Abundance Patterns of Species along Elevational Gradients

Ecological Insights from a Bird Community in the Eastern Himalayas

A thesis submitted in partial fulfilment of the requirements of the degree of
Doctorate of Philosophy

by

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Indian Institute of Science Education and Research, Pune

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To Mini, Cocoa, and the "Larkalog"

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.

Alakananda Maitra

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Date: January 30, 2023

Certificate

Certified that the work incorporated in the thesis entitled **“Abundance Patterns of Species along Elevational Gradients: Ecological Insights from a Bird Community in the Eastern Himalayas** submitted by **Alakananda Maitra** 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: January 30, 2023

Acknowledgements

I was somehow very sure that I wanted to do a PhD two weeks into my summer internship at the National Centre for Biological Sciences as a second-year undergrad. Of course, within months of starting graduate school, I realized that it wasn't going to be easy. Having been lucky enough to make it out with a smile, I take this opportunity to express my gratitude to the ones who inspired me to start a PhD in the first place, but more importantly to the ones who turned an uphill battle into a fantastic journey, that taught me so much about the world around me as well as myself.

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Synopsis

A species' distribution or range is the expanse of geographical space where it is commonly encountered. The abundance that a species achieves in a landscape is determined by its fitness, which is an emergent property of the linkage between the environment, species' traits and adaptation. Though environment-trait-fitness-abundance (ETFA) linkage is central to ecological and evolutionary theory, fitness remains inaccessible, as it can neither be estimated through observations nor modelled. The lack of testable theoretical frameworks, coupled with the complex, multivariate nature of most landscapes has limited studies in the field to being purely heuristic or empirical, with little progress towards an understanding of the processes that determine species distributions.

Using a database of ~ 35000 bird records collected by our research group in both summer and winter along a 2600 m gradient in the eastern Himalayas, we demonstrate that montane elevational gradients – which are effectively univariate, one dimensional and host high species diversity – are suitable for testing theoretical models which make predictions of species distribution patterns. We use this system to revisit two largely phenomenological but widely investigated biogeographical patterns of the ETFA linkage.

The first is the abundant centre hypothesis (ACH), which suggests that abundance is highest at the centre of a species' distribution and declines towards the edges. However, despite four decades of investigation, there is little consensus over its validity as a general rule. We recast the ACH to align with a mechanistic framework that predicts a gaussian abundance profile shape along a linear environmental gradient. We find that the species average abundance profile shape for our bird community across seasons is close to symmetric and peaked with extended tails on either side, which is in line with the model's prediction. We also detect a small but significant residual asymmetry arising mainly from outlier range-edge populations indicating that ranges are likely getting compressed by the limits of the mountain slope.

The second is the relationship between abundance and range width, which is generally expected to be positive, but there are a sizeable number of empirical reports of negative as well as non-significant relationships. We quantify range-width using two different metrics:

extent and SD. The extent is dominated by the statistically unstable and ecologically less relevant peripheral populations with possible vagrants. However, data for this metric is more widely available for a large number of species. The SD is a more robust metric determined from the bulk of the population. With a focus on understanding the mechanisms which determine species distributions, we formulate hypotheses predicting the relationship between extent/SD and abundance for different levels of environmental steepness and population densities. We find that both SD and extent increase with increasing abundance in summer, which is consistent with a shallow environmental gradient (relative to density-driven dispersal), with populations at carrying capacity. However, neither of these relationships are significant in winter, which is not consistent with any of our hypotheses. We can only speculate that perhaps species strategies are more mixed in winter.

Migration is another key component of the ETFA linkage, and the evolutionary origins and drivers of this behaviour are poorly understood. Several species from our bird community exhibit short-distance altitudinal migrations, and we explore the impact of this on species distributions by comparing abundance profiles between summer and winter. Species generally tend to move towards the warmer lower elevations in winter, but there are a few exceptions that move higher up. Range expansions and contractions are more or less equally likely between seasons. We also combine our distributions data with published species-level data on traits, habitat/dietary preferences and phylogeny. We find that altitudinal migrations are more likely to be driven by body size (related to thermoregulation) rather than flight ability. We also show a moderate relationship between migratory propensity and phylogenetic relatedness, as well as certain habitat and dietary preferences, but suggest that a more thorough investigation is required for the emergence of secure patterns.

Overall, our study suggests a path towards a more mechanistic understanding of the determinants of species distributions while bringing to light a highly diverse, yet understudied, tropical montane ecosystem which has been recognised as a globally important biodiversity hotspot.

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1 Introduction

> *'Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare?'*
>
> *Charles Darwin*
> *On the origin of species (1859)*

1.1 Background

The distribution or *range* of a species is the expanse of geographical space where it is commonly encountered. The location and extent of these distributions can be very different even for closely related species with similar life-history traits. Figure 1.1 shows the global distributions of two closely related bird species of the genus *Liocichla* obtained from the IUCN Red list of threatened taxa (IUCN, 2021). Both birds are similar in morphology, as well as dietary and habitat preferences. However, while the Red-faced Liocichla (*Liocichla phoenicia*) is found all across the eastern Himalayas, its sister species, the Bugun

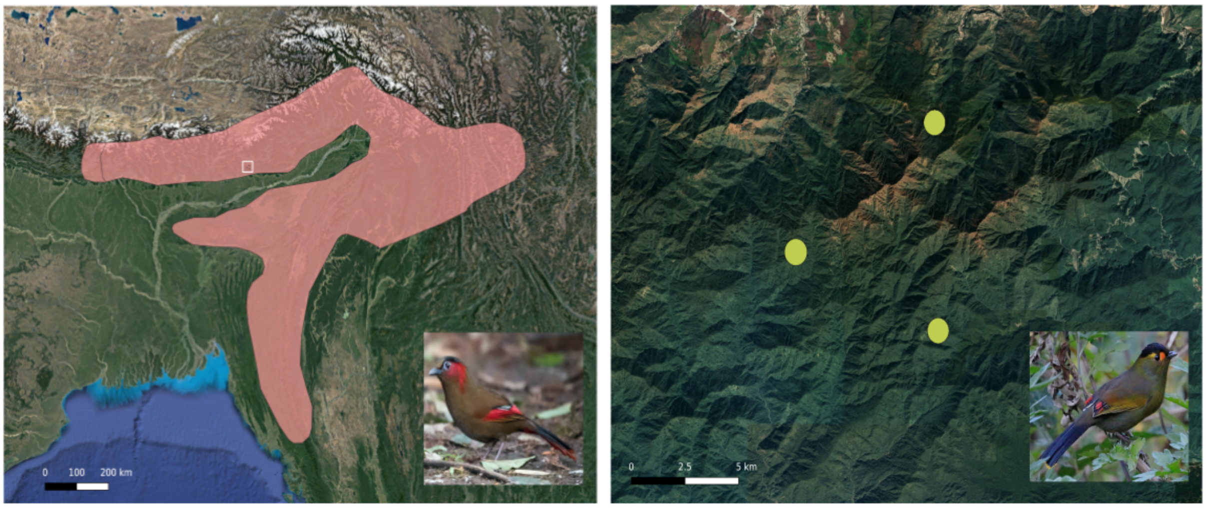

Figure 1.1: Global distributions of the Red-faced and Bugun Liocichlas. *The Red-faced Liocichla's range (left) spans a few hundred kilometres across the eastern Himalayas. The Bugun Liocichla on the other hand, is found only at three locations (right) within 10-15 km of each other in western Arunachal Pradesh. The panel on the right is a zoomed-in version of the small white rectangle that appears in the left panel.*

Liocichla (*Liocichla bugunorum*) is limited to 3 specific locations in western Arunachal Pradesh, all within 10-15 kilometres of each other.

A species' distribution is an emergent property of the interaction of its traits with the biotic and abiotic properties of the landscape. It is clear that the location at which a species first arises, and subsequent barriers to its dispersal play a crucial role in shaping its distribution. Geographical barriers (such as mountain ranges, large water bodies, and more recently human settlements) hinder dispersal by restricting the movement of individuals or through abrupt shifts in biotic regimes. However, evidence accumulated over the past several decades suggests that species distributions rarely expand indefinitely even in seemingly continuous landscapes devoid of such barriers, and the underlying processes are particularly interesting from an evolutionary perspective.

In order to delve deeper into these processes, we must ask what determines the survival of a species at a particular location (say, x) in a landscape (Figure 1.2). Biotic and abiotic factors together constitute the environment E(x), which has an optimal trait $T_0(x)$ associated with it. Suppose that the population of the focal species at x has a mean trait value $T_S(x)$. The difference between the optimal and the actual trait values, termed the trait discrepancy, determines the fitness (F) of the species at x. If F(x) is positive, the species survives and is able to maintain a non-zero abundance at x. If F(x) is negative, the

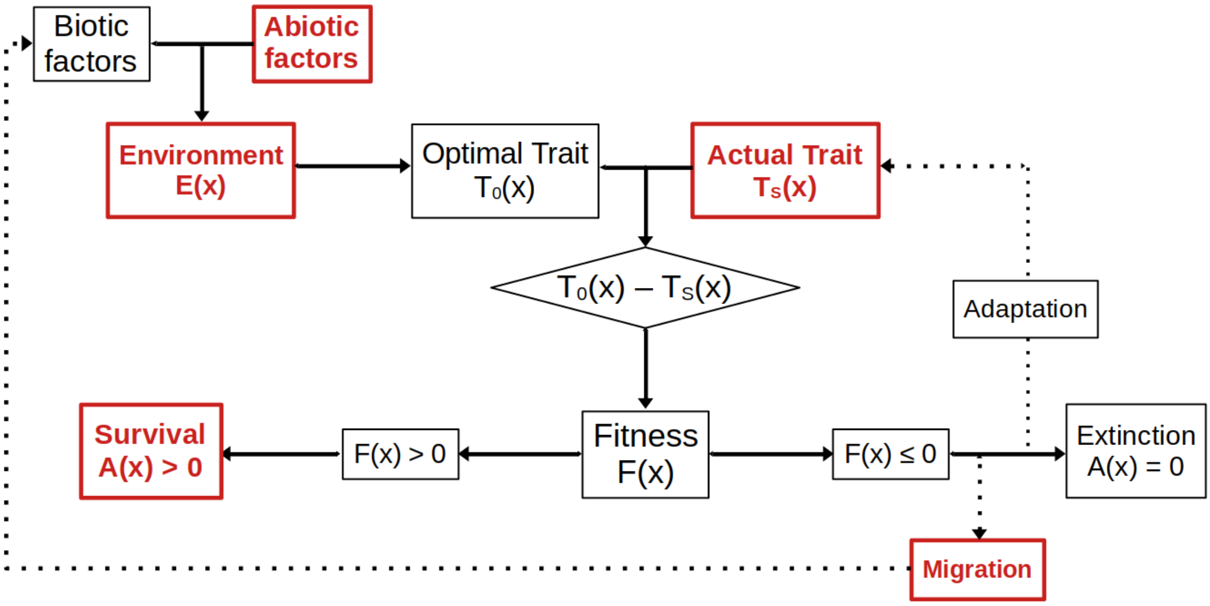

Figure 1.2: Factors influencing a species' survival in a landscape.
Biotic and abiotic factors together constitute the environment E(x), with an optimal trait value $T_0(x)$*. Species S has a mean trait value* $T_S(x)$*. The trait discrepancy determines fitness F(x). If F(x) is positive, the species maintains non-zero abundance at x. If F(x) is negative, the species can adapt to modify* T_S *or migrate to modify* T_0*, failing which it goes locally extinct at x. Only the components marked in red are observable.*

species may undergo local adaptation to modify the value of T_S or migrate to a different environment, thereby modifying the value of T_0. If it does neither, the species goes locally extinct at x.

In other words, the abundance that a species achieves in a landscape is determined by its fitness, which is a product of the linkage between the environment and species' traits and adaptation. The environment-trait-fitness-abundance (ETFA) linkage has several components and is central to ecological and evolutionary theory. However, very few of these components can be observed and/or measured for natural landscapes (marked in red in Figure 1.2). Additionally, fitness, which is the most crucial link, can neither be estimated empirically, nor modelled.

Studying the ETFA linkage is further complicated by the fact that most landscapes are complex and multivariate. Most species span vast expanses of geographical space across which multiple ecologically relevant variables (e.g., temperature, rainfall) fluctuate independently of one another. Therefore, identifying one, or even a few environmental factors that species abundances may be responding to is non-trivial. Another issue with studying distributions across vast landscapes is the intense sampling effort involved, even for a single species. Since changes in environmental variables are unpredictable across the landscape, abundances must be recorded at as many sites as possible - the abundance at one location cannot be derived based on other locations. The problem is further exacerbated when multiple species are considered. One way people have tried to work around this is by acquiring presence-absence data from large-scale surveys and citizen science initiatives. However, such data is affected by several biases - data heterogeneity, observer biases, non-uniform sampling effort and pseudo-replication from recording the same individuals repeatedly (Santini et al., 2019).

Consequently, even though studies have been investigating species ranges for the past several decades, they have mostly been either heuristic - attempting to identify "general" biogeographic patterns (Murphy et al., 2006; Ren et al., 2013; Reeve et al., 2016; Yancovitch Shalom et al., 2020), or species distribution models that use the environmental correlates from points of known occurrence to predict potential distributions (VanDerWal et al., 2009; Martínez-Meyer et al., 2012; Dallas et al., 2020). It seems that the lack of a theoretical framework, coupled with the complex, multivariate nature of most landscapes has limited ecological understanding of the processes that determine species distributions. Therefore, studies that combine ecological theory with empirical data are the need of the hour. Owing to reviews and meta-analyses that have collated information from hundreds of studies, we now have a fairly exhaustive list of factors that determine species range limits. However, there is progress to be made with regards to identifying the ways in which these factors interact to keep species distributions confined.

Several phenomenological and heuristic hypotheses have directly or indirectly formed the basis of all empirical studies in the field since its conception. The 1990s also saw the rise of a few mechanistic models, but these remain untested against empirical data, perhaps owing to the complexity of natural landscapes. Recent advances in technology and computation have yielded increasingly sophisticated species distribution models. However, most of these models predict distributions based on environmental correlates (Chandler et al., 2011), with little emphasis on understanding the underlying ecological processes.

As a result, most recent studies investigate species distributions in order to identify recurrent biogeographic patterns, in the hope that once their generality is established, it will be easier to arrive at the mechanisms that give rise to them. However, most of these patterns involve species distribution parameters alone, such as how abundance varies across the distribution, or the relationship between abundance and distribution width. Perhaps this is why studies typically disregard how environmental factors are changing across the landscape. Unsurprisingly, the high degree of variability in empirical studies involving different taxa, locations and geographic realms, as well as the definitions of range parameters has resulted in a large number of *case studies* but little consensus on general patterns.

The utility of investigations into processes that govern species distributions needs little advocacy in the current era of climate change and biodiversity loss. It seems the primary reason for the lack of directed effort towards validating process-based models is a dearth of natural systems that can be used as test beds. This dissertation is an attempt to investigate two of the most widely investigated biogeographic patterns associated with species distributions with a focus on the processes which may give rise to them. We argue that information on how the environment varies across the distribution is critical to understanding these processes. Further, multi-species studies using robust and ecologically relevant range parameter definitions that facilitate inter-specific comparison are an essential step to move beyond species-specific idiosyncrasies and identify general patterns.

While one aspect of the ETFA linkage involves local adaptation, migration, which is the alternative survival strategy is also poorly understood. Migration is expected to modify both the location as well as extent of species distributions between breeding and non-breeding seasons. However, we did not come across any study that uses abundance data to quantify such differences in our literature survey. Currently, there are several hypotheses regarding the evolutionary origins and drivers of migratory behaviour, few of which have been established through empirical studies. It is also as of yet unclear whether the same hypotheses are applicable to short-distance migration as well - a phenomenon that is poorly studied across taxa and geographic realms.

1.2 Study Region

In 1988, Norman Myers introduced the concept of biodiversity hotspots, leading up to his seminal article that identified regions in urgent need of conservation (Myers et al., 2000). Globally, 25 biogeographic regions qualified as hotspots based on their endemicity and threat from biodiversity loss. Each of these regions was found to host at least 0.5% (or 1,500) of the world's 300,000 plant species as endemics and had lost at least 70% of their primary vegetation. Currently, 36 regions qualify as hotspots and support more than half of the world's plant species and 43% of bird, mammal, reptile and amphibian species while spanning a mere 2.5% of the earth's land surface (www.conservation.org). India houses parts of four biodiversity hotspots: Indo-Burma, Himalayas, Western Ghats-Sri Lanka and Sundaland (Venkataraman & Sivaperuman, 2018), which are threatened by anthropogenic influences as well as climate change (Chitale et al., 2014). India has a combination of one of the largest populations and highest densities in the world, and the Western Ghats ranks first globally amongst biodiversity hotspots threatened by population growth (Cincotta et al., 2000). However, as is the case for most tropical ecosystems worldwide, the ecology of these regions are grossly understudied and poorly understood (Chitale & Behera, 2014).

1.2.1 The Eastern Himalayas

The Himalayas are a vast range of young fold mountains known to be unique from both paleo-geographic and ecological perspectives. They separate the plains of the Indian subcontinent from the Tibetan plateau and house the two largest river systems of the region - the *Indus* and the *Ganga-Brahmaputra* basins, in the west and the east respectively (Gaillardet et al., 2003). These mountains have a profound influence on the climate of south Asia and exhibit immense diversity in climatic regimes and habitat types - from humid subtropical in the foothills to a cold and dry desert on the Tibetan side of the range. They receive precipitation predominantly from the south-west monsoons, generally higher in east than the west. However, there is significant local variation between exposed slopes and rain-shadow regions. Combined with variations in altitude, soil type and a very high snow line, this gives rise to unique micro-habitats supporting distinct forest communities (dominated by broad-leafed evergreen taxa) that span 3000 kilometres in east-west extent and over 3000 m in elevation (Zobel & Singh, 1997).

The eastern Himalayas comprise a particularly precipitous landscape at cusp of the

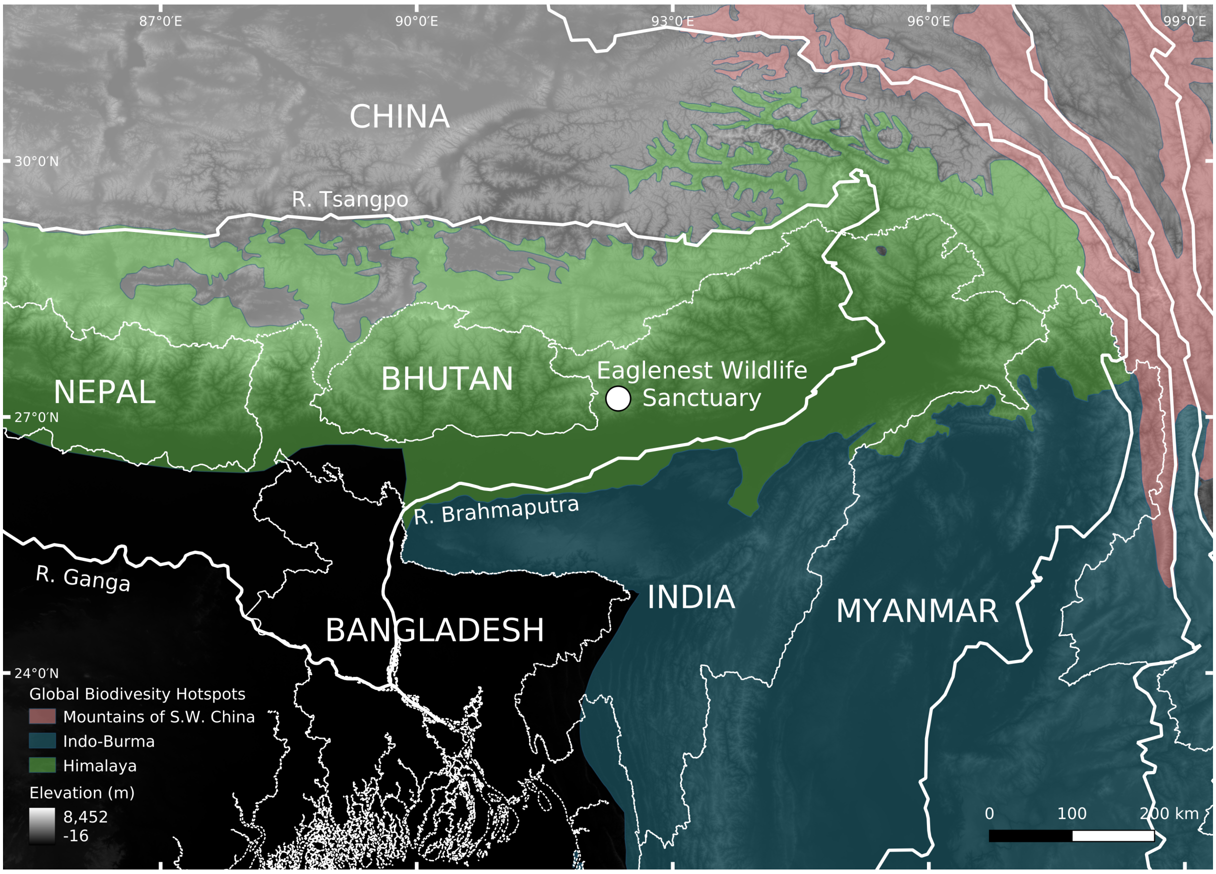

Figure 1.3: Our study region in the eastern Himalayas.
It is located at the cusp of three global biodiversity hotspots: the Himalayas, the Indo-Burma region and the mountains of south west China. This, coupled with an elevational gradient of over 8000 m gives rise to a wide variety of habitat types.

Indo-Burma and Himalayan biodiversity hotspots (Figure 1.3). It extends from eastern Nepal across Bhutan, north-east India, south-east Tibet, China's Yunnan region and northern Myanmar. This region was previously considered the interface of the Indo-Malayan and Palaearctic biogeographic realms (Wallace, 1876), but a recent revision based on phylogenetic relationships puts it at the confluence of the Oriental and Sino-Japanese biogeographic regions (Holt et al., 2013).

The climate of the region is best described as tropical montane - moderate but wet all year round with no dry season in the foot hills and chilly winters at higher elevations. Summer commences mid-April, peaks in June and is over by August end (average summer temperature $\sim$ 20°C). The eastern Himalayas are significantly wetter than their western counterparts, with an average annual rainfall as high as 10,000 mm on southern slopes (Soja & Starkel, 2007). However, heavy snowfall is uncommon, even at higher elevations.

The river basins of this region feature dense forests that sustain a diverse array of wildlife. While tropical forests are common at lower elevations, the most biodiverse cloud

Figure 1.4: The precipitous terrain of the eastern Himalayas.
Left: The low flat plains dominated by agriculture transition into towering, snow-capped mountains over a distance of less than 150 km. Right: Its dense cloud forests host the second highest biodiversity in the world. Photo credits - Chris Walker (WWF species discovery report, 2015).

forests and wet grasslands in the world are found at higher elevations in this region (Figure 1.4). These unique habitats are are home to more than 10,000 plant species, 300 mammal species, 977 bird species, 281 reptiles and amphibian species and 269 freshwater fish species, including countless rare endemics (WWF India, 2009). At least 211 new species have been discovered in this region between 2000-2014 alone - an average of 34 new finds every year. However, these forests are also currently under threat due to unsustainable and illegal logging, agriculture, unsustainable fuel wood collection, overgrazing by domestic livestock, poaching and wildlife trade, mining, pollution and poorly planned infrastructure (WWF India report, 2015). Only about 25% of the original habitats remain intact (www.conservation.org).

