species dominance can be more influential than evenness in maintaining ecosystem process and function. *Scientific reports*, *6*, p.39325.

529. Wohlgemuth, D., Solan, M. and Godbold, J.A., 2017. Species contributions to ecosystem process and function can be population dependent and modified by biotic and abiotic setting. *Proc. R. Soc. B*, *284*(1855), p.20162805.

530. Wolda, H., 1981. Similarity indices, sample size and diversity. *Oecologia*, *50*(3), pp.296-302.

531. Wu, Y., Colwell, R. K., Han, N., Zhang, R., Wang, W., Quan, Q., Zhang, C., Song, G., Qu, Y., Lein, F. 2014. Understanding historical and current patterns of species richness of babblers along a 5000-m subtropical elevational gradient, Global Ecol. Biogeogr. 23 (11) : 1167 – 1176

532. Xu, X., Zhang, H.Y., Luo, J., Zhang, D.J. and Ma, A., 2017. Area-corrected species richness patterns of vascular plants along a tropical elevational gradient. *Journal of Mountain Science*, *14*(4), pp.694-704.

533. Yela, J.L. and Holyoak, M., 1997. Effects of moonlight and meteorological factors on light and bait trap catches of noctuid moths (Lepidoptera: Noctuidae). Environmental Entomology, 26(6), pp.1283-1290.

534. Yom-Tov, Y. and Geffen, E., 2011. Recent spatial and temporal changes in body size of terrestrial vertebrates: probable causes and pitfalls. *Biological Reviews*, *86*(2), pp.531-541.

535. Yom-Tov, Y., Benjamini, Y. and Kark, S., 2002. Global warming, Bergmann's rule and body mass–are they related? The chukar partridge (Alectoris chukar) case. *Journal of Zoology*, *257*(4), pp.449-455.

536. Yom-Tov, Y., Yom-Tov, S., Wright, J., JR Thorne, C. and Du Feu, R., 2006. Recent changes in body weight and wing length among some British passerine birds. *Oikos*, *112*(1), pp.91-101.

537. Zambre, A.M. and Thaker, M., 2017. Flamboyant sexual signals: multiple messages for multiple receivers. Animal Behaviour, 127, pp.197-203.

538. Zamora-Camacho, F.J., Reguera, S. and Moreno-Rueda, G., 2014. Bergmann's Rule rules body size in an ectotherm: heat conservation in a lizard along a 2200-metre elevational gradient. *Journal of evolutionary biology*, *27*(12), pp.2820-2828.

539. Zhang, Y., Chen, H.Y. and Reich, P.B., 2012. Forest productivity increases with evenness, species richness and trait variation: a global meta-analysis. *Journal of ecology*, *100*(3), pp.742-749.

540. Zillio, T. and Condit, R., 2007. The impact of neutrality, niche differentiation and species input on diversity and abundance distributions. *Oikos*, *116*(6), pp.931-940.

541. Zinger, L., Amaral-Zettler, L.A., Fuhrman, J.A., Horner-Devine, M.C., Huse, S.M., Welch, D.B.M., Martiny, J.B., Sogin, M., Boetius, A. and Ramette, A., 2011. Global patterns of bacterial beta-diversity in seafloor and seawater ecosystems. *PLoS One*, *6*(9), p.e24570.

542. Zomer, R., Ustin, S. and Ives, J., 2000. Using satellite remote sensing for DEM extraction in complex mountainous terrain: landscape analysis of the Makalu Barun National Park of eastern Nepal. International Journal of Remote Sensing, 23(1), pp.125-143.