1.2.2 Arunachal Pradesh

With an area of 83743 km^2, Arunachal Pradesh is the largest state of north-east India. Elevation rises precipitously from 100 m at its southern border to nearly 7000 m at its border with Tibet - over an aerial distance of less than 150 km (Figure 1.5). The mountains form an effective barrier against the northward progression of the monsoon resulting in rainfall of over 3500 mm on southern slopes. Deep north-south river gorges drain this heavy rainfall and eventually become tributaries of the *Tsangpo* or *Brahmaputra*, making

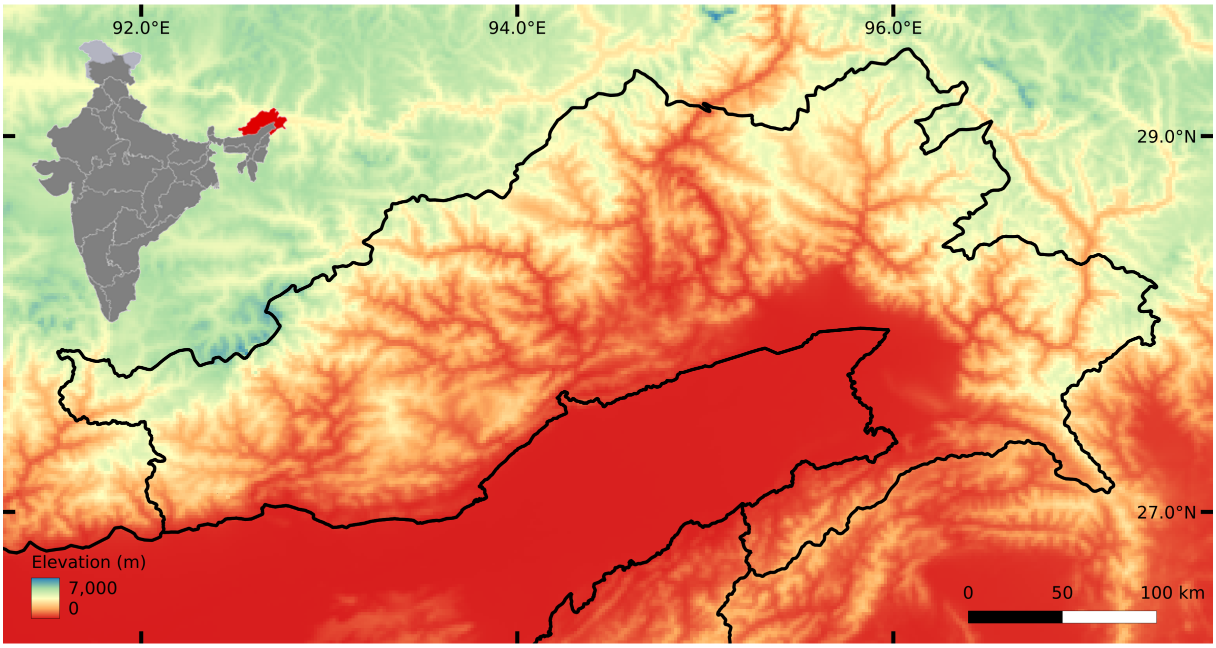

Figure 1.5: Elevational map of Arunachal Pradesh.
Arunachal Pradesh is the largest and northernmost state of North East India (Inset). Note the stratified landscape with elevations ranging from sea-level to 7000 m in a short stretch of $\sim 1°$*latitude.*

it the largest river basin of the Indian subcontinent.

Primarily owing to the vast elevational and precipitation gradient, this region ranks 6th among the "hottest" of biodiversity hotspots in the world (Myers et al., 2000) and also features among the top 200 ecoregions of the world (Olson & Dinerstein, 1998). The topographical complexity with its interleaved steep mountains and deep river gorges has forged isolated islands of habitats.

81% of the state's area is under forest cover, and rights and ownership of 60% of this ($\sim 31,800km^2$) remain with local indigenous communities. The protected areas of western Arunachal Pradesh collectively dubbed the Kameng Protected Area Complex (KPAC) comprise the largest contiguous track of pristine forests of the state. These include the Pakke and Nameri tiger reserves, the Sessa orchid sanctuary, the Eaglenest wildlife sanctuary and the reserve forests of Papum, Doimara, Amortola and Shergaon. This forest complex is bounded by the plains of Assam ($\sim 100m$) to the south and the Gori-Chen range ($\sim 6000m$) on the Indo-Tibetan border to the north and is drained by the *Kameng* river, a major tributary of the *Brahmaputra*. It encompasses over $3500km^2$ of diverse habitat types and 3300 m in elevation and is of critical importance to conservation (Athreya, 2006).

1.3 Study Taxon

Birds are one of the most widely studied taxa on the planet. Being hyper-diverse in terms of taxonomy, physiology and behaviour, and yet generally conspicuous, they are well suited for investigations in a wide variety of fields ranging from neurobiology to ecology and evolution (Konishi et al., 1989). They are relatively easy to spot and identify even in heavily forested areas owing to their distinct appearances and songs.

The eastern Himalayan region (especially Arunachal Pradesh) is ideal for studying birds as it hosts the second highest bird species richness (Orme et al., 2005), and the highest density of oscine passerines in the world (Price et al., 2014). An estimated 600 species of birds ($> 50\%$ of all birds in mainland India) breed in a 250 km quadrat centred on Arunachal Pradesh and another ~ 150 are winter migrants (Athreya, 2006).

There are several large-scale surveys that have been documenting bird distributions for over half a century (such as the North-American and British breeding bird surveys), global databases (such as the IUCN red list and Birds of the world) as well as citizen science programs (such as eBird). More recently, species-level data on traits, habitat preferences and diet have also been published. The availability of such comprehensive resources not only allows us to compare new findings to what we know of bird distributions in various contexts around the world, but also facilitates the exploration of relationships between distribution patterns and the ecology of species.

Birds from this region are known to undertake both long as well as short distance annual migrations. However, details on the seasonal movement of birds from this region are yet to be documented. Globally, very few studies have looked at altitudinal migrations, and we have not come across any studies that have specifically looked at this in the eastern Himalayas.

1.4 This Dissertation

This study is an attempt towards identifying a framework that allows investigations into the processes that determine species distributions. While mechanistic models are essential for progress beyond phenomenological patterns, the complex and multivariate nature of most landscapes renders such models empirically unverifiable.

We posit that montane elevational gradients are a category of systems that may be suitable test-beds for frameworks that invoke ecological processes to make predictions regarding the shape of species distributions. Using robust and ecologically meaningful parameters and anchored to such frameworks, we investigate elevational profiles of abundances for ~ 280 species of birds (~ 35000 individuals) recorded along a mountain slope in the eastern Himalayas.

In **Chapter 2**, we provide detailed descriptions of the study site, sampling design, as well as the statistical methods used in our analyses.

In **Chapter 3**, we revisit the Abundant Centre Hypothesis, a widely investigated biogeographical pattern with much confusion regarding its validity, recast in the light of a mechanistic model.

In **Chapter 4**, we test hypotheses that represent different scenarios of density-driven movement towards harsher environments by investigating the relationship between distribution width and abundance.

In **Chapter 5**, we look at altitudinal migrations in our bird community, and how they modify species distributions. We also look at relationships between species' migratory propensity and their traits, habitat and diet preferences, as well as their phylogenetic relatedness.

Besides proposing a step towards a better understanding of the ecological determinants of species distributions, this study also provides novel information on an under-studied tropical montane biodiversity hotspot.

2 | Field Data and Analysis

2.1 Study Area

2.1.1 Eaglenest Wildlife Sanctuary

Field sampling for our study was conducted in Eaglenest wildlife sanctuary (hereafter EWS), a protected area of $218km^2$ in the West Kameng district of western Arunachal Pradesh (Figure 2.1). Situated between 27°02' - 09' N and 92°18' - 35' E, it is bounded by the Eaglenest ridge and the Bugun community reserve forest to the north, the Sessa orchid sanctuary to the north-east, the Bhalukpong-Bomdila highway to the east, Doimara/Shergaon reserve forests to the south and the forests of the Sherdukpen community to the west. The Eaglenest and Sessa ridges (2700 - 3250 m) are the first major barriers to monsoon clouds as they move northwards from the plains of Assam. As a result, they get over 3000 mm and 1500 mm of rainfall on the southern and northern slopes respectively (Athreya, 2006).

The Eaglenest road (Figure 2.1) was part of the first motorable road between Tawang and Assam, constructed by the Indian Army in the late 1950's. It remained undisturbed for over 30 years owing to the subsequent construction of the neighbouring Bhalukpong-Bomdila highway. The army resumed construction in a short section of the road in 1996, which was finally halted by a judicial stay in 1998. The forests have recovered considerably since then, and this road now provides vehicular access to contiguous pristine forests from 100 - 3250 m.

Lower elevations are quite warm in summer (>25°C in May-June), while higher elevations remain pleasant when dry. However, overcast/rainy weather and cold winds from nearby snow-laden ridges can cause a substantial temperature drop any time of year. February is the coldest month, with occasional snowfall above 2000 m. The principal rainy season lasts from June to October, with occasional spells in March and April as well. Though the region is prone to rain and fog all through the year, December is the driest month of the year (Mungee, 2018).

The large diversity in environmental conditions has given rise to diverse habitat types

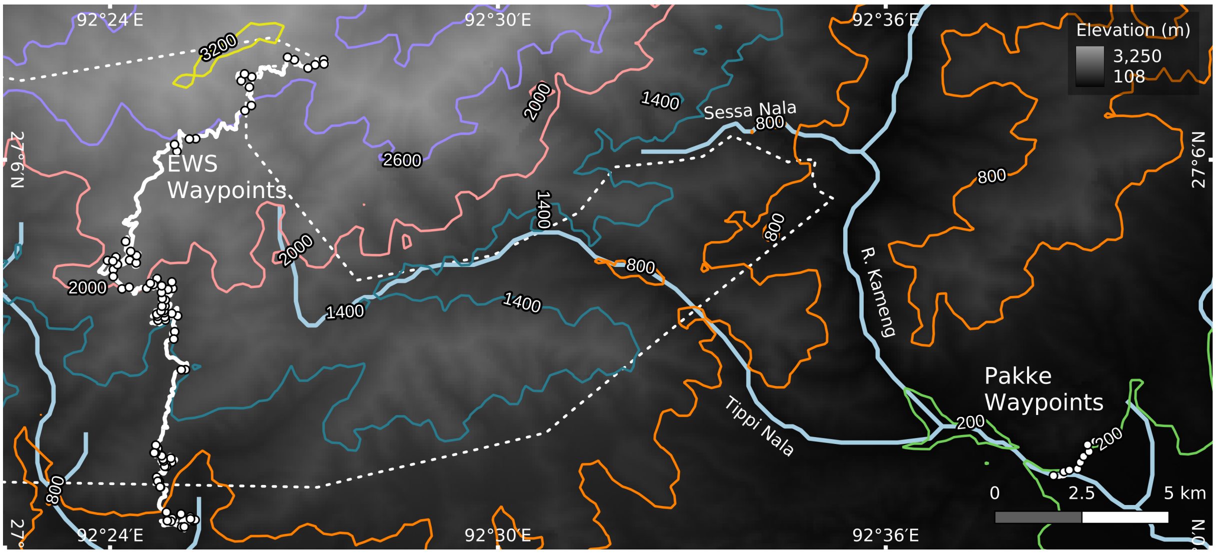

Figure 2.1: Elevational transect in Eaglenest Wildlife Sanctuary. *The plot shows the elevational contours and sampling locations. The 49 Eaglenest transects in 500-2800 m are along a vehicle track. The Eaglenest ridge at 3200-3250 m is shown in yellow.*

ranging from tropical wet evergreen (below 900 m) to coniferous temperate forests (>2800 m). Forests below 600 m are mostly tropical semi-evergreen (dominated by *Amoora wallichii*, *Pterospermum acerifolium*, *Stereospermum chelonoides*, *Altingia excelsa*) and tropical evergreen (*Kayea assamica*, *Mesua ferrea*, *Dysoxylum procerum*, *Echnocarpus sp.*). Tropical wet evergreen forests dominate from 600 to 900 m with a preponderance of species like *Phoeba paniculata*, *Actinodaphne obovata*, *Alnus nepalansis*, *Phoebe attenuata*. This is followed by sub-tropical broad leaved forests from 900 to 1900 m, 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).

An *a priori* checklist of the bird species found at our study site (Athreya, 2006) made birds a practical choice for our study. Since EWS is home to nearly 450 different species of birds (Figure 2.2), studying them allowed us to look past species-specific idiosyncrasies and identify general patterns at the community level arising from the influence of the environment. Furthermore, observed patterns for a highly vagile taxa like birds in a compact montane ecosystem is conservative in some sense - we expect these patterns only to be more definitive in case of more sessile species.

Figure 2.2: Some of the birds of Eaglenest Wildlife Sanctuary.
Left to Right: Rufous-necked hornbill (Aceros nipalensis), Sultan tit (Melanochlora sultanea), Bugun liocichla (Liocichla bugunorum) and Ward's trogon (Harpactes wardii). Image credits - Rohan Pandit.

2.2 Field Sampling

Several comprehensive resources are available as aids for choosing an appropriate sampling technique (Bibby et al., 2000). Available options include point counts, line transect surveys, mist netting, radio-tagging among several others. The choice of sampling method depends both on the data requirements as well as budgetary constraints of the study. We chose the line transect method for its several advantages in the context of our study. Firstly, the relative ease in spotting and identifying birds makes them a suitable taxon for transect surveys. Secondly, since we were only interested in the number of individuals of each species and did not need to capture or tag individuals, line transect surveys were sufficient in our case. Thirdly, line transect surveys are known to yield higher number of observations as compared to point counts (Järvinen, 1978). Finally, laying line transects was convenient in our study area as a dirt track allowed easy access to all target elevations which helped us identify transects that were sufficiently distant from one another.

Large-scale surveys are known to struggle with observer biases as they rely on observations made by multiple individuals with varying levels of expertise (Faanes & Bystrak, 1981). All birds in this study were recorded by a single observer, Rohan Pandit, with several years of experience in EWS. Pandit recorded bird abundances at (50 m elevational intervals) from 500 to 2800 m along our compact transect. Each 200 m transect was surveyed during a steady walk up and down (5 minutes each way) on 12 different days between May 02 and July 03, 2012-2014 in summer and between January 13 and March 13, 2012-13 in winter (Figure 2.3). Since we recorded birds along the same transect in both summer and winter, we also investigated altitudinal migrations. All individuals within 20 m from the path, detected visually or aurally were recorded. Elevations below 500 m were inaccessible in EWS, so in 2016, 4 transects (12 replicates each) were sampled

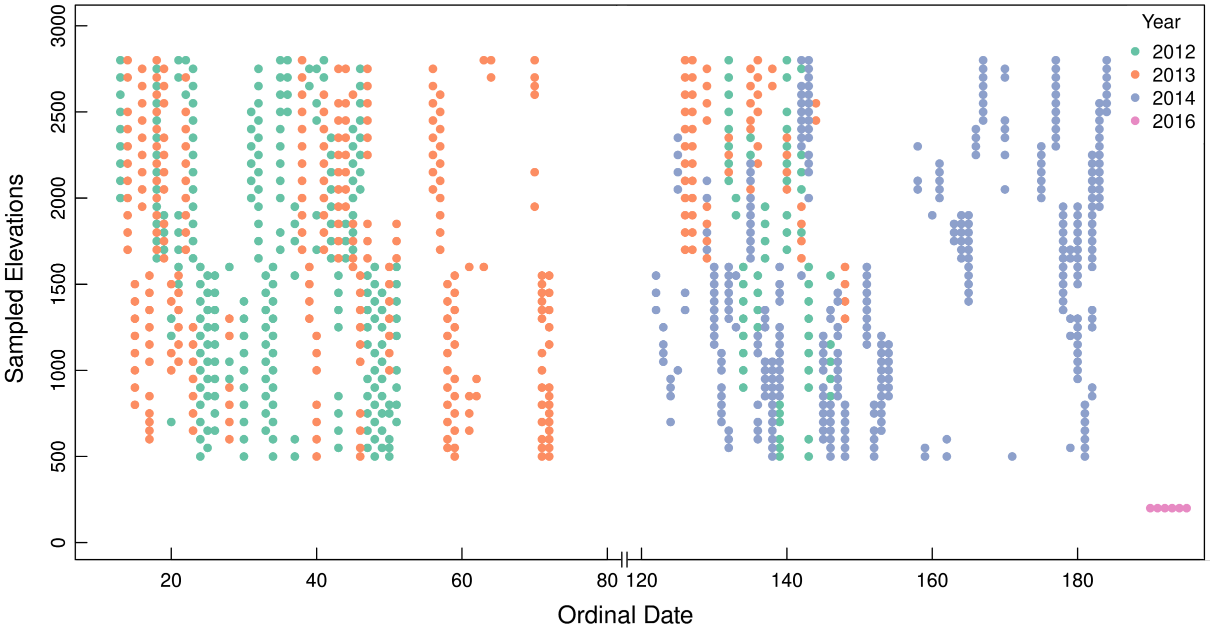

Figure 2.3: Distribution of sampling dates and transect elevations. *The ordinal date values are 13 for January* 13^{th}, *73 for March* 13^{th}, *122 for May* 2^{nd} *and 184 for July* 3^{rd}.

in the neighbouring Pakke Tiger Reserve (25 km away) across the Kameng river gorge (Figure 2.1). The 200 m observations were only used to determine if species distributions extended significantly below 500 m.

All observations were made during 0600-1200 hours, covering up to 12 elevations per day. Systematic biases in bird activity were minimised by distributing the 12 transects equally across three 2-hour slots – early morning (0600-0800 hrs), mid-morning (0800-1000 hrs) and late morning (1000-1200 hrs). Pandit used a motorcycle to commute from one transect to the next, as he was required to cover transects spanning $\sim$ 20 km every day. This meant that every transect was traversed twice in quick succession to get back to the vehicle. Though there potentially was a risk of having correlated records, the probability of sighting the same bird twice was highest at the far end, but variable across the transect. Therefore, birds were counted during both onward and return traverse (observations maintained as separate sets A and B).

2.3 Statistical Methods

One of the prime objectives of this study was to identify a procedure to parametrize species distributions in a statistically robust and ecologically relevant manner. Our field observations yielded abundance profiles for $\sim$ 280 species along a uniformly sampled elevational gradient. We explored several metrics of central tendencies (i.e., mean, median and modal elevations), distribution widths (i.e., min-max range, inter-quantile range and standard deviation), profile shape and asymmetry. Procedures for obtaining estimates all these metrics as well as their associated errors are described in the following subsections.

2.3.1 Abundance Profiles

Species-wise elevational abundance profiles were constructed by adding observed abundances from all replicates at each 50 m elevational "bin". With regards to deciding between sets A and B, we tried two ways of defining abundance for each species: $N_T \equiv (A+B)/2$ and $N_T \equiv Max(A,B)$. There was neither any obvious correlation, nor any significant difference between the two sets. Therefore, using either one of the sets resulted in little else other than a reduction in the number of records. Therefore, we used $A+B$ as our abundance measure for each transect replicate. Conceptually, this is equivalent to recasting our dependent variable from *abundance* to the *product of abundance and the time period for which a habitat is utilized* and will not change any of the final conclusions. Further, correlation between replicates is likely to have the same effect on statistical analysis as flocking and will result in underestimating the counting noise. Since we estimated the counting noise empirically from the data (see Estimating Errors below), any weak correlation between the two sets will manifest as noise in excess of the Poisson dispersion.

The counting error on a Poisson-like process depends on the absolute number of individuals counted in a particular spatial/temporal interval. In general, one is unlikely to spot all the birds of a species within the 20 m strip on either side of a transect. Since all transects were in a similar habitat structure - along a vehicle track passing through good forest, we do not expect much of a variation in detectability for a particular species at different elevations. This implies that the actual number of birds in any transect is the observed count scaled up by an unknown multiplicative factor. Though this can change the absolute counts and consequently the counting error, the use of an empirically determined Poisson factor (Figure 2.10) includes the contribution of this unknown detectability factor as well.

We examined each species for elevational movement across the sampling period by looking at the relationship between the elevation and ordinal date (regardless of year) of all records for each species. Only nine species in summer and six species in winter showed a significantly positive correlation (Figure 2.4). Translating their elevations to a standard date of June 30 for summer and January 30 for winter made no discernible difference to the community-level patterns we report. Thus, they were retained in their uncorrected form in further analyses. Interestingly, there were quite a few species that exhibited a

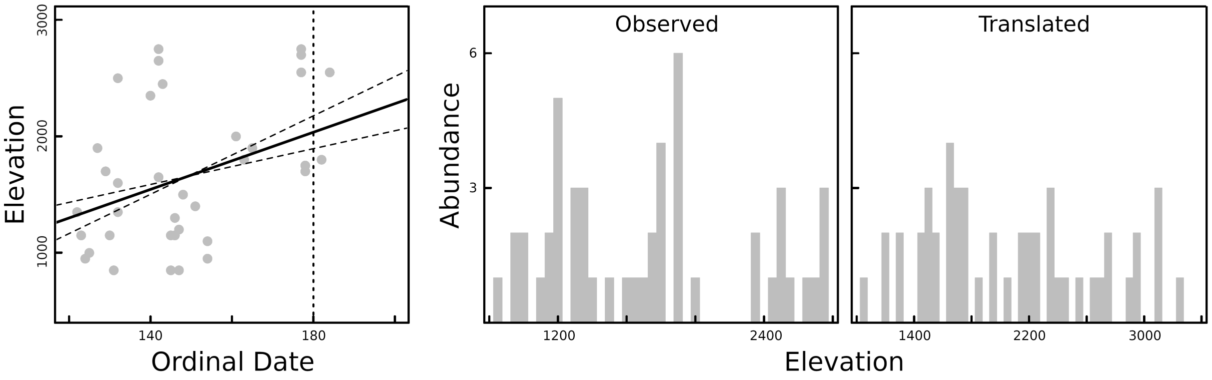

Figure 2.4: Correcting profiles for intra-seasonal movement.
We found a positive relationship between elevation and sampling date for 9 summer and 6 winter species. The correction performed on Eumiyas thallasina's summer profile is shown here. The regression slope (left) was used to translate the observed profile (centre) to the 180^{th} *ordinal day. Using the corrected profile (right) made no difference to the community-level patterns reported.*

negative trend between date of sampling and elevation in both seasons. This is somewhat unusual in the light of our knowledge of the seasonal movement of birds in the eastern Himalayas. Assuming that these are statistical artefacts provides an estimate of the error for the positive slopes.

In our study, elevation is the independent variable and is linearly correlated with ecologically crucial environmental factors such as mean annual temperature and precipitation, as well as vegetation indices (Mungee & Athreya, 2020).

Compilation of all records for a particular species resulted in an elevational abundance profile with unknown (presumably, well-behaved) stochasticity in abundances at each elevation. The eligibility of individual profiles for analyses was examined on four accounts: their total abundance, the number of elevations with non-zero records, a preliminary estimate of profile shape and whether or not our range of sampled elevations included the complete distribution of the species. Determining the first two among these was straightforward.

An estimate of profile shape was essential to shortlist species for certain analyses, but this was difficult for the *raw* profiles. To estimate the approximate shape, we smoothed each profile with the smallest full-width smoothing scale (from among $0.5 \times SD$, $1.0 \times SD$, $1.5 \times SD$ and $2.0 \times SD$) that rendered unimodality. A smoothing or moving window average operation allows only immediate neighbours to influence the value at each point, thus improving the signal to noise ratio while retaining information locally. This shape estimate was primarily used to determine whether the profiles were unimodal or multimodal, and to what extent the elevational range that we sampled covered the distribution

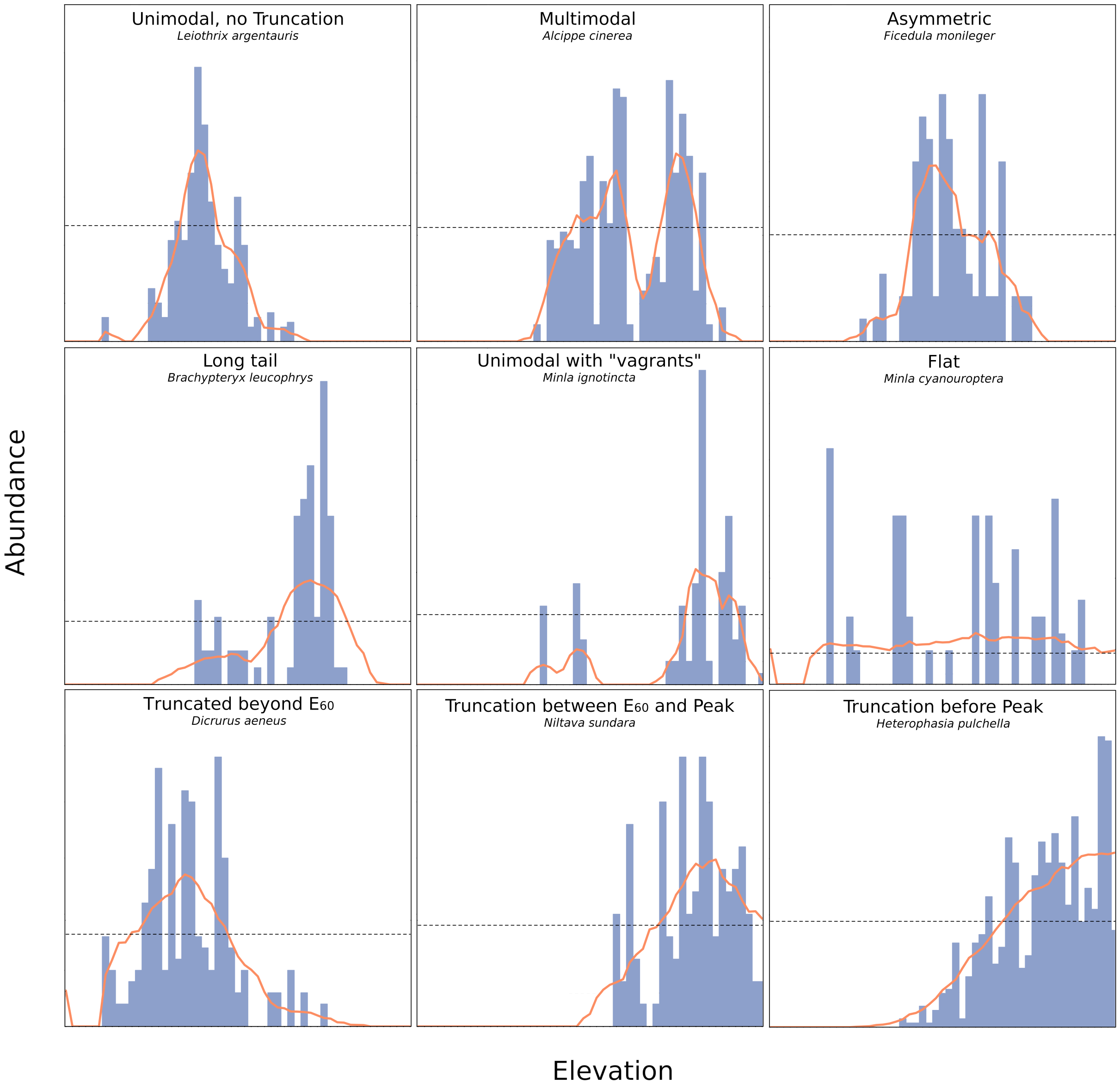

Figure 2.5: Examples of species abundance profiles in our dataset.
Blue bars represent the observed abundances at each elevation, while the orange line represents the smoothed values. The horizontal dotted lines are at 60.65% *of peak abundance. Profiles which were unimodal and untruncated were used in the study.*

of the species (Figure 2.5).

2.3.2 Estimating Central Tendency

We estimated species mean elevation in the usual manner. We determined the median elevation by uniformly distributing the counts within each 50 m elevational bin, followed by 2-point interpolation. This ensured that our estimate was no longer limited to the 50 m resolution of our data. To estimate the modal elevation, we coerced profiles to unimodality by smoothing (procedure same as above). The chosen full-width factor was

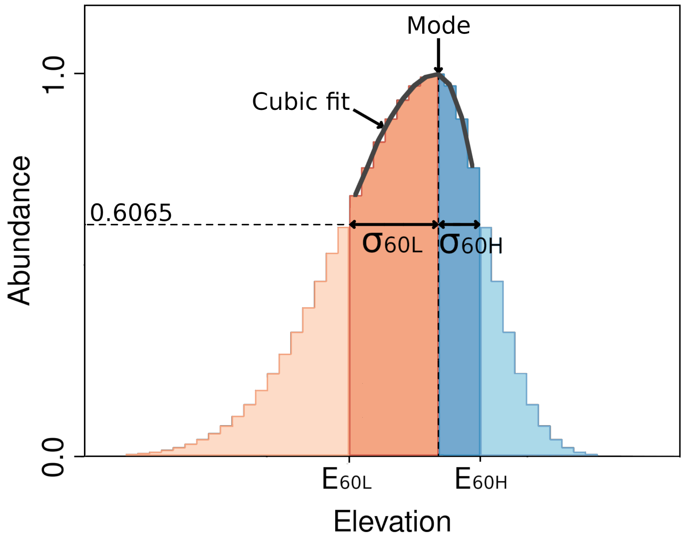

Figure 2.6: Estimating abundance peak and distribution width.
The abundance peak was located by determining the maximum of a cubic fit to the smoothed abundance profile. We then estimated distribution half-widths on either side of the peak using simple RMSD, total abundance and the scale-length of decline to 50% of peak abundance.

the smallest width that yielded a single peak with a monotonic decline out to 60% of the peak on either side. Profiles with persistent multiple peaks even at 2.0xSD were excluded from the analysis.

Since we were interested in estimating profile asymmetry, we modelled profiles as bigaussian or two-part normal distributions (Wallis et al., 2014, Figure 2.6). Such distributions can be completely described using four parameters: mode, RMS deviation on either side of the mode (σ_L and σ_H) and peak or total abundance. Asymmetry may be quantified as departure from symmetry by comparing the profile width on either side of the peak.

Any continuous differentiable function in a suitably small span can be represented as a polynomial, in which the higher order terms can be ignored. A cubic function is the lowest order polynomial that allows asymmetry about a peak. Therefore, we estimated the mode (at a higher resolution than 50 m resolution of the data) by fitting a cubic in a neighbourhood of ± $1.0SD$ around the maximum of the smoothed observed profile. It should be noted that this smoothing was only used to determine the location of the peak. Both modal abundance as well as elevation were obtained from the maximum of the cubic fit.

Smoothing tends to modify the location and height of the peak for asymmetric dis-

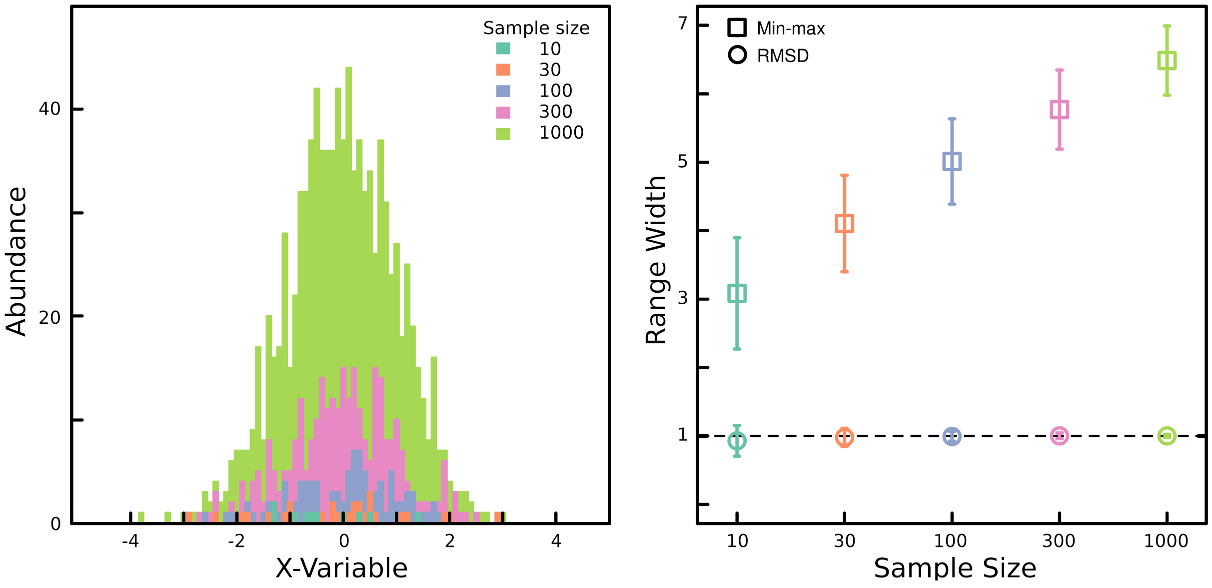

Figure 2.7: Outermost records are heavily dependent on sampling effort. *Left: Different magnitudes of sampling effort are akin to samples of different sizes being drawn from the same normally distributed population. Right: Range extents determined (from 1000 simulated distributions for each sample size) using outermost records is impacted by extreme outliers and show large variations regardless of the size of the sample drawn. Width estimates based on standard deviation or inner-quantile widths are far more robust.*

tributions. We quantified these offsets using simulated profiles (N = 10000, to minimise stochastic noise) with the following range of input parameters: σ_{iL} and σ_{iH} : 100-1000 m in steps of 50 m; smoothing width W_S: 0.5-3.0 × SD in steps of 0.5 SD. We measured the shift in the peak along with the resulting (output) σ_{oL} and σ_{oH} and created a look-up-table for reference values of W_S, σ_{oL} and σ_{oH}. We matched the output values σ_{oL} and σ_{oH} to the look-up table and corrected for the shift in the observed peak.

2.3.3 Estimating Profile Width

We considered several metrics to define the width of species distributions. The most prevalent width definition in the literature is the distance between the "outermost" records for a particular species. In the context of an elevational gradient, this would correspond to the difference between the lowest and highest elevation records (min-max width). However, such estimates can change considerably with sampling effort and vagrant records (Figure 2.7). Vagrants found far away from the bulk of the population are a regular feature in studies of wind-borne organisms, especially in montane landscapes where they can be blown across their entire range fairly quickly. Therefore, width metrics referenced to the outermost records are likely to be error-prone and may not even be of ecological relevance to the bulk of the species (Gaston, 1990).

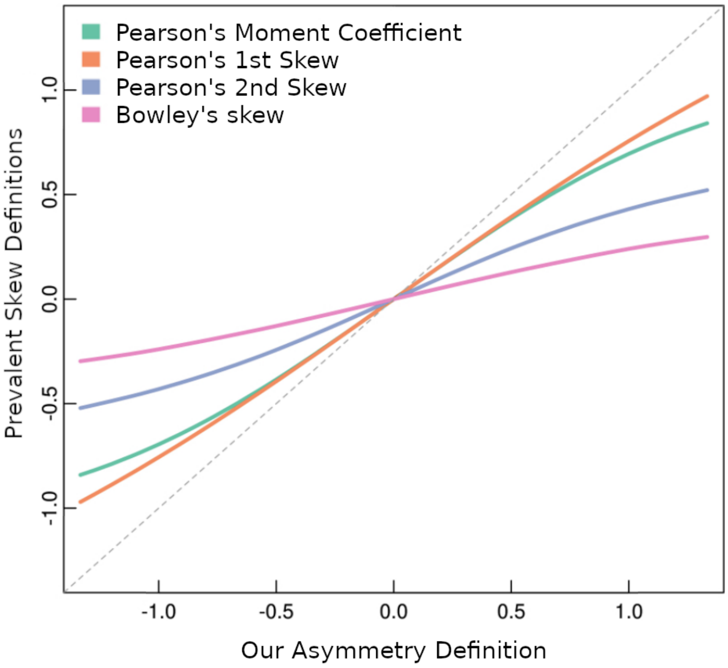

Figure 2.8: Prevalent skewness definitions vs. Asymmetry.
Commonly used definitions of skewness have a symmetric and tightly correlated relationship with our asymmetry definition.

In this regard, quantile and root-mean-squared-deviation (RMSD) based width estimates have several advantages. For one, they are well-defined for various different profile shapes, including infinite profiles such as gaussian distributions. For another, they make use of all the data (as opposed to just the two outermost records) and are therefore less impacted by vagrants and outliers. Additionally, RMSD is defined with respect to a measure of central tendency which is relatively more stable and can therefore be estimated more reliably than min-max width. Thus, subject to their eligibility (which will be discussed in subsequent chapters), we estimated the conventional min-max width, RMSD with respect to both mean and modal elevations, as well as the inner 95 percentile width for each species profile.

2.3.4 Estimating Profile Asymmetry

We estimated profile asymmetry using *half-widths* - root-mean squared deviations σ_{SL} and σ_{SH} on the lower and higher side of the abundance peak (mode) respectively. We defined asymmetry as

$$A_S = 2\frac{(\sigma_{SH} - \sigma_{SL})}{(\sigma_{SH} + \sigma_{SL})}$$

A_S ranges between -2 and $+2$ and is zero for symmetric profiles. There are several definitions of asymmetry or *skewness* prevalent in the literature (Figure 2.8), many of which involve the computation of third moment which is error-prone for low quality data. Our asymmetry definition is likely to be relatively less erroneous, especially for species with fewer records, and has a simple relationship with prevalent skewness definitions.

In case of bigaussian distributions, the same value of asymmetry can also be obtained by substituting σ_{SL} and σ_{SH} by other parameters such as (i) the total abundance on either side of the mode, N_L and N_H (number asymmetry A_N) and (ii) the elevational interval over which abundance declines to 60.65% of the peak, σ_{60L} and σ_{60H} (Scale-length based asymmetry A_{60}). For a gaussian distribution, this interval corresponds to one standard deviation. While both A_S and A_N are impacted by any section of the profile extending beyond the sampled range, A_S is sensitive to the distance of the records from the peak while A_N is not. A_{60} on the other hand, measures asymmetry only in the central $\pm$ $1.0SD$ of the distribution. A_S and A_N were estimated from the profiles as is, while smoothed profiles (procedure same as above) were used for A_{60} estimation.

2.3.5 Estimating Profile Shape

Broadly, we were interested in determining whether observed species profiles were best described as distributions with (i) a peak as well as tails or a peak but no tails. These shapes can be represented by gaussian or inverted-quadratic distributions respectively. One recipe for this would be to (i) fit both models to the observed data by turn, (ii) derive a goodness of fit (e.g.,χ^2) and (iii) use some criteria to pick one of the two as the best fit. This process has two disadvantages which could vitiate the entire exercise. Firstly, fitting a non-linear curve is not straight-forward and the fitted parameters will end up with large error bars, especially for the quantum of records we have for individual birds. Secondly, a two-step process, i.e., first identifying the best gaussian and best quadratic; and then determining which of the two is better - further reduces our ability to discern between hypotheses.

Instead, we “measured” profile shapes using the kurtosis (K) parameter which is characteristic of families of distributions: $K_G = 3.0$ for all normal distributions regardless of mean and SD and $K_Q = 2.14$ for all $\cap$-quadratic distributions. Kurtosis involves the fourth power of the coordinate in both the numerator and the denominator which results in large errors for small datasets. Therefore, we calculated the kurtosis for species-averaged community profiles for groups of species. The elevational profile of each species was normalised using $E_N = (E - E_M)/\sigma_E$ and $F_N(E_N) = N(E_N)/NT$, where, E_N is the normalised elevation, F_N is the fractional abundance at elevation E_N, E_M is the modal elevation, σ_E is the elevational SD, $N(E_N)$ is the unsmoothed abundance at elevation E_N, and N_T is the total abundance for the species. The normalised profiles of all the contributing species were averaged at each elevation after weighting it with the inverse of the variance. Finally, we smoothed the species-averaged profiles with a full width kernel of 1 unit and estimated their kurtoses.

We used simulations to determine the dependence of kurtosis on smoothing width and profile SD (Figure 2.9). Kurtosis was independent of profile SD for up to 600 m. The smoothing width, however, had some influence. We therefore estimated a weighted mean value of the expected kurtosis for gaussian and quadradic shapes considering smoothing scales for the species included in the analysis.

2.3.6 Estimating Errors

Flocking of birds, weather conditions and habitat heterogeneity may increase the dispersion of abundance counts above the Poissonian. Studies often use N-mixture models to obtain "true estimates" for abundance while accounting for flocking and detectability (Royle, 2004). However, this method relies on temporally as well as spatially replicated count data. Since we did not have spatial replicates, we smoothed observed species abundance profiles using a kernel width of five elevational bins. This was *our best estimate*

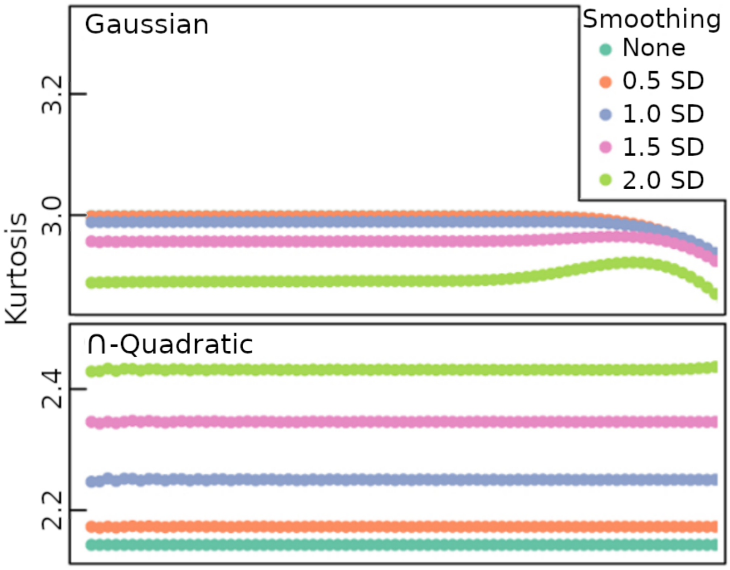

Figure 2.9: Impact of smoothing on the kurtosis.
Colours denote different smoothing levels going from no smoothing to a full-width of 2.0 times the standard deviation for simulated profiles. Even with smoothing, the kurtosis of gaussian (minimum 2.85) and ∩-quadratic (maximum 2.42) profiles are very different. The average predicted kurtosis for our smoothed elevational community samples were $K_G = 3.0$ *and* $K_Q = 2.23$.

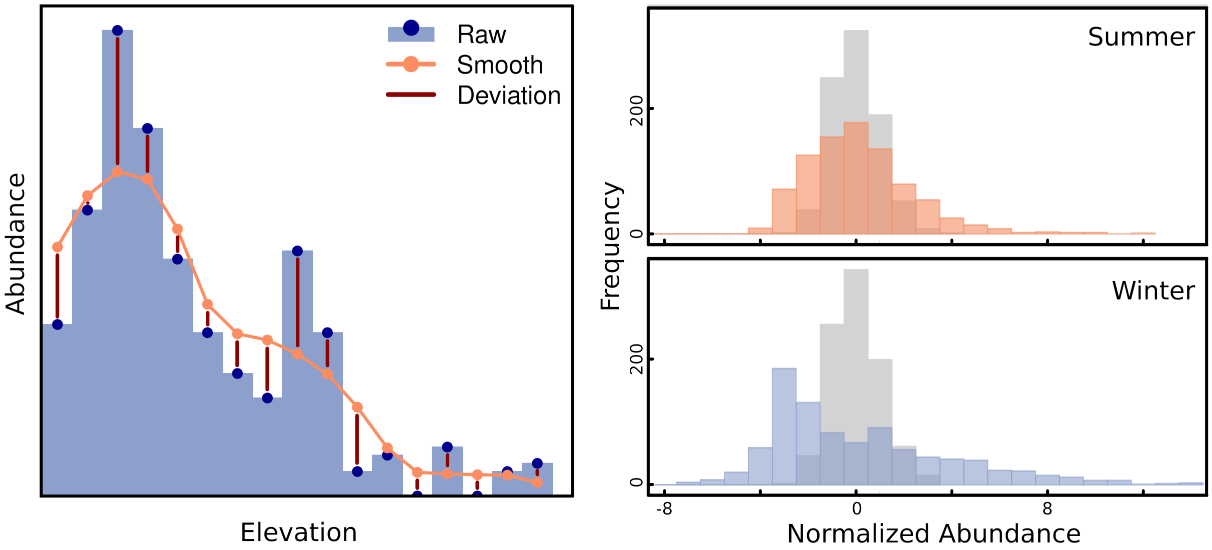

Figure 2.10: Estimating Poisson overdispersion in abundance.
Left: Stochasticity in abundance records was estimated using the difference between observed and smoothed abundances in each bin for each species. Right: We estimated the overdispersion in the summer and winter abundance records separately. The distribution of normalized abundances was wider than an equivalent Poisson distribution (grey) by a factor of 2.0 in summer (orange) and 3.4 in winter (blue).

for the true shape of each species profile, as the difference between the errors of this smoothed profile and those of the (unknown) "true" profile is a second order effect and can be ignored.

We then estimated the dispersion in counts using the difference between the smoothed $N_{SM}(E)$ and the observed $N_{OBS}(E)$ profiles (Figure 2.10). If $N_{OBS}(E)$ has an error statistic with standard deviation σ_ε in one elevational bin, smoothing it with a window of 5 bins yields an error statistic with standard deviation of $\sigma_\varepsilon/\sqrt{5} \approx 0.447\sigma_\varepsilon$. The difference between $N_{OBS}(E)$ and $N_{SM}(E)$ is another statistic with *mean* ~ 0 and $dispersion = \sqrt{(1 + 0.447^2)}\sigma_\varepsilon = 1.1\sigma_\varepsilon$. This should be valid for locally linear or low-curvature sections of the profile, i.e. all regions other than the peak. The statistic $Y = \{N_{OBS}(E) - N_{SM}(E)\}/\sqrt{N_{SM}(E)}$ should be approximately standard normal for bins with $N_{SM}(E) \geq 5$ and a standard deviation higher than 1.0 for this statistic indicates overdispersion. The corrected estimates of overdispersion were 2.0 and 3.4 in summer and winter respectively.

All profile parameter estimates of central tendency, profile width, asymmetry and kurtosis depend on the abundance profile in a non-linear manner, and some of these errors are correlated. Therefore, we used Monte Carlo simulations for error estimation. The poisson overdispersion factor (as estimated above), a negative binomial random number generator (*rnbinom in R;* R Core Team, 2021; Lindén & Mäntyniemi, 2011) and a model abundance profile to generate 400 simulated profiles for each species. The model profile for a species was the smoothed profile $N_{SM}(E)$ (kernel width = 5 elevational bins as described above) to which a 3-point linear interpolation procedure was applied to enhance smoothness. These profiles were processed in a manner identical to the observed profiles to obtain a set of 400 values for each parameter and each species. The simulated distribution function of these parameters (either standard error or the 95% confidence interval) were used as error estimates of the corresponding parameters.

2.3.7 Tests for Correlation

Most of the relationships that we looked at involved measurement errors in both variables. To check for correlation, we estimated both Pearson's (non-weighted) and Spearman's rank correlation coefficients. However, a simple linear regression was not appropriate in every case, since it requires a minimization of the sum of squared residuals in both x- and y- directions. Therefore, we used the *orthogonal* or *total least squares* regression method.

We suspected that computing perpendicular residuals for pairs of variables whose scales differed by orders of magnitude (for example, modal elevation ranging between 700 and 2500 m, and asymmetry ranging between -2.0 and +2.0) could be problematic. Therefore, we normalized measurements for each variable $[V' = (V_i - \mu_V)/\sigma_V]$, computed the regression for the normalized variables and then estimated the corresponding slope for the untransformed data.

We used an orthogonal regression in which each point was weighted by the sum of variances in the x- and y-directions to determine the slope of the regression, and the dispersion in the slopes from unweighted orthogonal regressions for the 400 Monte-Carlo iterations was our estimate of error on the slope. Functions for orthogonal regression are readily available in R. However, as has been discussed in some statistical papers, the weighted total least squares problem "has no closed-form solution and its computation involves solving a non-convex optimization problem" (Markovsky et al., 2006; Schaffrin & Wieser, 2007). It has also been shown that there exists a tight equivalence between the total least squares regression method and the maximum likelihood PCA (Schuermans et al., 2005). Therefore, we used the rotation from a weighted PCA (the *wpca* function from the *aroma.light* package in R) as our estimate for the slope of the corresponding weighted orthogonal regression. For relationships where we had error estimates for the y-direction alone, we used weighted ordinary least squares regressions.

3 | Identifying a Theoretical Framework for the Abundant Centre Hypothesis

3.1 Background

Brown (1984) recognised a general pattern with regards to distribution across a landscape, which seemed to hold for both plant and animal species - that "... density is greatest near the centre of the species' range and declines, usually gradually, towards the boundary". This gave rise to the *Abundant Centre Hypothesis* (henceforth the ACH) which although purely heuristic, is the most commonly tested macroecological pattern of the environment-adaptation-fitness paradigm even today. There have been hundreds of field studies over the past few decades to determine whether the ACH can be deemed a biogeographical rule (Sagarin & Gaines, 2002; Murphy et al., 2006; Rivadeneira et al., 2010; Fenberg & Rivadeneira, 2011; Baldanzi et al., 2013; Freeman, 2017; Pironon et al., 2017; Burner et al., 2019; Wen et al., 2020). However, most of these studies are almost entirely empirical in nature and have yet to result in a consensus.

A review of empirical studies about two decades ago found support for ACH in only 39% of 145 direct tests conducted in 22 field studies (Sagarin & Gaines, 2002). The situation has not clarified much since then (Santini et al., 2019), urging some to question the utility of looking for a general pattern (Sagarin et al., 2006; Gaston, 2009). Indeed, given the complex, multivariate nature of most landscapes, it is nearly impossible to identify one or even a few environmental variables that changing abundance may be attributed to. Perhaps the only secure conclusion from the welter of results amassed thus far across taxa and habitats is that ACH may not be valid in all contexts (e.g. Sagarin et al., 2006; Gaston, 2009).

Santini et al. (2019) identified a number of issues with previous studies that looked at ACH. These include confounding geographic/geometric and environmental/ecological def-

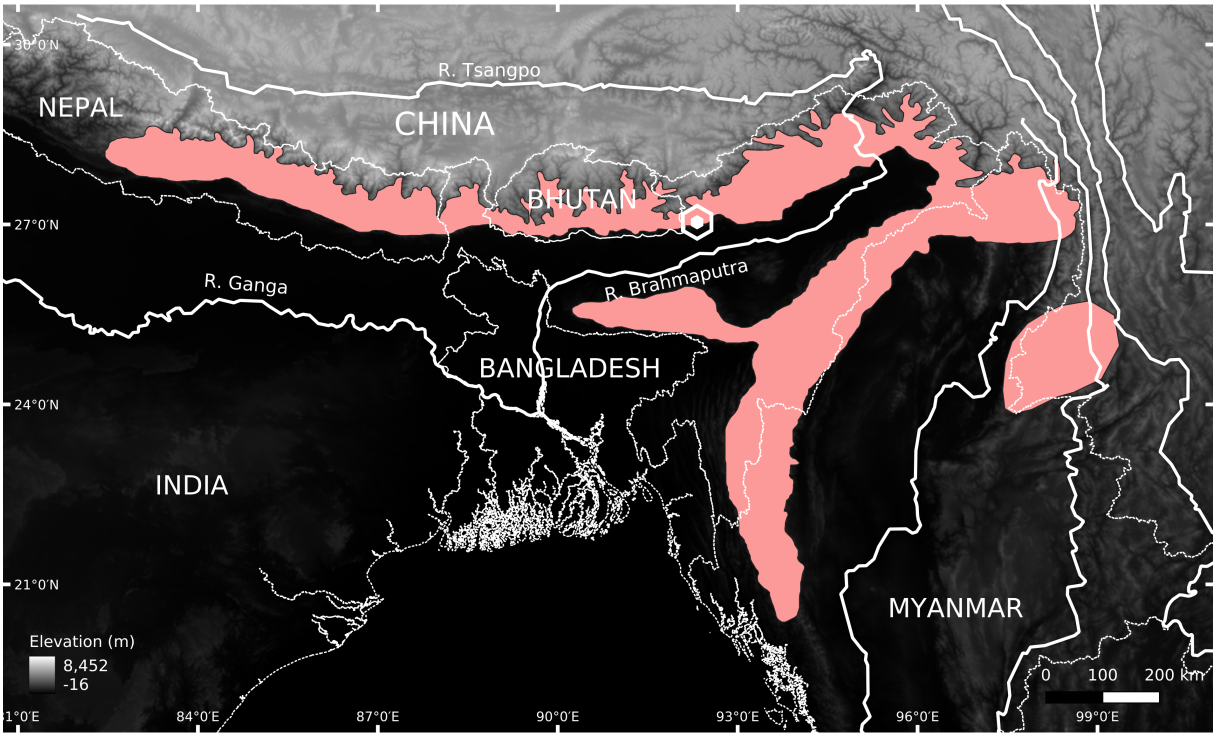

Figure 3.1: The typical distribution for species in our dataset. *The shaded region shows the global distribution of Actinodura egertoni. The geometric centroid of the complex shape has no ecological relevance and it may even lie outside the distribution. Pockets of absence of this species within the envelope will further complicate the issue. Our study transect lies within the spot inside the hexagon to the right of Bhutan.*

initions of a species range, multiple climatic variables across two-dimensional landscapes (also Sagarin & Gaines, 2002), confusion in terminology and definitions (also Borregaard & Rahbek, 2010), data quality (heterogeneity and insufficient normalisation for effort and species ecology), incomplete sampling of species ranges, and difficulty in separating location-specific patterns from peculiarities of particular species (Borregaard & Rahbek, 2010). Many of these issues are logistical or due to resource constraints.

We have identified two conceptual problems with the entirely heuristic and empirical approaches employed so far:

1. None of the previous studies have asked if ACH should at all have been expected at their locations.
2. The conflation of geography with environment, and the consequent confusion in identifying the "centre" of species distributions.

Studies typically described species distributions by the geographical coordinates of a convex polygon connecting the outermost records. Figure 3.1 shows the spatial distribution of a species from our dataset. The geometric centroid of the distribution may not even lie within it for some species; therefore it cannot be of ecological relevance in general. On the other hand, the determination of the ecological centroid is difficult in the absence of a theoretical framework which quantifies niche and fitness. Additionally, while patchiness of occurrence within the distribution (possibly at multiple scales), is expected to impact analysis and inference, there is logical circularity in weighting patches by abundance to determine the centroid (Sagarin et al., 2006).

Niche models have somewhat side-stepped ecological irrelevance by linking species abundance directly to environmental variables (e.g. VanDerWal et al., 2009; Martínez-Meyer et al., 2012; Dallas et al., 2020), but their entirely empirical approach makes mechanistic understanding of underlying processes difficult. Santini et al. (2019) weighted the locations using inputs from niche models (which itself is entirely empirical) but it did not improve the conclusions. Some have more appropriately interpreted the ACH as an increase in abundance away from the edge (e.g. Brown, 1984; Svensson, 1992; Telleria & Santos, 1993; Blackburn et al., 1999; Santini et al., 2019). However, this does little to establish a link between abundance and fitness.

3.2 Our Approach

3.2.1 Key Improvements

Our study differs from previous studies on four main counts:

Firstly, we used an established theoretical framework (Kirkpatrick & Barton, 1997, hereafter KB97) to identify an environmental context (a steep elevational transect in a large mountain chain) for which the ACH emerged as a prediction. The lack of a theoretical framework has contributed substantially to the dearth of progress in this field.

KB97 has incorporated several ecological processes (genetic diversity, directional selection of traits, intergenerational vagility) into a differential equation based on heat diffusion to investigate the evolution of a population trait across a 1-dimensional environmental gradient. Solving the equation along the environmental gradient under the assumptions of (i) a linear difference between the local population mean trait and the local environmental optimum trait (i.e. trait discrepancy), (ii) fitness being a quadratic (symmetric) function of trait discrepancy, and (iii) abundance being an exponential function of fitness - results in a gaussian abundance profile (Figure 3.2).

This prediction of a symmetric abundance profile - same as the formulation of the ACH - emerges naturally from a theoretical model based on ecological dynamics. Of

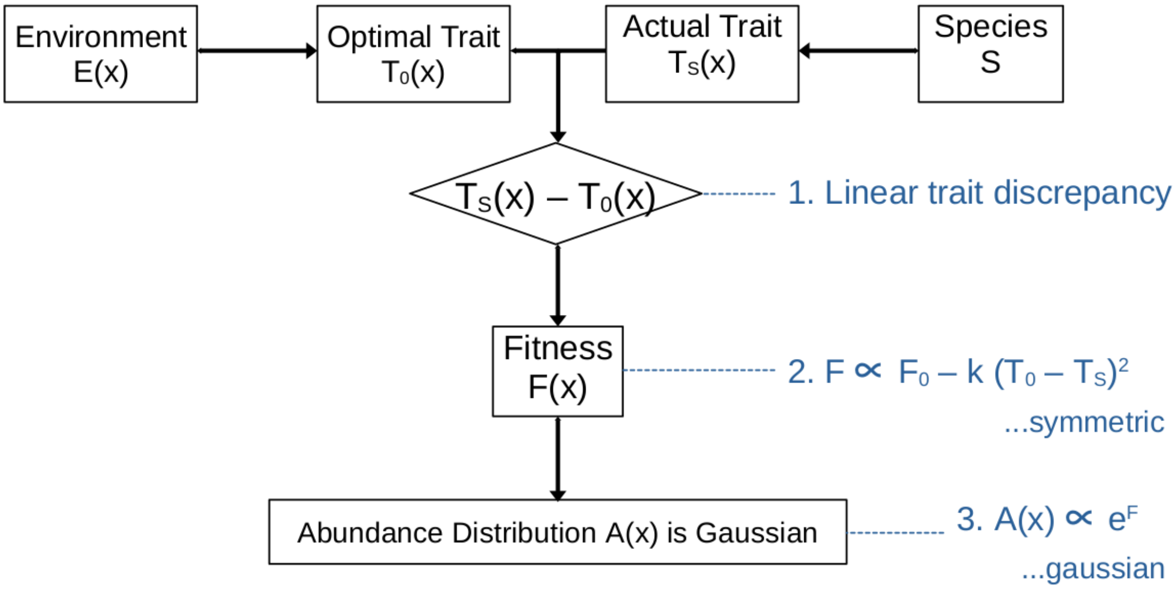

Figure 3.2: KB97 predicts an abundant centre.
The simplifying assumptions used in the model have been chosen such that they inherently introduce symmetry into the model, resulting in gaussian (symmetric) abundance profiles.

course, every environment-species context will have an associated abundance distribution as a testable prediction. However, dealing with the symmetry implicit in the ACH has observational and theoretical advantages. We also suspect that, generally, predictions of the ACH may be associated with simpler and hence mathematically more tractable environmental contexts. This would allow theory and observations to progress together and sustain each other. Even the rejection of ACH by data could contribute to progress by identifying inappropriate assumptions in the model - either (i) the trait discrepancy profile is not linear, or (ii) some assumptions were inappropriate, or (iii) KB97 is missing an additional ecological process (e.g. competition).

Secondly, through field observations we collected a large amount of primary abundance data ($\sim$ 280 species; 35147 individuals) across a large environmental gradient (2600 m in elevation) in a systematic manner (47 equispaced line transects under similar habitat visibility, 24 replicates matched for time of day across elevations; inside 3 years; by the same observer for uniformity). This facilitated the analysis of elevational abundance profiles for a *community* of birds.

Thirdly, we were able to measure species abundance responses along a relatively unperturbed environmental gradient. Montane elevation gradients are generally considered as effectively 1-dimensional (Freeman & Beehler, 2018) since changes in environmental variables are far steeper along the slope than along contours. Further, a previous study along this very same transect has shown that it is also essentially univariate as several biologically relevant environmental factors are tightly correlated with elevation (Mungee

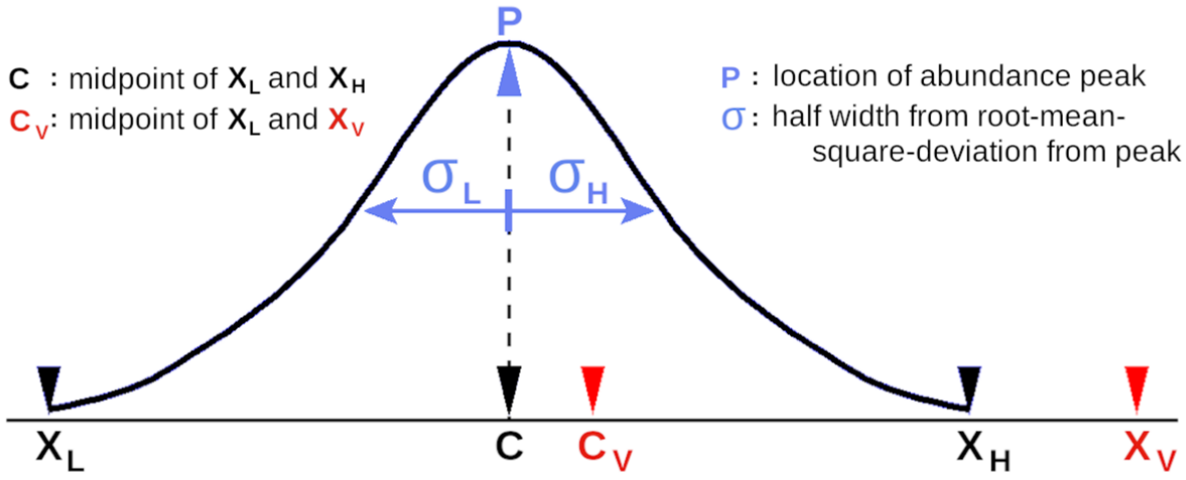

Figure 3.3: Our approach to the Abundant Centre Hypothesis.
X_L and X_H are the outermost records for a "well-behaved" distribution. Popular approach: The centre is expected to coincide with abundance peak and is determined from the two outermost records, ignoring all the rest. However, even a single vagrant record can bias this exercise substantially (C_V). Our approach: Half-widths (σ_L and σ_H) on either side of the abundance peak are estimated using all the data. If $\sigma_L = \sigma_H$, ACH is valid. Extreme outliers have little impact on our estimates of peak and half-widths.

& Athreya, 2020).

Finally, we shifted the reference for characterising range parameters from the peripheral populations to the abundance peak. Range edges are associated with small, fluctuating, sink populations (Hengelveld & Haeck, 1982; Brown, 1984; Lawton, 1993; Hoffmann & Blows, 1994). Vagrants far from the bulk of the population are a regular feature of organisms impacted by ocean and wind currents and human agency. This is even more problematic in montane ecosystems where a bird can fly (or be blown by wind) the short distance across its entire range in a few hours. Furthermore, as seen in chapter 2, the outermost records, can change considerably with sampling effort, especially in the presence of vagrants. Therefore, any metric referenced to the range edge is likely to be error-prone and may not even be of ecological relevance to the bulk of the species. The abundance peak is the ecologically relevant *centre* of a species range and the relatively large number of records at this location make its estimation statistically more stable (Figure 3.7).

Thus, we propose an ecologically more appropriate and methodologically more robust version of ACH. Instead of coincidence between the geometric centre and the abundance peak, we tested the ACH by symmetry of half-range widths on either side of the abundance peak (Figure 3.3). This shifts the reference from the sparsest, least reliable, parts of the range to the densest (i.e. most robust). With the peak as the reference the half-range width can be quantified using the bulk of the data, rather than the distance to just the two outermost records. One can even use robust statistics to eliminate sporadic outliers and focus on the bulk of the individuals. Additionally, the use of the entire data provides more meaningful error estimates for both peak position and half-range widths for robust hypothesis testing.

3.2.2 Issues Addressed

Our approach addresses several of the aforementioned issues with previous studies:

1. Anchor in a theoretical framework: We started with KB97 to link an environmental gradient to a particular abundance profile using standard ecological processes and the species' life-history traits. The formalism is applicable to a one-variable (univariate) environment with a gradient along one geographical dimension. Multiple environmental variables can be considered as effectively univariate if they are strongly correlated.

2. Study system: Our study site along an elevational transect is effectively a 1-dimensional and univariate environmental gradient (with elevation as the predictor for multiple environmental variables). Its compact size (projected rectangle 6 km x 15 km) avoids the impact of confounding variables like zoo-geographical history, geographical climate variability, etc. Crucially, the elevational transect spans the entire local environmental range of many dozens of species.

3. Theory predicts an abundant centre for a particular context: KB97 predicts the ACH is valid for a linear environmental gradient - a reasonable assumption with regards to our study system.

4. Statistically robust hypothesis testing: owing to our large and systematically collected abundance data set, as described earlier.

5. Modified metric for ACH: Instead of coincidence between the geometric midpoint (of the outermost records) and the abundance peak, we test the ACH by symmetry of range half-widths on either side of the abundance peak. This is a more robust metric as

    (a) it shifts the reference location from the sparsest regions to the densest

    (b) the two half-widths are estimated using the entire species profile rather than the just the two farthest records.

6. Multiple species: We target the entire bird community in a species-rich eastern Himalayan site with the expectation that we could average over asymmetries that arise due to interactions and idiosyncrasies of individual species to reflect the impact of the environment.

S. No.	Categories	Filters	No. of species in Summer	No. of species in Winter
1	Total Abundance (N_T)	$N_T \geq 30$	112	90
2	Elevations with non-zero records ($E_{N>0}$)	$E_{N>0} \geq 5$	108	77
3	Smoothed profile shape (full-width $\leq 1.5 \times SD$; Only species with $N_T \geq 30$ were considered)	Unimodal Multimodal Uniform	96 7 5	63 12 2
4	Profile truncation due to sampling limits	None Beyond E_{60} Between Peak and E_{60} Peak outside sampling limits	**51** **24** 8 13	**32** **16** 8 7

Table 3.1: Criteria used to determine suitability of species profiles for analysis.
Numbers indicate the number of species retained after every screening stage.
Numbers in bold font indicate the number of species used in final analyses.

3.3 Analysis

3.3.1 Species selection

As previously mentioned, each species in our dataset was screened for suitability before inclusion in analyses. Cut-offs based on minimum total abundance and number of elevations with species presence were essential for statistical security while examining profile shapes and symmetry. EWS ridge spans 100-3250 m, but only elevations between 200-2800 m were sampled for this study. Therefore, we only selected species distributions that were adequately covered by our sampling limits to ensure that our range parameter estimates were not impacted by truncated distributions. Only unimodal profiles were selected for the analyses in this chapter. Distant, secondary peaks were acceptable only if they were at least $\pm 3.0SD$ away from the primary peak and comprised less than 20% of the species total abundance. Only 75 of the 245 species recorded in summer and 48 of the 210 species recorded in winter were unimodal, sufficiently numerous and complete to at least 60% decline from peak abundance on either side - therefore suitable for A_{60} estimation. Further, only 51 summer species and 32 winter species were complete to less than 10% of peak abundance and allowed the estimation of A_S and A_N. Details on these estimates and their significance can be found in chapter 2. The selection criteria, along with the corresponding number of species that satisfied them are listed in Table 3.1.

3.3.2 Parameter Estimation

All the parameters mentioned in this section, along with their significance have been described in details earlier (chapter 2). We estimated the abundance peak (using cubic fit to the smoothed profile) and range half-widths based on scale length of decline (σ_{60}, and subsequently asymmetry A_{60}) for 74 and 47 of the species shortlisted in summer and winter respectively. Half-widths based on RMSD and total abundance (σ_S and σ_N) and were likely to be impacted in case profiles extended beyond sampling range. The corresponding asymmetry metrics (A_S and A_N) could be estimated only for the subset of complete profiles, since they take the entire distribution into account - A_S is sensitive to the distance of records from the peak, while A_N is not. A_{60} measures the asymmetry in approximately the inner $\pm 1.0 SD$ of the profile, and therefore could be estimated for partial profiles as well.

The overdispersion factor was estimated to be 2.0 and 3.4 for summer and winter respectively. We used this to estimate errors on all parameters of interest using Monte-Carlo simulations as described earlier. We also calculated Pearson and Spearman's correlation coefficients as well as the orthogonal linear regression for all three measures of asymmetry vs. the elevation of peak abundance.

We estimated profile shape by calculating kurtosis for species-average community profiles in 3 elevational bands - 800-1500 m, 1501-1850m, 1851-2600 m in summer and 700-1600 m, 1601-2200 m, 2201-2500 m in winter. The band limits were chosen so as to equalize the number of species included in each band.

Season	Asymmetry	N	Mean	SE	CI 95%
Summer	A_S	51	0.054	0.087	(-0.101, 0.239)
	A_N	51	0.069	0.079	(-0.122, 0.189)
	A_{60}	75	0.068	0.123	(-0.201, 0.290)
Winter	A_S	32	0.087	0.164	(-0.558, 0.078)
	A_N	32	-0.117	0.134	(-0.377, 0.140)
	A_{60}	48	0.125	0.156	(-0.328, 0.285)

Table 3.2: Community mean asymmetry of profiles in summer and winter. *All estimates are weighted by the inverse of variance from 400 Monte-Carlo iterations. The community mean asymmetry is consistent with the value zero, i.e. profiles are by-and large symmetric across seasons.*

Season	Relationship	N	r	CI 95%
Summer	$A_S \sim E_M$	51	-0.46	(-0.60, -0.29)
	$A_N \sim E_M$	51	-0.40	(-0.59, -0.18)
	$A_{60} \sim E_M$	75	-0.13	(-0.37, 0.12)
Winter	$A_S \sim E_M$	32	-0.68	(-0.88, -0.41)
	$A_N \sim E_M$	32	-0.50	(-0.74, -0.18)
	$A_{60} \sim E_M$	48	-0.15	(-0.46, 0.18)

Table 3.3: Correlation between asymmetry and elevation.
We determined the Spearman's ranked correlation coefficient for our data. The 95% confidence intervals were determined by Monte Carlo simulations of the observed profiles.

3.4 Results

The statistics of the community average asymmetry metrics are shown in Table 3.2. The mean asymmetry for the three metrics across seasons varied between 2.7% and 6.3%. The 95% confidence interval for all asymmetry estimates across 75 summer species and 48 winter species included $A = 0$, suggesting symmetry that the community as a whole was consistent with symmetry.

The correlation coefficient and linear regression for asymmetry-elevation relationships are shown in Tables 3.3 and 3.4, and Figure 3.4. Both correlation and regression analyses show a significant dependence of A_S and A_N on elevation across seasons, but not for A_{60}.

Average community profiles in 3 elevational bands, along with kurtoses of the corresponding half-profiles in summer and winter are shown in Figure 3.5. The analytical expected values for kurtosis are well defined and are constant for "families" of distribution shapes regardless of parameter values. Kurtosis for a gaussian profile (K_G) is 3.0, whereas for a $\cap$-quadratic (K_Q) is 2.14. Smoothing the profiles in the same manner as the data

Season	Relationship	N	Slope	CI 95%	p-value
Summer	$A_S \sim E_M$	51	-1.55×10^{-3}	$(-1.8, -1.3) \times 10^{-3}$	< 0.01
	$A_N \sim E_M$	51	-1.12×10^{-3}	$(-1.4, -0.8) \times 10^{-3}$	< 0.01
	$A_{60} \sim E_M$	75	-0.93×10^{-3}	$(-3.7, 5.5) \times 10^{-3}$	< 0.01
Winter	$A_S \sim E_M$	32	-1.87×10^{-3}	$(-2.3, -1.5) \times 10^{-3}$	< 0.01
	$A_N \sim E_M$	32	-2.22×10^{-3}	$(-2.7, -1.9) \times 10^{-3}$	< 0.01
	$A_{60} \sim E_M$	48	-0.83×10^{-3}	$(-2.7, 1.6) \times 10^{-3}$	0.42

Table 3.4: Linear Regression between asymmetry and elevation.
We determined the orthogonal or total least squares linear regression for our data. The 95% confidence intervals and p-values were determined from Monte Carlo simulations on the observed profiles. Unit of slope: Asymmetry/m.

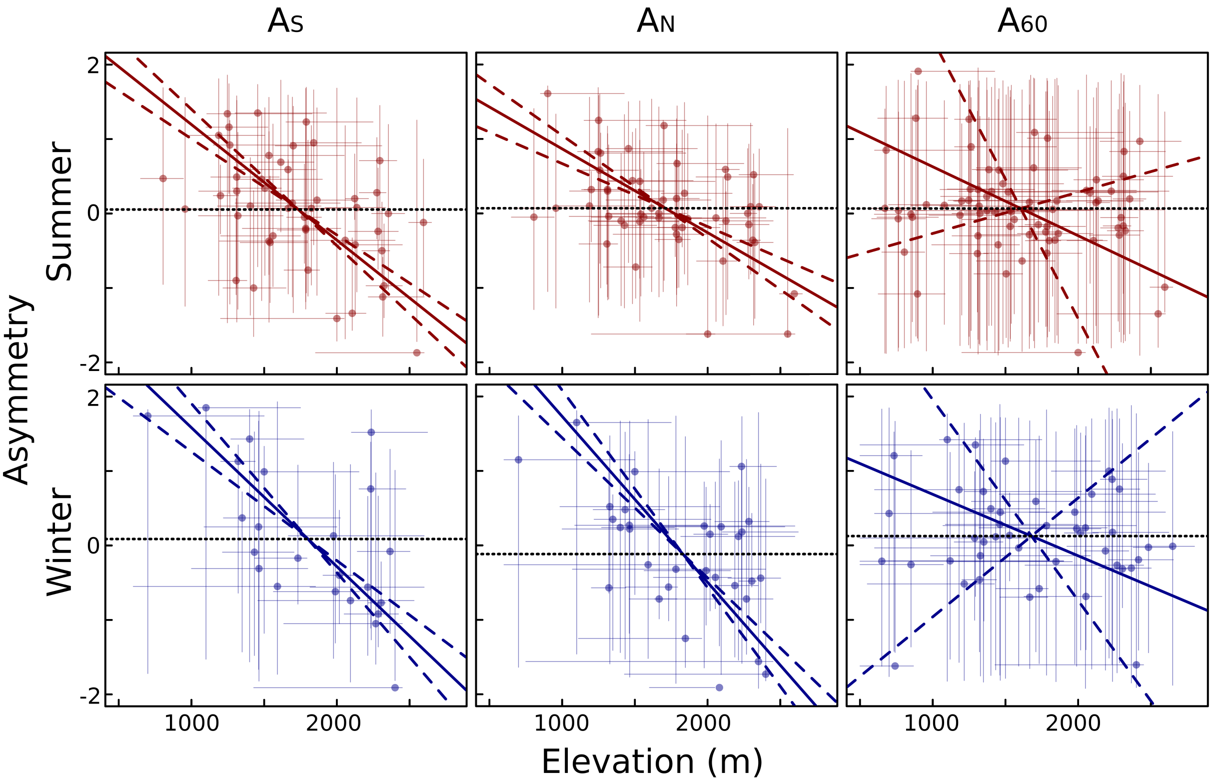

Figure 3.4: Linear Regression between asymmetry and modal elevation. *Summer data is shown in red, winter data is in blue. Solid lines denote the best fit and 95% confidence intervals of the slope are denoted by dashed lines. All error bars represent 95% confidence intervals. Corresponding regression parameters are listed in Table 3.4.*

marginally modified the expected values to 2.99 and 2.25 respectively. The mean kurtosis for the six half-profiles from our observations was 3.37 ($CI_{95}[2.71, 4.10]$) in summer and 3.23 ($CI_{95}[2.25, 4.47]$) in winter. Both these measurements were consistent with the expected kurtosis for a gaussian profile shape. Estimates from the summer profiles rejected the ∩-quadratic profile shape at $\alpha < 0.001$, while K_Q lay on the lower bound of the 95% confidence interval for the winter data.

These kurtosis values suggest that the community average profiles are consistent with gaussian, perhaps best described as leptokurtic in both summer and winter, i.e., are distributions that have a peak as well as tails.

3.5 Discussion

We studied the abundance profile of bird species within a compact region ($15 \times 6 km^2$ projected area) in a montane ecosystem in the eastern Himalayas. In a departure from the prevalent approach, we considered the ACH as a prediction of a theoretical model when applied to a particular environmental context. We suggest that recasting the ACH in

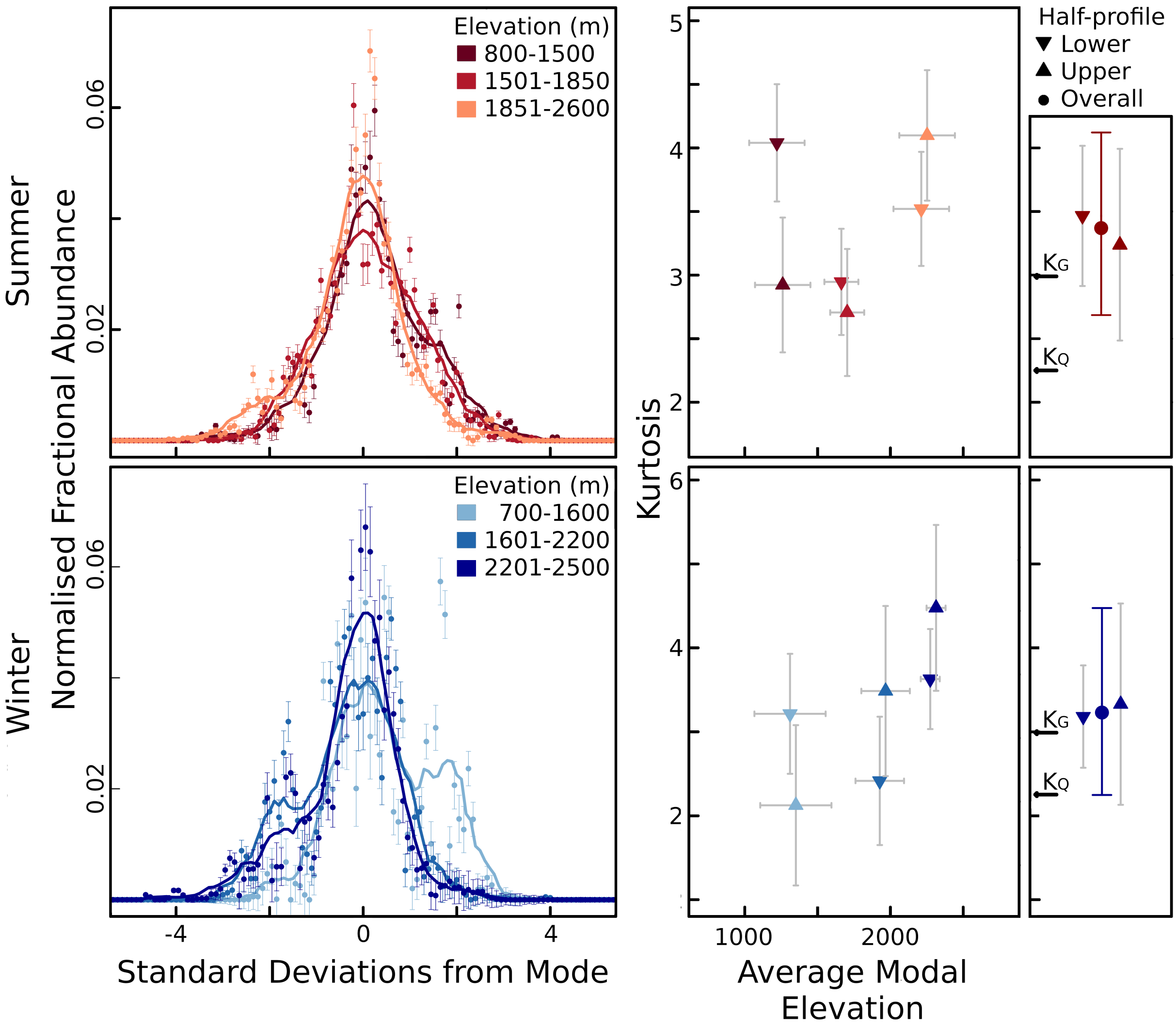

Figure 3.5: Community average profile shape in 3 elevational bands. *Left: The scatter and smoothed profiles were constructed by averaging the SD-normalised profiles of the species in the community for summer (reds) and winter (blues). Right: Kurtosis of half-profiles (split at the mode). The mean and ±1 SE values for each elevational band are shown in colour in the left half of the plot. Their weighted averages and 95% C.I. bars are shown separately for upper and lower halves (3 each) and overall (all 6) in the right half. The expected smoothed community profile kurtoses are also shown for reference:* $K_G = 2.99$ *for gaussian,* $K_Q = 2.25$ *for ∩-quadratic, and* $K_U = 1.95$ *for uniform distributions.*

terms of symmetry about the abundance peak is ecologically and methodologically more appropriate than seeking coincidence between the abundance peak and geometric centroid of a species range. We also parametrized distribution widths in a more robust manner using root-mean-squared-deviation and scale length of decline, rather than defining them solely on the basis of the sparse and unreliable outermost records.

We found that in both summer and winter, the mean asymmetry for the community of birds in EWS is consistent with zero and departures from symmetry in individual species profiles were consistent with expected measurement errors. This implies that the data for the community as a whole is consistent with the abundant centre hypothesis. We also found a significant negative correlation between asymmetry and elevation using the two metrics that considered the entire distribution, but found no correlation when we considered only the region around the peak. The community average shape for species distributions across both seasons was best described as one with a peak as well as tails (characterized as gaussian), and ruled out the ∩-quadratic profile shape (a peak but no tails) with a high degree of statistical significance.

Overall, observed trends largely remain conserved between summer and winter. However, the usable data we were able to obtain in winter was significantly less than that from summer. The *noisier* winter estimates prevented us from pursuing a more subtle comparison of patterns between seasons.

3.5.1 Grafting a theoretical framework onto ACH

Despite its simple and insightful formulation, we have not come across any study that tests KB97 - or any other theoretical framework describing the spatial distribution of individuals - with field data. We suspect that this is due to the daunting form that such differential equations may assume when applied to complex multi-variate environmental patterns in a two-dimensional landscape. Since the ACH emerges as prediction for a particular kind of environmental gradient, we approach the problem by first identifying a "simple" landscape for which KB97 yielded testable predictions. This, of course is true only under some simplifying assumptions (Figure 3.2), the details of which are discussed in upcoming sections.

Compact, one-dimensional landscape

Most landscapes across which species distributions are recorded are manifestly two dimensional in terms of geography and correspond to multiple environmental variables. KB97 is difficult to solve and is also limited in its utility in two dimensions. Nevertheless, one-dimensional analysis may be applied (with a suitable change of coordinate axes) if the environmental gradient is much steeper along one dimension as compared to the other. This is true of elevational transects, with environmental gradients being very steep along the slope and essentially zero along contours (Freeman & Beehler, 2018).

Coastlines have often been considered as one-dimensional systems in the ACH context since their length is typically orders of magnitude larger than their width (Sagarin & Gaines, 2002; Defeo & Cardoso, 2004; Sorte & Hofmann, 2004; Gilman, 2005; Wares

& Castañeda, 2005; Samis & Eckert, 2007; Tuya et al., 2008; Rivadeneira et al., 2010; Baldanzi et al., 2013). In our opinion, this may be inappropriate. Transects parallel to the coast may be effectively one-dimensional *geographically*, but not in the context of the ACH. Coastal species ranges in such studies span thousands of kilometres, with complex variations in multiple biotic, abiotic and anthropogenic factors and lack a "unifying" feature akin to elevation in montane gradients. A transect perpendicular to the coastline (e.g., the intertidal region), however, may be suitable for studying the ACH.

In a region spanning merely $75km \times 75km$ around our study site, the elevation changes from 100 to 5000 m ($\sim 30°C$ in mean temperature), while the highly folded 2000 m elevational contour traverses $\sim 1500km$ of essentially unchanging environment. Our 500-2800 m study transect fits into a projected area of just $15 \times 6km^2$ on the southern slope of the east-west oriented Himalayas. The temperature gradient across the transect corresponds to a latitudinal gradient spanning 2300 km. At such continental scales, other ecologically relevant aspects such as biogeography, ecology, geology as well as dispersal barriers change unpredictably and preclude the applicability of theoretical models. Our compact study site is far less likely to be influenced by such factors.

Optimizing a single trait v/s overall fitness of the individual

This is the major hindrance in translating environment and traits to fitness. The sampling effort required to map the interaction for multiple traits that determine survival for dozens of species that comprise a community is non-trivial. KB97 describes the spatial distribution pattern for individuals with *a* particular trait value across an environmental gradient governed by a single environmental variable. The fitness of an organism, on the other hand, is known to be influenced by multiple traits responding to multiple environmental variables. However, this may not be an issue for our study for several reasons:

1. If the fitness due to *a* trait results in a gaussian abundance profile, it is easy to show analytically that a combination of traits in a smoothly varying environment will also result in gaussian abundance profile. Further, simulations have shown that smooth gradients involving multiple environmental variables (and hence multiple response traits) in a 2-dimensional landscape can lead to a smooth unimodal abundance profile (Brown et al., 1995).

2. Multiple variables can be reduced to the univariate case if they are strongly correlated with one another.

Multiple environmental factors along a steep elevational transect are likely to be strongly correlated with elevation. This was certainly true at our study site: a principal component analysis of mean annual temperature, mean annual precipitation, plant productivity, and air density/partial pressure of oxygen yielded a first principal component (PC1) which accounted for 91% of the variance, and $R^2 0.95$ for the linear regression of PC1 and elevation (Mungee & Athreya, 2020). Therefore, elevation was an appropriate single-variable representative for the multi-variate environment.

Symmetry

KB97 links symmetry in the environmental gradient to that of the abundance profile, and this is key to the environment-fitness paradigm. In the model, the trait discrepancy gradient is linear and *antisymmetric* (magnitude symmetric about peak, but has opposite signs). They explicitly imposed this symmetry by defining fitness as a quadratic - *square* of the trait discrepancy function. In terms of analysis and logistics, the amount of data needed to invalidate a prediction of symmetry is far less than that for falsifying a particular abundance profile. Symmetry can be disproved by showing that a metric is dissimilar about a putative symmetry location (here, the abundance peak). In contrast, testing a predicted profile shape with data requires sufficient sampling effort at multiple locations along the environmental gradient. Therefore, at this early stage in testing theories it is perhaps simplest to identify environmental gradients for which models predict symmetric abundance profiles. These may be more frequent, or at least easier to identify, in compact one-dimensional and univariate landscapes than two-dimensional and multivariate landscapes at a continental scale.

Further, symmetry aids in mitigating the trait to fitness conundrum. Invoking Occam's razor we construct a “consistency” argument as follows: a symmetric fitness profile (as opposed to an arbitrary asymmetric one) is far more likely to give rise to a symmetric abundance profile. Ergo, a symmetric abundance profile observed along a symmetric (linear) environmental gradient is likely to have passed through a symmetric fitness function. This argument is somewhat circular, but self-consistent and the best that can be done at the moment for a quantity (fitness) that can neither be directly measured nor theoretically calculated.

Biotic v/s abiotic influences

Communities are shaped by a combination of external (abiotic) and internal (biotic) filters (Albert et al., 2012). The former push to converge species traits towards the local optimum, while the latter increase dispersion of traits within the community. KB97 only takes environmental factors into account and ignores biotic interactions. However, such interactions (especially interspecific competition) are likely to be a very important deter-

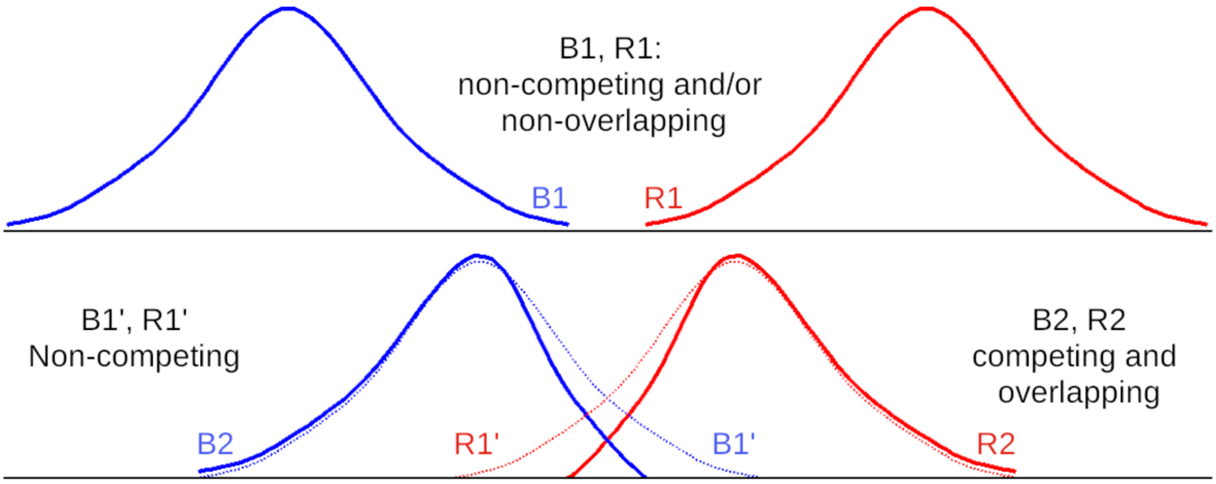

Figure 3.6: The effect of competition on species abundance profiles. *Consider two species for which the environmental gradient underlying the shape of the abundance profile is symmetric. Competing species pairs are likely to impact each other much more in the zone of overlap, leading to asymmetric fitness, and hence abundance distributions. However, the asymmetry will be in opposite directions and the net average asymmetry introduced by the competitive interaction will be zero.*

minants of limits to species distributions (Case & Taper, 2000; Price & Kirkpatrick, 2009).

If we consider two competing species (Figure 3.6), the impact of each species on the other is expected to be higher in the zone of overlap (Legault et al., 2020) since the effect of competition is known to be density dependent (Keddy & Shipley, 1989). While the precise nature of the modification to the abundance profile shape may differ from the representation in our schematic, it is reasonable to assume that the interaction will introduce an asymmetry, but in opposite directions for the two species, with a net asymmetry of zero for the species pair. Therefore, the average asymmetry for the entire community should be a measure of the environmental influence on the shape of profiles. Measuring the individual profiles of just a few species may not correctly reflect the effect of the environment.

3.5.2 Abundance v/s occupancy and completeness of sampling

Sagarin & Gaines (2002) found that 21 out of 23 separate studies of the ACH did not sample the full distribution of the focal species. This statistic is not surprising from a logistic point of view. If sampling a species distribution requires N grids along one dimension, it needs N^2 grids in two dimensions (usually with increased inaccessibility.

While we agree that it is essential to sample the entire distribution (Santini et al., 2019), we offer a more nuanced approach to achieving this. We sampled only a tiny part of a species' geographical distribution (Figure 3.1), but covered its entire *local elevational* and hence *environmental* distribution. Our objective was not to describe the entire range of environments occupied by the species, but to co-opt theoretical tools to educe quantitative principles of the environment-fitness linkage.

Grid occupancy data from multi-decade surveys such as the North American Breeding Bird Survey or the British Bird Survey (Blackburn et al., 1999; Péron & Altwegg, 2015; Osorio-Olvera et al., 2020) have been used to circumvent the resource-intensive abundance sampling of wide-ranging species but are impacted by issues of data heterogeniety and quality (discussed in Santini et al., 2019). We estimate a dispersion as high as a factor of 2-3 in the relationship between occupancy and abundance from a plot in Gaston (2009), which translates to an uncertainty of 60-78% of the distribution width in locating the abundance peak for a gaussian profile. Sagarin & Gaines (2002) have reported differences of up to 50% between published ranges (largely determined by occupancy information) and their own estimates from systematic sampling. Crucially, even with our large field effort collecting abundance data we were only able to retain only a quarter of all the species we encountered for analysis. This is similar to the bird study in New Guinea in which 5000 records yielded only 7 profiles numerous enough and completely contained within the sampled range (Freeman & Beehler, 2018).

3.5.3 Appropriate range parameter definitions

The geometric midpoint of the polygon encompassing the outermost points of occurrence is of little ecological relevance in case of multi-variate and non-linear environmental gradients. Additionally, vagrant records found far away from the bulk of occurrences are a regular feature, especially for organisms impacted by human agency, and ocean and wind currents. In montane landscapes, wind dispersed organisms (like insects and birds) can fly or be blown by wind very easily across the short distance of their entire distribution in a short timespan. Furthermore, these outermost records can change considerably with sampling effort (chapter 2). Therefore, metrics referenced to edge populations are likely to be error-prone and ecologically irrelevant with regards to the majority of individuals of a species (Gaston, 1990). Figure 3.7 shows results from simulations attempting to locate the peak of a gaussian (i) by fitting it and (ii) as the midpoint of outermost records. The fit approach is insensitive to vagrants and its accuracy increases with sample size. The midpoint approach, on the other hand, is very sensitive to the fraction of vagrants and does not improve with sample size.

Even in characterising distribution widths, root-mean-squared-deviation scores over outermost record-based estimates on several counts.

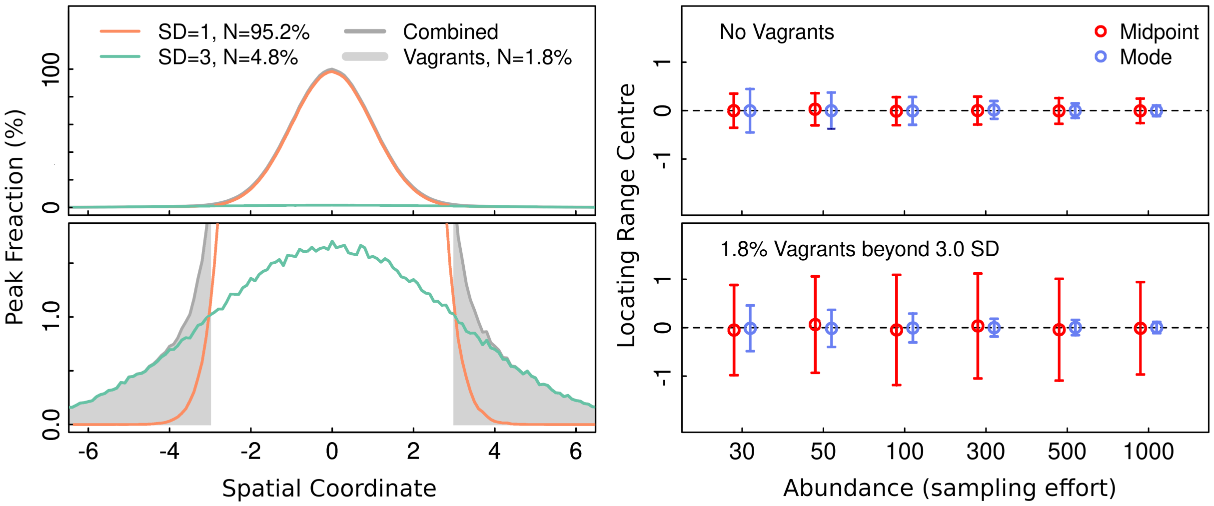

Figure 3.7: Dispersion in locating the centre of a simulated gaussian profile.
We compared identifying the centre (i) as the midpoint of the outermost records and (ii) by fitting the mode for different abundance values. Left: The simulation model (black curve) consists of an admixture of 95.2% "well-behaved" individuals from a gaussian distribution with $SD = 1$ *(orange curve) and 4.8% individuals with* $SD = 3$ *(cyan curve). All records outside* $X = \pm 3.0$ *were assumed to be vagrants (grey-shaded region), since their probability is very low for a "well-behaved" distributions. The ratios were chosen to reproduce the 1.8% "vagrants" in our data. The lower plot is a magnified view of the relative distributions of the two components in the outer parts of the range. The composite curve follows the "well-behaved" profile for the most part; only a small fraction at the edge makes all the difference. Right: The centre coincides with the abundance peak for a normal distribution. The dispersion in the location of the centre from the midpoint of the outermost records (red) is much larger than that from mode-fitting (blue) in the presence of vagrants. Increased sampling effort hardly increases the accuracy of the midpoint-as-centre as it is estimated from just two records regardless of the sample size.*

1. It is referenced to the abundance peak, which is statistically more robust and ecologically more relevant.

2. It makes use of the full dataset, as opposed to just the two outermost records.

3. It is well defined even for infinite distributions (e.g., gaussian) that are frequent components of theoretical models.

4. It facilitates the identification of the role of different traits in determining species distributions, and eventually interspecific comparisons to understand the link between trait values and range widths (Kirkpatrick & Barton, 1997).

3.5.4 Insights into montane bird communities

Community average abundance profile

The existence of an abundant centre (i.e., $A = 0$) is an appropriate null hypothesis for this study, and the data for the community of birds across both summer and winter is consistent with the ACH. Table 3.2 suggests that the asymmetry in species abundance profiles, if any, is small. We do not have sufficient data to speculate further at the moment, but several interesting observations, including the higher number of species showing intra-seasonal movement (which can cause departures from unimodality) in winter are probably worth investigating in future. We recognise that the errors on symmetry values are large, despite a systematically sampled dataset. An even larger dataset is likely to limit this departure to only a few percent. However, it is important to remember that a large number of simplifying assumptions went into making the model mathematically tractable. It may be more useful to repeat the study in other transects, than collect more data in one site.

The departure from symmetry for a few species may be due to specific life-history idiosyncrasies or interspecific competition. However, the set of 15 most abundant species in our data set had no congeneric pairs in them. Therefore, we could not test for signatures of interspecific competition Understanding competitive networks will likely require intensive sampling for a sizeable number of congeneric pairs.

Asymmetry and elevation

We detected a significant relationship between asymmetry and elevation in case of metrics that considered the complete species abundance profile (A_S and A_N) in both summer and winter. Generally, species tended to have larger range half-widths away from the elevational limits of the mountain, and this was particularly apparent at the extremes. We looked investigated changes in asymmetry by imposing an artificial cut-off on the untruncated side for 5 summer species profiles whose abundance peaks were below 800 m or above 2400 m, and can confirm that this is not an artefact of the limits of our sampling effort (500 and 2800 m). This seems to suggest that perhaps the hard limits to elevation (100 m in the Brahmaputra valley, and 3250 m at Eaglenest ridge) is responsible for this pattern.

Despite being a part of the Lesser Himalayas (Shivalik range), at 3250 m, Eaglenest ridge is somewhat high. It is akin to a "sky island" (Warshall, 1995), 23 and 40 km away and isolated above the 2275 m contour from the nearest locations at the same elevation on the mid Himalayan range. It is reasonable to assume that species found above 2800 m are somewhat isolated. The hard boundaries of the hill slope are likely to distort abundance profiles by compressing the upper half-width of high elevation species, consequently pressurizing the lower half. A cascade of competition (both inter- and intra-specific) set in motion by this compression may give rise to the observed pattern between asymmetry and elevation (Jankowski et al., 2010; Stanton-Geddes et al., 2012; Huntsman & Petty, 2014; Péron & Altwegg, 2015; Wen et al., 2020). Our highest elevation transects are less than 2 km from Eaglenest ridge, and perhaps close enough to feel its effect. A similar explanation is likely to apply at the lowest transect as well, as lowland hill forests transition to the tall grassy plains of the Brahmaputra valley somewhat abruptly (Rana et al., 2019).

Alternatively, KB97's assumption of fitness being independent of the sign of trait discrepancy is not valid. Higher elevations are considered to be high-stress environments (Louthan et al., 2015; Cunningham et al., 2016), and a trait that deviates from the optimum may have a higher penalty above the abundance peak than below it. This results in a non-linear trait discrepancy profile. Such a function with small curvature can be approximated by two linear functions with different slopes intersecting at the abundance peak. This naturally invokes a bi-normal model for abundance profiles - linear trait discrepancy functions with differing slopes result in gaussian abundance profiles with different widths on either side of the abundance peak. However, this explanation would result in largely symmetric profiles at lower elevations that transition towards negative asymmetry values at higher elevations. But this is not borne out in our observations - asymmetry is zero closer to the mid-point of the elevational range.

Profile shape

Kurtosis values of averaged profiles (estimated for three elevational communities separately above and below the peak) across summer and winter indicate that abundance profiles have peaks and tails *at least* as broad as that of a gaussian. This corroborates the widespread "bell-shaped" expectation assumed by studies (Hengelveld & Haeck, 1982; Tuya et al., 2008; Boucher-Lalonde et al., 2012; Freeman & Beehler, 2018), while rejecting the $\cap$-quadratic. However, it is important to note that this does not *prove* that abundance profiles in nature are gaussian; it demonstrates that theoretical models can reproduce observed data when backed by reasonable assumptions.

The community mean profiles suggest a tapering off in abundance profiles from the peak towards the periphery. Additionally, the trend with elevation in A_S and A_N but not A_{60} suggests that the observed asymmetry arises from the small fraction of data at the periphery. This suggests that the hard ecological elevational limits *push back* peripheral populations without appreciably modifying the central regions of the profile and beyond. This may also explain the lack of consensus amongst previous studies, most of which depend on the outermost records to define the distribution centre, and many of which used grid occupancy as a surrogate for abundance. The symmetric central part of the range includes most of the and population may be more relevant for understanding the environment-abundance linkage - the profile periphery is a distraction to be ignored. On the other hand, peripheral populations may be more important for understanding the dynamics of selection and range expansion (Caughley et al., 1988; García et al., 2010; Rehm et al., 2015).

Most studies assume that abundance distributions are either uniform or gaussian in shape - the former for the sake of methodological simplicity and the latter because of the ubiquity of the shape in nature. This work shows that abundance profiles are likely close to gaussian. The ACH is only one of the many patterns, though perhaps the simplest to test, characterising the environment-abundance linkage. However, the symmetrical abundance profile implicit in ACH can only arise in environmental gradients with particular characteristics. Theoretical models based on quantifiable ecological processes are essential to identify such ACH-specific environments, and to progress beyond reports on the validity of biogeographical patterns like the ACH. We suggest that compact elevational transects and transects perpendicular to the coast may be more appropriate for testing the ACH. We also suggest that systematic collection of abundance data for a large number of species in such transects may offer the best option for gaining insights into the environment-abundance paradigm.

4 | The Relationship between Abundance and Range Width

4.1 Background

The relationship between the range of environments over which a species is able to persist and the total abundance it achieves is central to both ecology and evolutionary theory. Life history strategies that determine the variety of niches a species can utilize directly influence its survivorship in changing environments, and are particularly pertinent in the current era of global change driven biodiversity loss. Besides furthering our ecological understanding of the strategies species adopt to accommodate population growth, identifying a general relationship between species abundance and how widespread its distribution is can potentially facilitate better informed conservation policies.

However, as was the case with investigations into the Abundant Centre Hypothesis, it is important to keep in mind that geographic space is a mere surrogate of the conceptual niche hypervolume, primarily for ease of observation. While it is reasonable to assume that occurrence locations collectively reflect the range of environments a species can endure and that local abundances are a measure of its fitness (Brown, 1984), translating geographic-space to niche-space is non trivial in most cases. As discussed in chapter 1, most real-world systems encompass vast, complex landscapes across which ecologically relevant environmental factors vary in an unpredictable manner across space, making them virtually impossible to track. With the advent of powerful remote sensing technologies, it may be possible to obtain local measurements to identify a species' *niche-width* (in terms of one or a few variables) based on its geographic distribution, but mapping abundance records onto niche space is practically impossible in most cases.

It follows that a wider species geographic range does not always correspond to a wide distribution in niche space. In other words, a species with a vast geographic distribution is not necessarily more resilient to environmental variability. This, along with the diversity in species strategies in dealing with adversities is reflected in the varied relationships between abundance and distribution-widths that have been observed in nature. This suggests that it is perhaps inappropriate to assume that the Abundance-Range Width Relationship (henceforth ARWR) has a universal or general form. That being said, in this chapter we argue there is still plenty of scope to examine ARWRs for clues on how species perceive and respond to the environment across a landscape that they inhabit.

Over the past five decades, a large number of studies have attempted to ascertain whether the width of species distributions track their abundances (Ricklefs, 1972; Gaston & Lawton, 1988; Gaston, 2000; He et al., 2002; Holt et al., 2002; Wen et al., 2018; Sreekar et al., 2021). While most field studies have found positive ARWRs (Brown, 1984; Gaston, 2000), there is a sizeable number of studies that report non-significant (Reif et al., 2006; Freeman, 2019) and even negative relationships (Päivinen et al., 2005; Ferenc et al., 2016).

At least a dozen different mechanisms have been proposed to explain how species whose populations persist in a wide range of sites can also maintain larger population sizes. A majority of these invoke ecological mechanisms, including resource availability (Brown, 1984; Hanski, 1993), vital rates (Holt et al., 1997) and metapopulation dynamics (Hanski, 1991; O'Connor, 1987; Venier & Fahrig, 1996). Some suggest that there is little value in looking at ARWRs since the spatial aggregation that is characteristic of most species will inevitably result in positive relationships (Wright, 1991; Hartley, 1998; Harte, 1999; Bell, 2000). Others attribute the various forms of ARWRs to differences in range width and abundance measures or biases in sampling design (Bock, 1987; Steenweg et al., 2018).

Owing to the variability in empirically observed forms of ARWRs, the conclusion that their nature (and by extension, perhaps their causal mechanism) is largely context dependent is not inaccurate. In their review, Borregaard & Rahbek (2010) suggested that the various proposed mechanisms need not necessarily constitute competing hypotheses but may be acting at different scales. Inferences of ARWR studies are also known to be highly sensitive to idiosyncrasies of study design (Gaston, 1996), choice of abundance and range width metrics (Wilson, 2011), spatial scale of the study (Blackburn et al., 2006) and life history or evolutionary traits of study taxa (Johnson, 1998).

Despite several decades' worth of studies, the field lacks structured enquiry into the underlying ecological processes that determine ARWRs. We posit that the *shape* of species distributions in a particular landscape, and by extension ARWRs can provide vital information on the coping strategies of species in the face of changing environments. In fact, an in-depth investigation of the nature of the ARWR for a particular landscape can potentially aid rigorous hypothesis testing with regards to how species perceive and respond to it.

In this chapter we argue that despite the welter of confounding factors and the lack of a general expectation, studying ARWRs can still enhance our understanding of the processes that shape species distributions. In combination with methodically collected data and hypotheses, ARWRs can potentially offer insights into how a combination of environmental factors as well as population density determine the shape of species distributions.

4.2 Our Approach

The nature of ARWRs may indeed be context-dependent, but it has the potential to provide information on how favourable the environment is towards species moving into novel niches in order to accommodate population growth. In chapter 3, we saw that species distributions for the bird community in our study area show patterns consistent with KB97 (Kirkpatrick & Barton, 1997), which models density-driven (net) movement from the favourable, high-fitness range centre into the less conducive range edges. The effectiveness of a species' adaptation determines this density-dependent pressure, and consequently the push that local populations experience, forcing individuals into novel environments.

The other factor that determines the rate of movement is the "steepness" of the environmental gradient as perceived by the species - how rapidly the environment changes across space. Given that species can only adapt within physiological limits, a steep environmental gradient is likely to impose hard limits on the movement of individuals into environmental extremes. In case of a *shallow* gradient, on the other hand, boundaries remain *soft*, making it relatively easier for individuals to move into previously unoccupied regions.

Therefore, a combination of density-dependent and environmental pressures determines the relationship between the total abundance and range width of a species. Once again, observing multiple species along the same environmental gradient allows us to infer the *average* trajectory, assuming they are merely at different stages of eliciting the same adaptive response. Therefore, the ARWR across a community may allow us to make general observations on how species handle the trade-off between growing populations and expanding into novel environments.

Thus, determining the nature of ARWR relies heavily on the accurate estimation of both range width and abundance for a large number of species. However, the logistical and conceptual challenges associated with the current paradigm for ARWR studies provides little scope for systematic and unbiased interspecific comparisons to arrive at a general expectation, let alone the processes that give rise to them. Obtaining local abundances across the geographic distribution even for a single species typically involves intensive sampling across vast, at times inaccessible landscapes. The logistics are only compounded when sampling multiple species. As a result, most studies rely on large scale surveys for multi-species data, but these have their own heterogeneity issues stemming from observer biases and non-uniform sampling effort. Additionally, since mapping abundance onto one or a few environmental variables in a reliable manner is non-trivial, such studies remain limited to a statement on the relationship between abundance and geographic range width, which may or may not translate to niche space.

We once again invoke the compact, one dimensional and univariate nature of our study system to aid an ecologically meaningful interpretation of ARWRs. The steep elevational gradient in our study area is tightly correlated with several biologically relevant environmental parameters (Mungee & Athreya, 2021) that allows us to reduce multi-dimensional niche hypervolumes to unidimensional *elevational ranges*. Additionally, all our transects are located within 15 km of each other in a region with the second highest diversity of breeding birds on the planet (Orme et al., 2005). This facilitates an unbiased community-wide analysis where all species range-widths and abundances are measured against an identical environmental gradient. In this manner, we can look beyond the idiosyncratic life histories of individual species.

In keeping with enquiry into the ecological processes that determine species distributions, we introduce two broad classes of range-width definitions - absolute extent and Root-Mean-Squared-Deviation, or RMSD. Besides a qualitative positive/negative label for the form of the ARWR, these different measures offer insights into how the shape of species distributions change when abundance increases. Broadly, extent-based measures provide information on whether the external environment sets hard limits on the movement of individuals, while RMSD is indicative of internal density-driven pressures that species experience.

Figure 4.1 illustrates how local population densities influence the shape of species distributions. When populations are below carrying capacity, they can accommodate more individuals at each location. Local densities increase, resulting in a more inflated distribution of essentially the same shape - all the profiles in the panel on the left differ in extents, but have the same RMSD. However, if the central population reaches carrying capacity, it can no longer accommodate an increase in density. New individuals get dis-

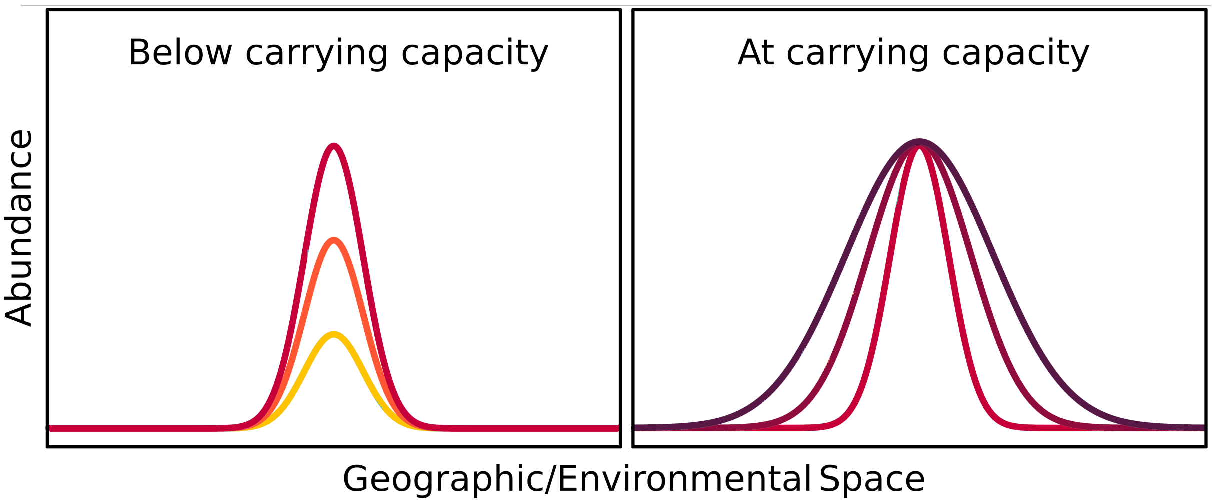

Figure 4.1: Impact of carrying capacity on distribution shape.
Left: When local populations of a species distribution are below carrying capacity, they are able accommodate increasing abundance. Local densities increase, without a change in actual shape - extent increases but RMSD remains the same. Right: When the central population reaches carrying capacity, it can no longer accommodate newer individuals locally. They overflow into the surrounding regions, changing the RMSD as well as extents of the distribution. The outermost profile in the left panel is the same as the innermost profile on the right.

placed to neighbouring regions, resulting in broader profiles, with density at the central region remaining unchanged. This is characterized by a change in extent as well as RMSD.

The shape of species distributions is ultimately determined by the interaction of populations with the environment. If the environmental gradient is steep, the landscape has hard boundaries - it restricts range expansion despite increasing abundances. The resultant ARWR is expected to be flat or saturating if extent is used as a measure of range width. On the other hand, density-dependent pressures are more crucial in determining the nature of ARWR when RMSD is used. If populations are below carrying capacity in a landscape with hard boundaries, the species distribution must accommodate new individuals without expanding outwards. The resultant abundance profile gets sharper with increasing abundance as new individuals keep piling up at the range centre, producing a negative ARWR with RMSD. Once the carrying capacity of the central region is reached, new individuals overflow into neighbouring regions, but are still restricted by the hard-limits of extreme environment. As a result, the abundance profile becomes flatter as abundances increase and shows a positive ARWR using RMSD.

If the environmental gradient is not very steep, individuals are relatively free to move towards the extremes of the gradient, i.e., boundaries are “soft”. Below carrying capacity, species distribution can accommodate new individuals both by increasing local densities

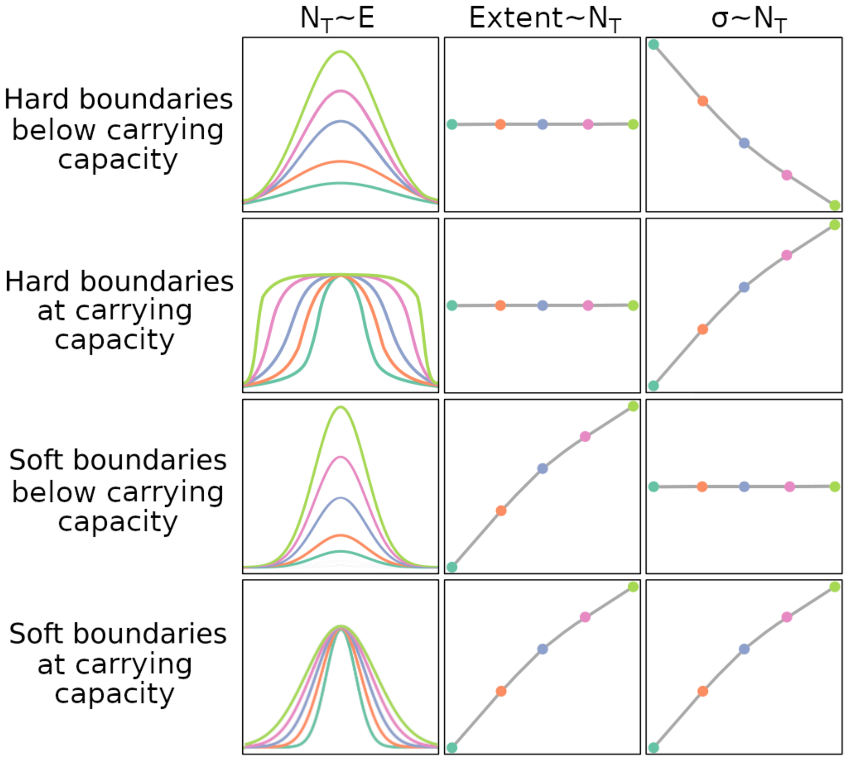

Figure 4.2: Possible Abundance-Range Width Relationships.
Schematic illustrating the possible mechanisms by which species colonize novel niches along environmental gradients; and the resultant ARWRs that may arise (for both extent- and RMSD-based metrics). A shallow gradient with hard boundaries gives rise to broad, flattish distributions as abundance increases, resulting in saturating and increasing extent- and RMSD-based ARWRs, respectively. Profiles get sharper with increasing abundance for a steep gradient with hard boundaries, resulting in flat extent-based, but decreasing RMSD-based ARWRs. Distributions increase in extent as well as RMSD when boundaries are soft. However, an increasing extent-based but flat RMSD-based ARWR is likely to be indicative of an insufficient sampling effort.

as well as gradually expanding outwards, with little change in shape. Thus, while the extent-based ARWR is positive, the RMSD-based ARWR is flat. However, beyond carrying capacity, distributions can no longer accommodate new individuals in the central regions and they are forced to move outwards. As a result, both the extent- as well as the RMSD-based ARWRs are positive.

Therefore, our framework allows us to differentiate between four possible cases that may arise with regards to species distributions along any environmental gradient (Figure 4.2):

1. The gradient has hard boundaries and is below carrying capacity:
   Flat/saturating extent-based and decreasing RMSD-based ARWR.
2. The gradient has hard boundaries and is at carrying capacity:

S. No.	Categories	Filters	No. of species in	
			Summer	Winter
1	Truncation due to sampling limits	None	85	114
2	Total Abundance (N_T)	$N_T \geq 5$	65	63

Table 4.1: Criteria used to determine suitability of species profiles for analysis.
Numbers indicate the number of species retained after every screening stage.

Flat extent-based and increasing RMSD-based ARWR.

3. The gradient has soft boundaries and is below carrying capacity:
   Increasing extent-based and flat RMSD-based ARWR.
4. The gradient has soft boundaries and is at carrying capacity:
   Increasing extent-based and RMSD-based ARWR.

4.3 Analysis

4.3.1 Species selection

Once again, we screened each species in our dataset for suitability before including them in our analyses. This time, we only retained species with a minimum total abundance of at least 5. In addition, we ensured that all included species were well within the elevational limits of our sampling. Only 65 of the 245 species recorded in summer and 63 of the 210 species recorded in winter satisfied both of the above criteria and could be used to estimate R_{SD} and R_{95}. Details on the selection criteria, along with the corresponding number of species that were included in final analyses are listed in Table 4.1.

4.3.2 Parameter Estimation

We examined abundance-range-width relationships using several measures of range extent. The most prevalent measure, in the literature is defined as the distance between the outermost records. In our case, this corresponds to the difference between the lowest and highest elevation records for a species. We refer to this as the min-max range extent or R_{MM}. However, as demonstrated through Figure 2.7 in chapter 2, R_{MM} is based on only the two outermost records. Range edges are known to harbour fluctuating sink populations, making R_{MM} unreliable, with a high degree of associated errors. Instead, we suggest using quantile based range-width (e.g., the extent of the inner 95% of all individuals or R_{95}) as a more robust measure. We used abundance profiles in their unmanipulated (raw) form to estimate R_{95} and R_{SD} for each species.

Small sample sizes tend to underestimate range widths, leading to spurious positive ARWRs. Therefore, we constructed a null model using the average RMSD for the community (separately for summer and winter) to simulate 400 sets of abundance profiles with constant RMSD but differing in sample sizes. Using these simulated sets, calculated the slope for the null model of no change in range width with abundance.

We quantified measurement errors in our width estimates through Monte-Carlo simulations in the same manner as in chapter 3 - as the dispersion in width measures from 400 simulated profiles for each species. These simulated profiles were generated using the smoothed profile as the model, an overdispersion factor and a negative binomial random number generator as described in chapter 2 (function *rnbinom*; R Core Team, 2021; Lindén & Mäntyniemi, 2011).

Orthogonal least square regressions were performed for the width metrics against abundance at the end of each iteration (for data as well as the null). We present the mean and 95% confidence intervals for the slopes so obtained, as well as difference between the data and the null in our results.

We also examined the average profile shape by constructing average community profiles in 3 abundance classes and estimating kurtosis for the same. Profiles were normalized using a similar transformation as in chapter 3, but using *median* as the central tendency instead of mode: $E_C = (E - E_M)/\sigma_E$ for elevation, and $F_{C,E} = N_E/N_T$ for fractional abundance, where E_C and F_C were the normalised elevation and fractional abundance values for each species, E_M was their median elevation, σ_E their elevational standard deviation, N_E their abundance at elevation E, and N_T their total abundance. We used median elevation for this exercise since it makes no assumptions regarding the shape of the profile and is more stable than mean for smaller sample sizes.

The fractional abundance of all the contributing species in each category was averaged at each (normalised) elevation after weighting it with the inverse of its variance. The kurtosis value (K) for the community average profile was used to determine whether profile shapes could be best described as gaussian (G; $K_G = 3.0$), ∩-quadratic (Q; $K_Q = 2.14$) or uniform (U; $K_U = 1.8$).

All analyses mentioned above were performed separately on both the summer and winter datasets, using scripts written for the statistical computing platform R (R Core Team, 2021).

Season	$logR \sim$ $logN_T$	N	Data		Null	
			R	CI 95%	R	CI 95%
Summer	R_{95}	65	0.55	(0.42, 0.66)	0.25	(-0.02, 0.54)
	R_{SD}	65	0.48	(0.31, 0.61)	0.20	(-0.10, 0.49)
Winter	R_{95}	63	0.12	(-0.09, 0.31)	0.27	(-0.01, 0.55)
	R_{SD}	63	0.04	(-0.19, 0.27)	0.23	(-0.12, 0.56)

Table 4.2: Correlation between $log(Rangewidth)$ ***and*** $log(TotalAbundance)$***.***
We determined the Spearman's ranked correlation coefficient for our data and the null model in both summer and winter. The 95% confidence intervals were determined by Monte Carlo simulations on the observed and null models.

4.4 Results

We used the average of the standard deviations of all species in the community (218.5 in summer and 214.2 in winter) to construct the null model, whose 95% confidence interval is depicted as a grey envelope in subsequent figures. Spearman's ranked correlation coefficients for the various metrics of distribution width vs. total abundance for the species in our dataset, along with those of the corresponding null models for summer and winter are listed in Table 4.2. We prefer the Spearman's ranked correlation coefficient over Pearson's because it is non parametric and checks for a monotonic relationship rather than specifically a linear one. Corresponding orthogonal linear regressions for the same variable pairs for summer and winter are shown in Figure 4.3 listed in Table 4.3.

Overall, both log-transformed R_{SD} and R_{95} were significantly correlated with log-transformed total abundances in summer. In contrast, correlations for neither were significant at the 95% confidence level in winter. Interestingly, null models for the conventionally used extent-based measure R_{MM} for both summer and winter, were significantly correlated with log(Abundance).

Season	$logR \sim$ $logN_T$	Data		Null		Data - Null		
		Slope	CI 95%	Slope	CI 95%	Mean	SD	p
Summer	R_{95}	0.42	(0.29, 0.57)	0.06	(0.003, 0.13)	0.35	0.08	< 0.01
	R_{SD}	0.41	(0.29, 0.56)	0.05	(-0.01, 0.11)	0.28	0.07	< 0.01
Winter	R_{95}	0.11	(-0.06, 0.29)	0.05	(0.001, 0.10)	0.31	0.10	< 0.01
	R_{SD}	0.07	(-0.10, 0.25)	0.04	(-0.01, 0.08)	0.24	0.09	0.01

Table 4.3: $log(Rangewidth)$ ***vs.*** $log(TotalAbundance)$ ***Regression.***
We determined the orthogonal linear regression for our data and the null model in both summer and winter. The 95% confidence intervals were determined by Monte Carlo simulations on the observed data and the null.

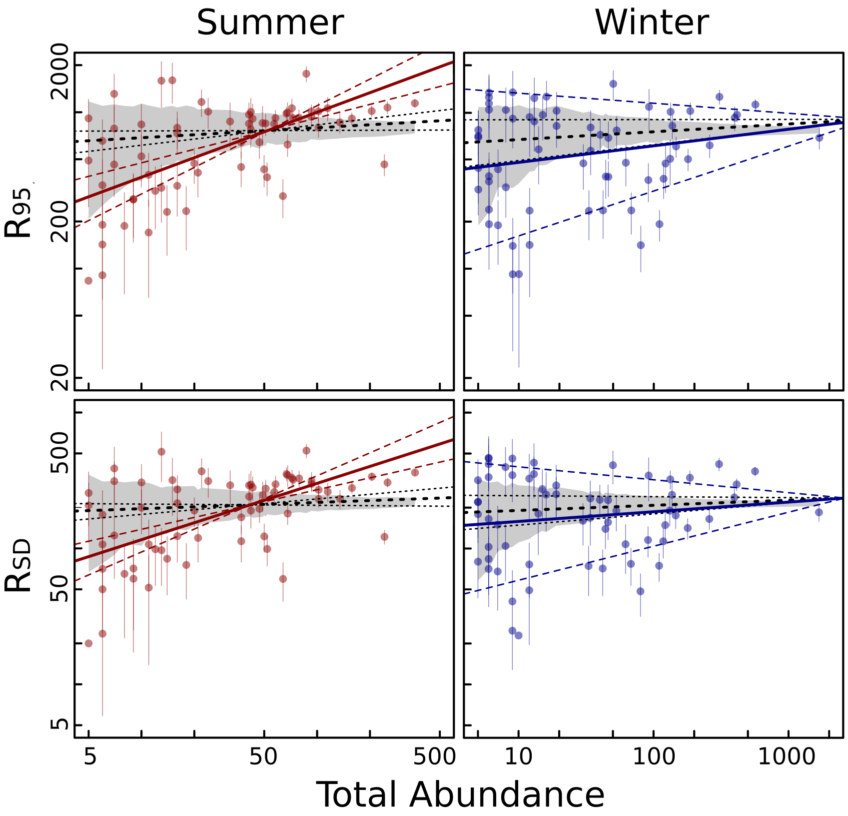

Figure 4.3: Linear Regression between range width and total abundance. *We plot the data for the inner 95th quantile of the distribution and root mean squared deviation, which are representative extent-based and RMSD-based metrics respectively. The orthogonal regression parameters for these as well as all other metrics are listed in Table 4.4. Summer species are shown in red, winter species in blue. Solid lines denote the best fit and 95% confidence intervals of the slope are denoted by dashed lines. An envelope that includes 95% of the scatter for the null model and the null regression are shown in grey and black respectively. All error bars represent 95% confidence intervals.*

Log-transformed orthogonal regressions for extent as well as RMSD in summer had positive slopes, significantly in excess of the 95% confidence interval of the null model, with a p-value of less than 2.5×10^{-3} for our set of 400 simulations. On the other hand, slopes for both R_{95}, as well as R_{SD} had a significant overlap with the null expectation at the 95% confidence level in winter. The contrasting regression plots for R_{95} and R_{SD} in summer and winter are shown in Figure 4.3.

The average profile shape for all abundance classes in both summer and winter rejected both ∩-quadratic and uniform distributions at the 95% confidence interval. All of the above were also consistent with a gaussian profile shape, except the highest abundance class in winter which was more leptokurtic than a gaussian (Table 4.4). The profiles for the smallest abundance class in both summer and winter were characterised by higher fluctuations than the other abundance classes (Figure 4.4).

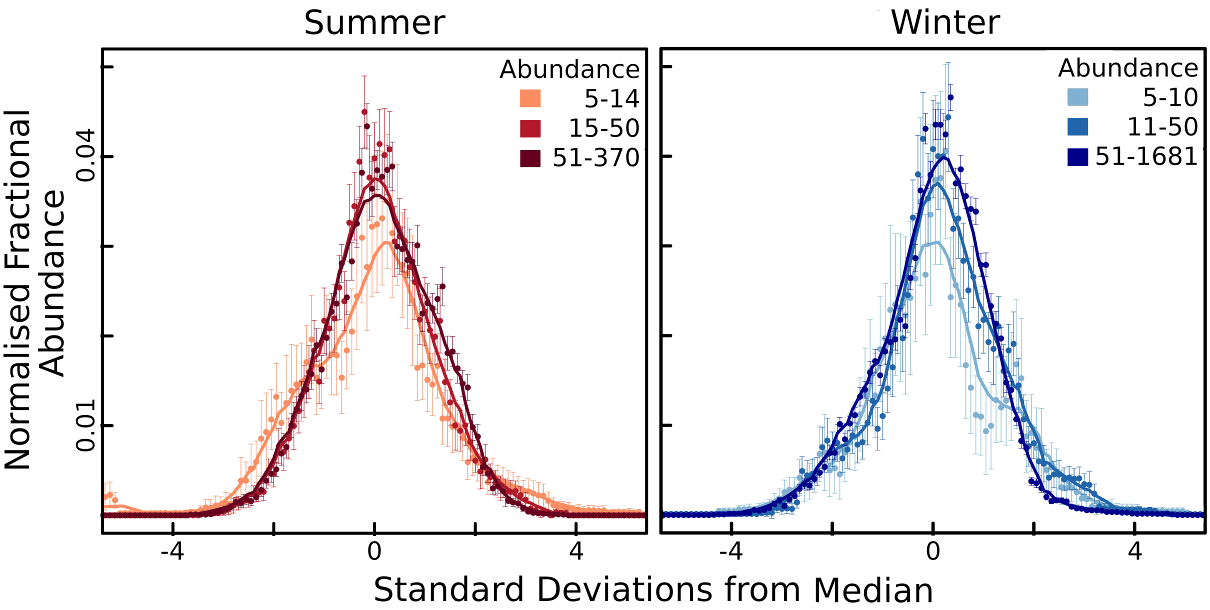

Figure 4.4: Community average profiles in 3 abundance bins.
The scatter and smoothed profiles were constructed by averaging the SD-normalised profiles of the species in the community for summer (reds) and winter (blues). All error bars represent 95% confidence intervals.

4.5 Discussion

In this chapter, we have explored the ARWR as a manifestation of the strategies by which species accommodate population growth along an environmental gradient. We began with the premise that a species' abundance distribution in geographic space is a surrogate for its response to changes in an underlying cocktail of environmental variables. Therefore, we ascribe primacy to identifying study systems that aid a reliable estimation of environmental factors and the fitness of the focal species at each location. We argue that a compact elevational transect like ours has two major advantages over other

Season	Abundance Range	N	Kurtosis	CI 95%
Summer	5 - 14	22	4.62	(2.82, 6.58)
	15 - 51	21	3.11	(2.75, 4.25)
	52 - 361	22	2.83	(2.59, 3.72)
Winter	5 - 10	22	3.59	(2.50, 6.23)
	11 - 50	20	2.85	(2.84, 5.46)
	51 - 1681	21	3.53	(3.37, 4.21)

Table 4.4: Kurtosis of community average profiles in 3 abundance bins.
Profiles were constructed by averaging the SD-normalised profiles (both observed and Monte-Carlo simulated) of all species in a particular abundance bin. Their kurtoses were compared to the expected kurtoses: $K_G = 3.0$ *for gaussian,* $K_Q = 2.14$ *for* $\cap$*-quadratic and* $K_U = 1.8$ *for uniform profile shapes.*

landscapes. Firstly, since most ecologically relevant factors are tightly correlated with elevation, range widths can be estimated in an objective and unbiased manner in terms of elevation. Secondly, it facilitates simultaneous abundance estimation across the *complete range* of several species with considerably lower sampling effort. This in turn enables us to look past species-specific idiosyncrasies to infer how the landscape is perceived by the "average" species.

Additionally, we propose that a comparison of the ARWR using *extent* vs. that using the *RMSD* of distributions holds information on how challenging the landscape is perceived to be - and is ultimately a commentary on the how the shape of species distributions changes to accommodate increasing numbers. Therefore, we identified two classes of ARWR relationships - extent and RMSD-based - that together yielded a framework with testable hypotheses with regards to how a combination of density-driven pressures and environmental factors shape species distributions across landscapes. We then used this framework on the summer and winter bird communities in our study area to determine differences in how the same landscape is perceived between seasons.

We designed our null model in order to estimate variability in our range estimates due to measurement errors alone when samples of various sizes are drawn from a gaussian population with a fixed standard deviation. We found that both extent- and RMSD-based ARWRs were significantly positive in summer (in excess of the null model at least at the 90% confidence level). This was consistent with expectations in case of an environmental gradient with soft boundaries and populations at carrying capacity.

In winter, the community showed no significant relationship between abundance and range-width for extent- or RMSD-based range width. This was evident from both the correlation coefficients as well as the regression slopes, none of which were significantly different from the null model. The lack of a relationship in winter was not consistent with any of the proposed hypotheses, but perhaps suggests that the dynamics of species distributions changes between seasons.

The average profile shape for summer records (across all abundance classes) was best characterised as gaussian, i.e. it had a peak as well as tails. We were able to rule out alternative shapes - ∩-quadratic (peak but no tails) and uniform (neither peak, nor tails) with a high degree of confidence. The presence of a peak as well as tails was corroborative evidence for soft boundaries at carrying capacity as species fitness tapered off towards the (relative) extremes of the environmental gradient in summer. The results were similar in winter, except the highest abundance class, which exhibited a higher kurtosis value than a gaussian at the 95% confidence level. Such distributions are expected to have a sharper peak than gaussian distributions. Invoking a change in the inherent shape of the distribution may well be a strategy by which species accommodate increasing numbers along a steep gradient with hard boundaries without increasing range width, but a more definitive statement requires further investigation which is perhaps beyond the scope of our study. However, it is safe to say that the strategies adopted are different, perhaps more variable between species in winter.

4.5.1 The ecological underpinnings of ARWR

The nature of ARWRs is context dependent

The expectation of positive abundance-range width relationship has by and large been deemed a "general" biogeographic pattern to the extent that deviants, no matter how numerous, are merely treated as exceptions to the rule. Despite the majority of studies that are in agreement on the ubiquity of positive ARWRs, we maintain that the nature of such relationships is wholly dependent on the nature of the landscape as well as taxa under consideration.

While it is easy to see the utility of establishing a general rule with regards to ARWR (from the perspective of conservation or the biology of invasive species, for instance), it contributes little to furthering our understanding of the ecology of density-driven range expansions. We argue that investigations into ARWRs are fascinating independent of the pursuit of a universal rule, as they provide insights into how species interact with the landscape they inhabit.

Width in geographic- and niche- spaces are not equivalent

One of the main flawed assumptions in the quest for universally valid ARWRs is that a species with a broad distribution in geographic space can also withstand a wide range of environmental conditions. While this may be true in certain contexts, there are several commonplace examples where it is not. A species endemic to vast deserts may span several hundred kilometres in terms of their geographic distribution, and yet be incapable of surviving in non-arid habitats. On the other hand, although such instances are much rarer, a montane endemic with a global distribution of a few square kilometres may be tolerant to large environmental fluctuations.

As mentioned earlier, it is important to remember that though we record species observations in geographic space; from the ecological perspective, we are interested in mapping a species' fitness in niche space. While it may seem trivial, this basic distinction between geographic- and niche space is overlooked in most studies, be it temporal tracking of changes in the range width of a single species, or multi-species surveys.

Montane elevational gradients are a few of those unique systems where the geographic width of species distributions (measured in terms of elevation) corresponds directly to width in niche space, since nearly all biotically relevant factors are linearly and strongly correlated with elevation. Contours, especially in case of young fold mountains span several thousand kilometres of practically unchanging environment, making such systems effectively one-dimensional. This reduces sampling effort by several orders, enabling unbiased and comparable width estimation for several species (an entire community in our case) simultaneously.

Choice of width metrics influence ARWR inference

Some studies have pointed out that inference on the nature of ARWR depends on the metrics and transformations used (Wilson, 2011). However, they most often refer to a choice between local abundance, total abundance or occupancy. To our knowledge, the range width metric used is invariably min-max based (e.g., a convex hull of all sites of occurrence) and there have been no alternative considerations. As discussed in the previous chapter, this method relies on a small, statistically unreliable fraction of fringe populations and can be highly erroneous for small sample sizes. We not only suggest metrics that utilize all (or at least a much larger fraction) of the data, but also speculate how they are subtly different in the information they provide.

Assuming the model proposed by Brown (1984) in which individuals overflow from a central, optimally adapted population into neighbouring regions, the extent-based width is a measure of how far out into extreme environments new individuals are able to disperse, while RMSD-based width measures density-dependent pressures, i.e., whether new individuals can remain at their location of birth or are forced to move into other niches available to them. The two measures in combination essentially describe how species handle the trade-off between overcrowding and venturing into environmental extremes in a particular landscape. The hypotheses we formulated for this study describe different combinations of these two strategies, and tie them to how challenging the landscape is perceived by species to be. In studying all the species in the community together, we infer the strategy that an *average* species in the landscape adopts.

4.5.2 Insights from the EWS bird community

Positive RMSD- and extent-based width metrics in summer suggest that populations are at carrying capacity and perceive the elevational gradient to have soft boundaries - new individuals keep moving outward and are not particularly clumped near their point of origin. In other words, the resistance that the gradient offers to individuals moving into previously unoccupied environmental regimes is not steep enough to challenge their physiological limits. This is not to say that all species distributions extend indefinitely into the gradient's extremes. The average species abundance profile shape indicates that fitness tapers off, eventually to a point where a species is unable to persist. However, observed patterns are consistent with our hypothesis that suggests that this limit is determined by the abundance and density-dependent efflux, rather than the hostility of the environment.

The contrast between ARWRs along the same gradient between summer and winter is especially fascinating since it highlights the importance of characterising the nature of the landscape. Besides the spatial variations in environmental factors across landscapes that we have already discussed, most of them are also extremely dynamic temporally. Therefore, studying ARWR relationships without an understanding of how ecologically relevant factors are changing across the landscape has little ecological meaning. The observed patterns in winter are not clear enough for us to make any definitive statements about how the landscape is perceived in winter. But perhaps what they do suggest is that different species may be accommodating growing populations via different strategies.

Despite being the most biodiverse and threatened regions of the world (Myers et al., 2000), there are very few studies from the tropics in general, and tropical montane systems in particular. As a result, there exists a fair bit of ambiguity in the literature with regards to the ARWR for montane ecosystems (especially in the tropics). Tropical mountains have been considered akin to islands (typically associated with unusual biogeographic patterns), and this has given rise to the expectation that specialist montane endemics are likely to be broadly distributed (Reif et al., 2006). Indeed, a number of studies have reported negative ARWRs (Reif et al., 2006; Nana et al., 2014; Ferenc et al., 2016; Reeve et al., 2016, 2018). However, like the rest of the literature, there are several others that find no relationship (Theuerkauf et al., 2017; Freeman, 2019), positive relationships (Wen et al., 2018; Hu et al., 2021; Sreekar et al., 2021), and even hump-shaped relationships (Sam & Koane, 2020). In general, we are far from a clear understanding of ARWR in most landscapes, let alone tropical mountains.

In this study we have attempted to interpret ARWRs from the perspective of delving deeper into patterns that may illuminate the mechanisms that determine species distributions in the face of changing environments. Montane gradients in biodiversity hotspots such as ours (Myers et al., 2000; Orme et al., 2005), provide the unique opportunity of tracking the fitness response (in terms of abundance) for a large number of species along a smoothly changing environment. Additionally in our case, the east-west orientation of the Himalayas due to which the environment remains relatively unchanged for large stretches along contours; and a single observer conducting the entire sampling procedure minimised the confounding influences that studies using survey datasets are known to struggle with. It is important to note that despite having nearly 35,000 records across summer and winter, only a quarter of the 280 species passed our quality check and could be included in hypothesis testing. This reiterates the importance of large, systematically collected datasets.

Another crucial aspect of studying species distributions is characterising them in an ecologically relevant manner. In case of ARWR studies, it is important to parametrize distributions using definitions that are reasonable approximations for the actual environmental variations that elicit the change in species fitness. In our case, the compact study system provided the added advantage of rendering measurements fit for inter-specific comparison without additional transformations. Choosing definitions that disregard irrelevant outliers (e.g. vagrant records) while retaining legitimate records that form the tail of the distribution is equally important. This is evident from a comparison of the different metrics used in our analysis, and the subtle, yet insightful variations in the ARWR forms obtained. In other words, there is much information to be gained from well defined, ecologically relevant metrics that can be applied across the board in a systematic manner.

In conclusion, we highlight the value of frameworks that look beyond the quest for a universally valid ARWR and focus on rigorously testing ecological hypotheses instead. We demonstrate this for a subset of several possible hypotheses pertaining to mechanisms that underlie ARWRs, in a system that simplifies species range measurements. Undoubtedly, a general pattern may emerge from a vast network of similar studies. However, the strength of such frameworks lies in deepening our understanding of the strategies organisms adopt to cope with spatio-temporally changing environments. There is an urgent need to understand the determinants of species distributions in different systems across the world, especially those that are vulnerable to biodiversity loss and climate change. More widespread implementation of frameworks such as this is likely to facilitate better informed and more effective conservation strategies.

5 | Seasonal Changes in Species Distributions

5.1 Background

The last two chapters primarily dealt with species persistence and proliferation by local adaptation, and the related patterns observed in their distributions. Species are known to have evolved several strategies in order to improve fitness and survival, especially in non-conducive environments. In temperate or montane environments like our study regions, cold survival strategies are particularly important. We find several forms of such avoidance mechanisms across the animal kingdom, of which torpor, resistance and migration are most common (Auteri, 2022).

Birds are known to have evolved all three forms of cold avoidance (Bech & Reinertsen, 2014). Several species of birds including swifts, doves and hummingbirds reduce their activity, body temperature and metabolic rate in winter (McAtee, 1947; Schleucher, 2004). The Bergmann's pattern, which predicts smaller body size in warmer climates is also generally well established in case of birds (Ashton, 2002; Salewski & Watt, 2017). In addition to waterproof feathers that act as insulation by trapping in air pockets, their feet and beaks are also known to have thermoregulatory functions (Tattersall et al., 2009). As expected from Allen's rule, birds in colder climates have been shown to have smaller beaks (Danner & Greenberg, 2015; Friedman et al., 2017). Several behavioural adaptations such as shivering (West, 1965), puffing up feathers, tucking in beaks and legs (Friedman et al., 2019) as well as communal roosting (Eiserer, 1984) are also well known. Additionally, birds are adept at flying - which happens to be the most effective mode of terrestrial dispersal, and a large number of species across the evolutionary tree have evolved migratory behaviours.

Migratory flights invariably coincide with seasons, with most involving movement of individuals to warmer areas in order to avoid cold, difficult winters. Despite the same underlying cause, birds exhibit immense diversity and complexity in their migratory behaviours, and it is clear that they do not always pick the closest conducive location to migrate to. Some birds like terns migrate halfway across the world (Egevang et al., 2010), while birds in montane environments like ours make short flights of the order of only a few kilometres. Crucially, despite decades of research, we have little knowledge on the evolution of long-distance migration, especially on the decisions involved in the choice of migratory refugia; and even fewer studies have addressed short-distance migration. In this chapter, we try to understand the factors that influence short-distance migrations in montane communities.

Migration is exhibited by several taxa across the animal kingdom, and has interested biologists for centuries. From Linnaeus' hypothesis of swallows hibernating under water in winter (von Linné, 1757) to the extensive documentation of animal movement and theories about its causes (Dingle, 2006; Dingle & Drake, 2007), the field has come a long way. There is a fair bit of variation in migration patterns of different taxa. Insect migrations involve any mass flight of individuals steadily in one direction, perhaps several times during a breeding season (Williams, 1957), while fish may move in circuits between feeding, breeding and wintering sites (Dingle, 2014). Broadly, they may be categorized as *one-way*, *to-and-fro*, *loop*, *vertical* or *altitudinal*, and *nomadic* (Dingle & Drake, 2007)

The sheer diversity (and plasticity, see Newton, 2012) that birds exhibit is probably why they are the most widely studied migratory taxon by far. But despite years of research, there is still a fair bit of disagreement regarding the evolutionary origin of migration. Most evolutionary theories address long-distance to-and-fro migrations, in the form of annually repeated, seasonal movement between the breeding and non- breeding ranges (Rappole, 2013). These trips are especially interesting since they almost always involve significant energetic investments and, by extension, the risk of mortality.

Initially, it was believed that long-distance migrations involved adaptations specific to tropical species, in order to take advantage of the plentiful resources and low competition in temperate latitudes (Cox, 1968; Rappole, 1995). However, more recent studies argue that it is actually the harshness of conditions in temperate regions (Salewski & Bruderer, 2007), and breeding site fidelity (Winger et al., 2019) that drive species to migrate *into* the tropics. The driving forces of long distance migration may be any one or a combination of these theories. However, it is perhaps safe to assume that the same drivers apply (albeit, less strongly) to short-distance elevational migrations as well (Hsiung et al., 2018).

Despite the ubiquity of elevational migrations across taxa, habitat types and climatic regimes, they are relatively ill-studied. In their review, Hsiung et al. (2018) found only 216 studies of altitudinal migration across taxa and continents, $\sim 60\%$ of which were on birds and ∼ 50% in temperate regions. There are recent reports of migratory patterns changing in response to global warming (Wilcove & Wikelski, 2008; Wilcove, 2010). Given the vulnerability of montane ecosystems to climate change (Fort, 2015), preferentially more so in the tropics (Eguiguren-Velepucha et al., 2020), elevational migrations (especially in tropical montane environments) are threatened and warrant urgent attention (Barçante et al., 2017).

Besides extrinsic influences such as food-availability, weather and predation, there have been lengthy discussions on intrinsic physiological adaptations that birds have evolved in order to aid migration, and it has also been suggested that such traits and migratory behaviours have perhaps been co-opted (Piersma et al., 2005). However, the empirical association between traits and migratory propensity is poorly understood. We only came across a handful of studies that looked for a relationship between elevational migration and morphometry (Norbu et al., 2013; Lundblad, 2014; Vágási et al., 2016; Cheng et al., 2022) or dietary/habitat preferences (Boyle, 2010; Loiselle & Blake, 1991) and even fewer that look for a genetic/phylogenetic basis (Merlin & Liedvogel, 2019; Lugo Ramos et al., 2017; Tsai et al., 2021).

5.2 Our Approach

In this study, we simultaneously sample close to 280 bird species across a tropical montane elevational transect to obtain their complete elevational distributions in both summer and winter. Community wide records across breeding and non-breeding seasons allowed us to quantify shifts not only in terms of the central tendency, but also the width of these distributions. Once again, our robust and unbiased estimates, in combination with the univariate, unidimensional gradient facilitated meaningful inter-specific comparisons.

Besides looking at community-wide changes in elevation and range width between seasons, we also looked for associations between morphology and altitudinal migration. Though we had not performed morphometric measurements on the individuals we sampled, we were able to compile species-level estimates from the multiple trait data repositories that are freely accessible (Price et al., 2014; Schumm et al., 2020; Tobias et al., 2022). Specifically, we obtained estimates for body mass and wing and beak morphology.

We also examined the relationship between altitudinal migration and dietary, foraging and habitat preferences. Once again, we utilized species-level data available in the literature for this analysis (Wilman et al., 2014). Additionally, we tested if the distribution of a species extending outside the Himalayas had a bearing on altitudinal migration. We

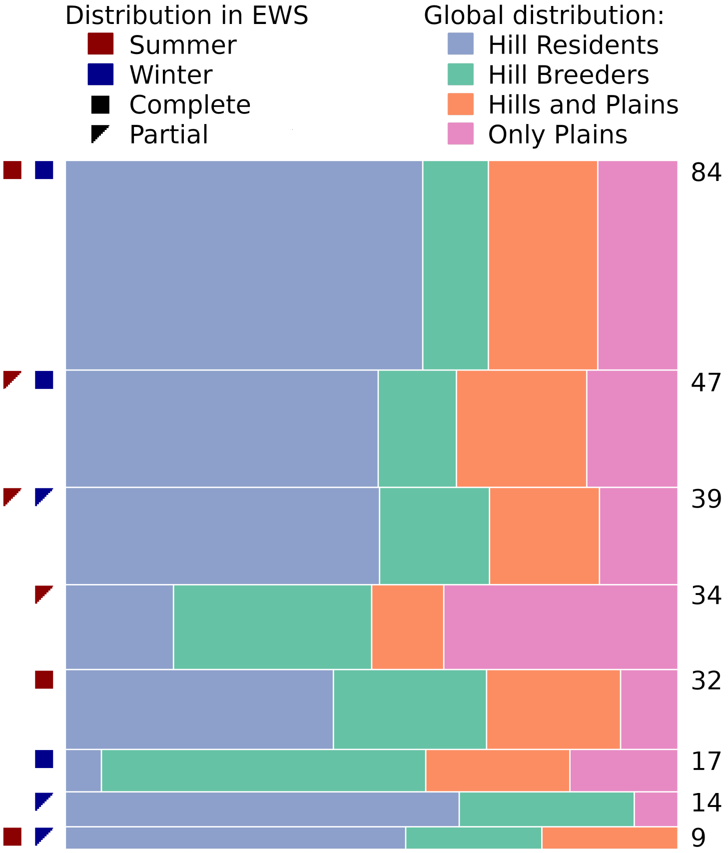

Figure 5.1: Break-up of species distributions recorded in EWS.
The spine plot shows the proportion of data we have for each category. Categories are defined based on completeness of data for species distributions between summer and winter, designated by the symbols on the left. The corresponding total number of species in each category is mentioned on the right. Each category has been classified into subcategories based on their global distributions as listed by BirdLife International. Note that we have only used the 84 species in the topmost category in the analysis for this chapter.

did this using information on the global distribution of species from the IUCN Red List of Threatened Species (IUCN, 2021).

Finally, we checked for phylogenetic relatedness between species with similar migratory propensities. For this, we used the complete dated global phylogeny for extant birds of Jetz et al. (2012).

5.3 Analysis

5.3.1 Shortlisting species

Unless specified otherwise, we used species mean elevation (and standard error) to estimate extent of altitudinal migration, and RMSD for the distribution to estimate changes in range extent. Figure 5.1 shows the extent of the distribution we were able to sample for all the species we recorded in Eaglenest Wildlife Sanctuary. Evidently, for a large number of species, we had no, or only partial information in one or both seasons. However, the *completeness* of their distribution was crucial for the accurate estimation of both central tendency as well as extent.

Importantly, our sampling was limited between 500-2800 m in elevation, while Eaglenest ridge extends from 100 all the way up to 3250 m. Therefore, while truncated distributions confirmed species presence beyond the lower/higher sampling limits, they would yield inaccurate estimates of width and central tendency. Species that we recorded in only one season were even more problematic, since we could neither confirm, nor rule out the possibility of them being found beyond our sampling limits. We tried to obtain this information by examining the IUCN spatial data across breeding and non-breeding seasons. Essentially, we wanted to check whether the species ranges were restricted to the Himalayas or also extended into the Indo-Gangetic plains, peninsular India or the Malay peninsula. However, this exercise was not very useful, as the IUCN spatial data was far too coarse-grained for most species.

Thus, for the current analysis, we had no data selection criteria based on the profile shape, or even minimum total abundance, or number of non-zero elevations. We only checked for completeness of the distribution sampled across both seasons. All the analysis reported in this chapter are for the 84 species for which we had complete information on the elevational distribution across both seasons. We argue that this "clean" dataset yields conservative inferences for all our analyses, since recording species in EWS in only one season very likely implies they had migrated beyond the sampled range - this would yield large differences between summer and winter distributions.

5.3.2 Examining relationships

Migratory propensity and traits

We obtained trait data for all our species primarily from the Price et al. (2014) and Schumm et al. (2020) datasets with trait measurements for species specifically from the eastern Himalayas. For the species for which we were still missing information, we extracted data from AVONET, the recently released global trait dataset for birds (Tobias et al., 2022). Specifically, we extracted measurements for body mass, wing length, beak length, beak width and beak depth. Body mass measures were used as-is to test whether large bodied species indeed have shorter migrations (Ketterson & Nolan, 1976). The relationship between altitudinal shift and wing length was a measure for the impact of dispersal ability on migratory propensity. Additionally, we posit that beak area is directly proportional to heat loss by radiation and by extension, the sensitivity of a species to colder climates (Friedman et al., 2017, 2019). Therefore, we estimated beak area by modelling the beak as an irregular triangular pyramid using the beak measurements.

We also checked whether altitudinal shift showed a significant trend with *residual wing* and *residual beak*. These two quantities are a measured *in excess of allometry*, and hence are capable of telling us whether there is a signal *other than* that coming from the altitudinal shift $\sim$ body mass relationship, since wings and beaks are known to scale with body size. Therefore, these are perhaps truer estimates of heat loss and flight ability.

Migratory propensity and diet/habitat

We obtained dietary and habitat preference data from EltonTraits, a global dataset on species-level foraging attributes for birds and mammals (Wilman et al., 2014). We extracted information primarily on four attributes:

- Diet: Insects, Vertebrates, Fruits, Omnivore, Nectar
- Habitat: Forest, Open
- Foraging Height: Mid-canopy, Top of the canopy, Bush, Ground, River-bed
- Primary Substrate: Leaf, Ground, Fruiting bodies, Flowers, Bark, Air, Moss

We asked whether the average elevational shift differed between species grouped based on these different attributes. Essentially, we were clubbing together all species with the same habitat/dietary preferences. We then plot the median and its 95% confidence interval for each group to check for patterns.

Migratory propensity and being hill-restricted

We obtained breeding, non-breeding and resident global distributions (subject to availability) for each species in our dataset from the IUCN red list IUCN (2021). This spatial data was used to determine whether species maintained distributions in the Himalayas alone, or also had other populations in other warmer southern regions.

Based on the IUCN range maps, we classified species based on whether they had (i) resident populations exclusively in the hills, (ii) only breeding distributions in the hills, (iii) resident populations in both hills and plains, (iv) resident populations in plains alone.

Much like the previous analysis, we looked for significant differences in the median elevational shift between summer (breeding) and winter (non-breeding) among the four groups.

Migratory propensity and phylogenetic relatedness

To look for phylogenetic signal (if any) in species elevational shift, we used the global bird phylogeny which contains all extant species published by Jetz et al. (2012). We used their online tool to obtain 1000 Bayesian trees, pruned to contain only the species in our dataset. We constructed a consensus tree from the 1000 trees and plotted it against the elevational shift for the corresponding species to visually look for clusters.

Additionally, we calculated Pagel's λ, a measure of phylogenetic correlation for each of the 1000 trees and our elevational shift data, and used the dispersion in these values to estimate the 95% confidence interval. Pagel's λ has a value between 0 and 1; 0 would indicate no correlation, and 1 perfect correlation between migratory propensity and phylogeny. All the phylogenetic analysis mentioned above was done using mainly 4 R packages: *ape* (Paradis & Schliep, 2019), *phytools* (Revell, 2012), *phylosignal* (Keck et al., 2016) and *phylobase* (Bolker et al., 2020).

In general, all the analysis mentioned above were performed using scripts written for the R statistical computing platform (R Core Team, 2021).

5.4 Results

Figure 5.2 shows histograms for the shift (summer - winter) in mean elevation and range width (RMSD) of distributions. The histogram for altitudinal shift had a mean value of 253.35 m ($SD = \pm 447.4$ m). The distribution's thick upper tail comprised the bulk of individuals and sparse lower tail contained only six species with a shift of more than 200 m. This indicated that species in this community were more likely to move to (relatively) lower elevations in winter. Although there were instances of migration in the other direction, they were fewer ($\sim$ 7%). The distribution for % change in range width

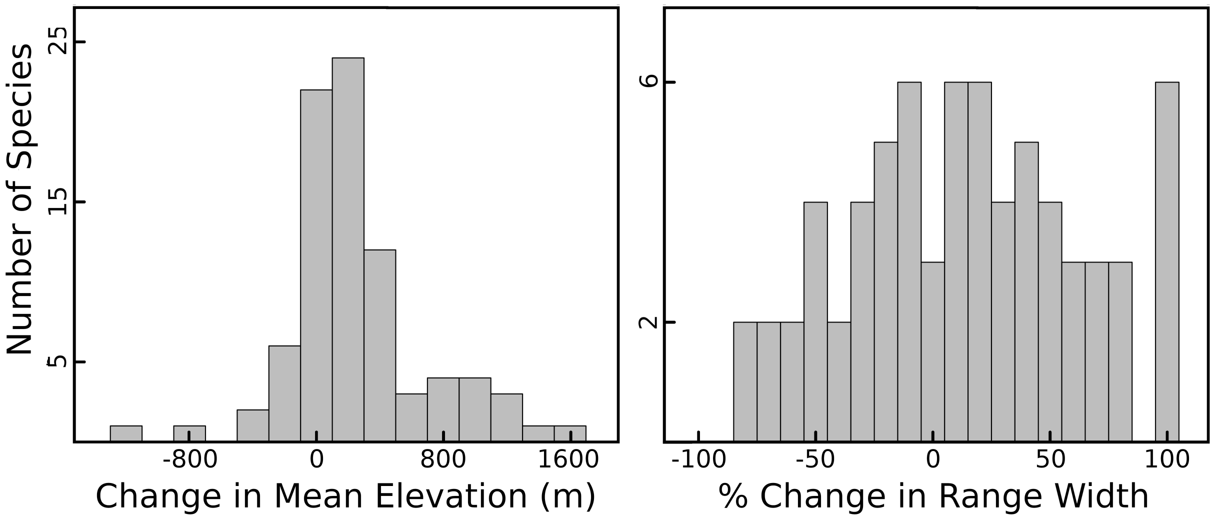

Figure 5.2: Changes in mean elevation and range width between summer and winter.
A majority of the elevational shifts are positive, i.e., barring a handful of exceptions, species usually move to lower elevations in winter. In case of range widths however, expansions (albeit, marginal) seem to be just as common as contractions.

from summer to winter had a mean value of -8.45% ($SD = \pm 116.9\%$). The distribution was slightly skewed towards range contractions in winter, though there were instances of range expansions as well. There were few extreme outliers, other than some 6 species with small numbers which were recorded at only 1 or 2 locations in winter.

Regressions for altitudinal shift and mass, residual wing and residual Beak are shown in Figure 5.3. Table 5.1 shows the Spearman's rank correlation and weighted linear regression values of the difference between mean summer and winter elevations against species-level traits. There was a significant negative correlation between change in elevation and body mass, wing length as well as beak area ($p < 0.005$). Negative regression slope values at the 95% confidence interval corroborated this result. However, neither residual wing, nor residual beak showed a significant relationship with migration propensity.

Of the 5 groups based on dietary preferences (Figure 5.4), nectarivores and birds of prey had too few species for meaningful inference. The median value for shift in insectivores was significantly positive ($\alpha = 0.05$), which indicated that they tend to move to lower elevations in winter. Corresponding values for omnivores and frugivores were not sufficiently different from zero (no change). Based on habitat preferences, there were only 3 species that preferred open habitats and 81 that were found in forested areas. Comparisons between such disproportionate groups would provide little wisdom. Of the 5 groups based on foraging height, only one species belonged to the river-bed group. Among the

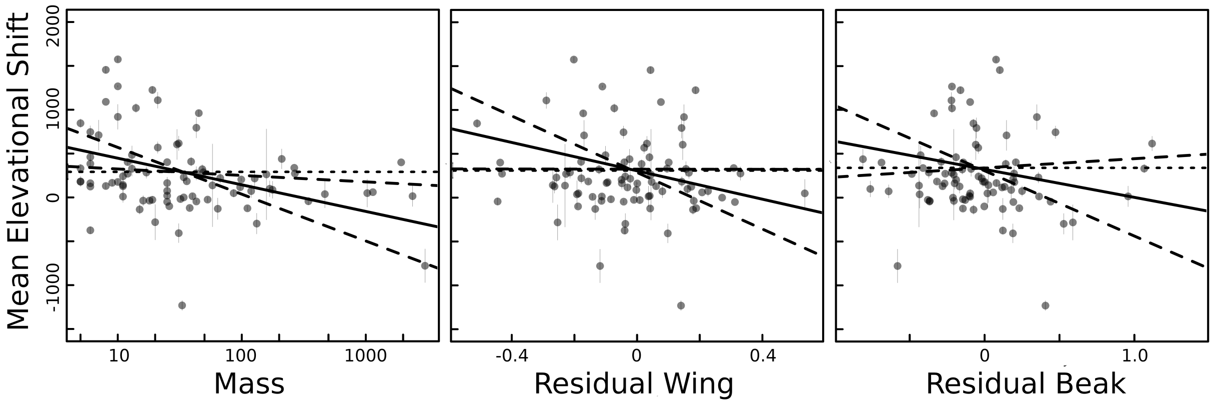

Figure 5.3: Weighted Linear regressions of species mean elevation shift against traits.
There is a significant negative correlation between shift and body mass, and perhaps residual wing. However, residual beak does not show a significant correlation at the 95% confidence level.

rest, species that preferred mid-canopies and bushes tended to move to lower elevations in winter, while those that were ground dwelling or preferred canopy tops were consistent with no change. Based on primary substrate, those that prefer leaves, mosses or are airborne seemed more likely to migrate to lower elevations in winter, whereas those that prefer the ground, fruiting bodies or tree barks showed no significant change in mean elevations between seasons. There were too few species in our dataset that preferred mosses or flowers for us to be able to infer their migratory patterns.

Based on classification by spatial distribution (Figure 5.4), hill residents, hill breeders and species that maintained distributions in both hills and plains showed significantly positive median values for elevational shift, whereas those species which had known distributions only in the plains were consistent with no shift. However, for this as well as the previous set of characterizations, differences between categories were not significant.

Our estimates for Pagel's λ across the 1000 phylogenetic trees (consensus tree in Figure

Relationship	Correlation			Regression		
	R	CI95%	p	Slope	CI95%	p
$\Delta E_M \sim log(Mass)$	-0.32	(-0.48, -0.12)	0.0034	-303.3	(-533.2, -73.4)	0.01
$\Delta E_M \sim log(Wing)$	-0.33	(-0.50, -0.13)	0.0021	-557.0	(-871.2, -242.9)	< 0.01
$\Delta E_M \sim log(Beak)$	-0.38	(-0.54, -0.19)	0.0004	-517.2	(-767.8, -266.6)	< 0.01
$\Delta E_M \sim Res.Wing$	-0.08	(-0.29, 0.13)	0.4463	-808.3	(-1611.7, -5.0)	0.049
$\Delta E_M \sim Res.Beak$	-0.13	(-0.34, 0.09)	0.2319	-319.6	(-744.2, 104.9)	0.138

Table 5.1: Correlation and Regression between elevational shift and traits.
Statistics quoted are of Spearman's rank correlation and weighted linear regression respectively.

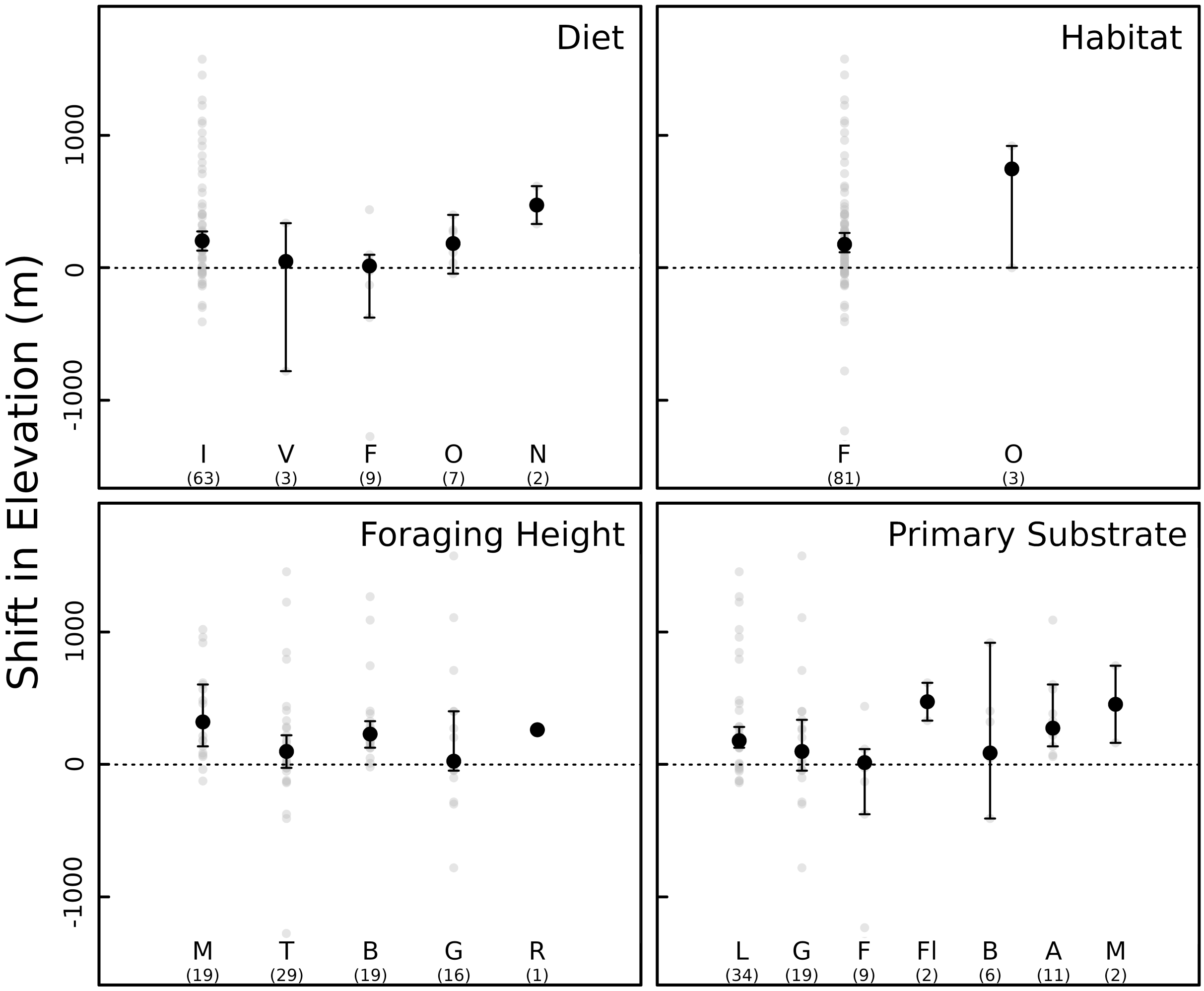

Figure 5.4: Elevational shift in species categorised by dietary/habitat preferences.
We grouped species based on Diet (Insects, Vertebrates, Fruits, Omnivore, Nectar); Habitat (Forest, Open); Foraging Height (Mid-canopy, Top of the canopy, Bush, Ground, River-bed); and Primary Substrate (Leaf, Ground, Fruiting bodies, Flowers, Bark, Air, Moss). Black dots denote the median values of elevation difference between summer and winter, while whiskers denote the 95% confidence interval of the difference in medians. The number of species in each category is mentioned within parentheses.

5.6) had a mean value of 0.39 and a 95% confidence interval of [0.29, 0.44], indicating a moderate consensus between altitudinal migration and phylogeny.

5.5 Discussion

In this chapter, we looked at altitudinal migrations, both in terms of changes in mean elevation as well as the width of species distributions between breeding and non breeding seasons. Additionally, we tried to determine the role of intrinsic factors on the migratory propensity of species. Specifically, we looked for relationships between mean shift in ele-

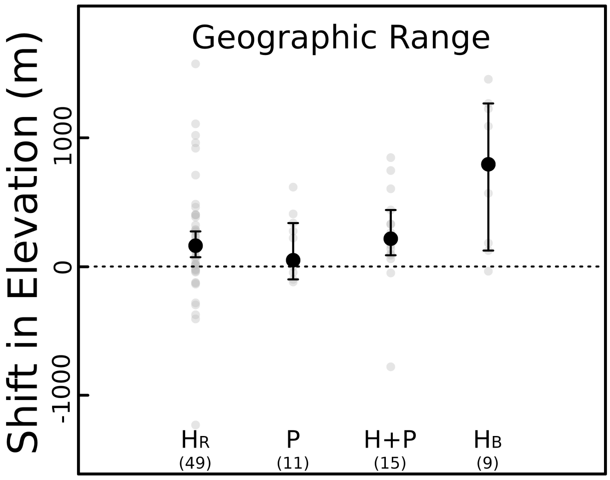

Figure 5.5: Elevational shift in species categorised by their global distribution.

We grouped species based on whether they had (i) Resident populations in the hills alone, (ii) Breeding populations in the hills, (iii) Resident populations in the hills and plains and (iv) Populations in the plains alone. Black dots denote the median values of elevation difference between summer and winter, while whiskers denote the 95% confidence interval of the difference in medians. The number of species in each category is mentioned within parentheses.

vation from summer to winter and traits (body size, wing span and beak size), dietary and habitat preferences and spatial distribution (whether the species has known distributions outside the Himalayas).

We found that a sizeable number of species tend to migrate to lower elevations in winter. However, there also were species that showed no change in elevation, as well as a few others that seemed to move to higher elevations. We also found that instances of range contraction were slightly less common than range expansions. Either way, changes (especially expansions) of the order of the range width itself (or greater) were rare. Small-bodied species were more likely to migrate to lower elevations in winter, while larger species tended to remain stationary. We found no influence of wing length or beak area in excess of allometry. Insectivores were the only dietary group that showed a clear propensity to move to lower elevations in winter. Based on foraging height in canopies, mid-canopy and bush dwellers showed a clear signal of moving to lower elevations in winter. Additionally, species that preferred leaves, mosses or were mostly airborne seemed to migrate to lower altitudes. Hill residents, hill breeders as well as species that have distributions in both hills and plains seemed to move to lower elevations. Only species with described distributions in the plains alone seemed to show no significant change in elevation between summer and winter. In our phylogenetic analyses, we found some signs of species with similar migratory propensities clustering together and a moderately sig-

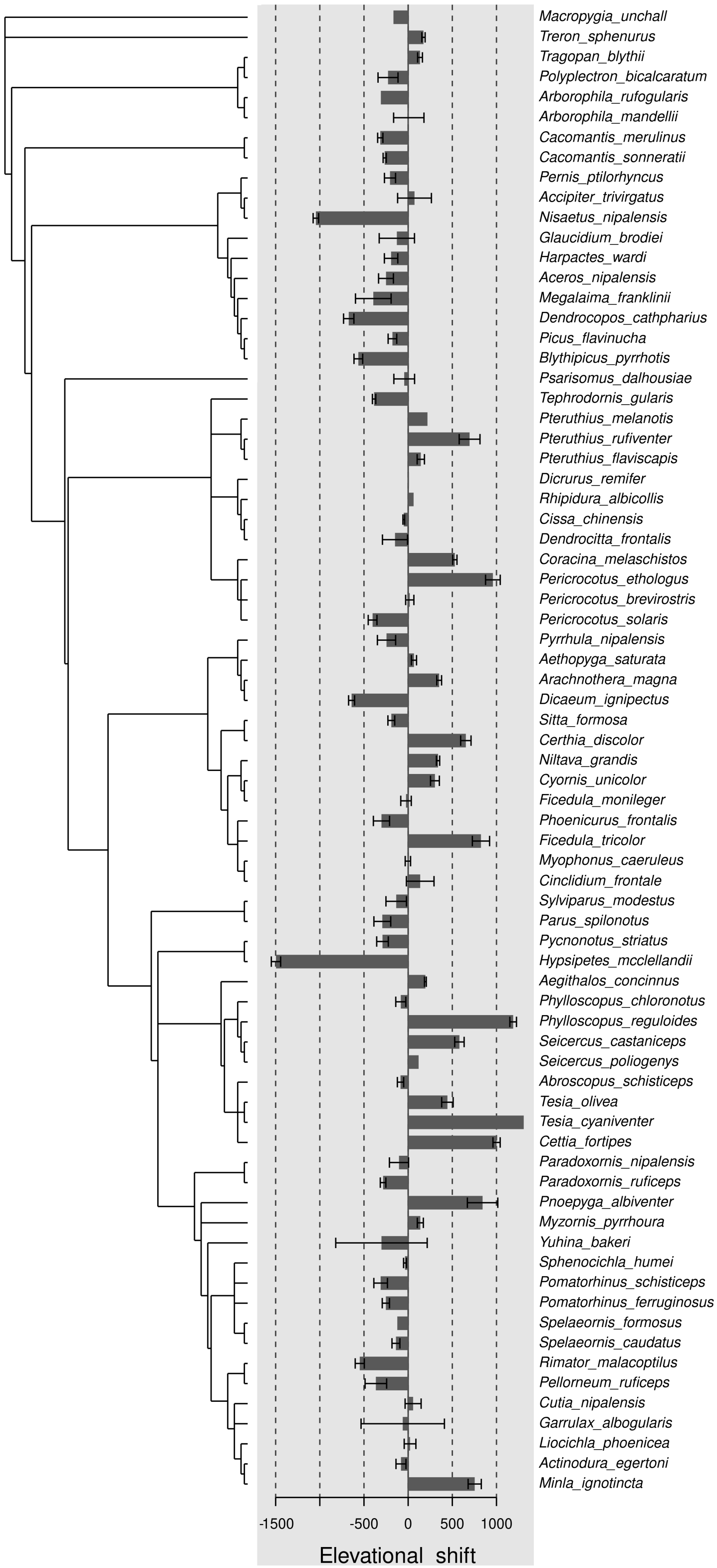

Figure 5.6: Mean elevation shift in species plotted against their phylogeny. *The phylogeny is a consensus of 1000 trees derived from Jetz et al., 2012. We notice some clustering in species that show a big shift between summer and winter.*

nificant correlation between migratory propensity and phylogeny.

Thus, in general montane species either remain stationary, or move to lower elevations in winter, barring a few exceptions that move to higher elevations in winter. These species are perhaps cold-adapted and have evolved strategies to make the best of the low levels of competition in these high elevation habitats while the bulk of the community migrates to warmer regions downhill. However, we know very little about such species at the moment and would require focussed studies to understand their strategies. The width of species distributions seemed marginally more likely to contract in winter rather than expand or remain unchanged. This result is consistent with our previous findings of narrow, but sharply peaked winter distributions.

The propensity for altitudinal migration has a clear relationship with body size, which in turn is directly related to metabolism and thermoregulation. That larger bodied organisms are better at maintaining body temperature has been known for nearly 200 years (Bergmann, 1847), but there is considerable disagreement over its generality (Salewski & Watt, 2017; Meiri & Dayan, 2003; Fan et al., 2019). A study on the same community of birds from our lab along this very gradient (Mungee et al., 2021) found strong evidence for a negative-Bergmann pattern, i.e. body size declined with increase in elevation in summer. This information in combination with our current findings may indicate that montane gradients allow small-bodied birds to exploit high altitude resources in summer and move to warmer lower elevations in winter at the cost of a (relatively) short journey.

We find no evidence for any relationship between flight ability and migratory propensity - which is perhaps because the entire elevational gradient can be covered in a trip as short as 15 kilometres. We also report the absence of any dependence on beak area despite our thermal radiation hypothesis. Though there is evidence of using beak surface area for thermoregulation (Friedman et al., 2017, 2019), beak structure is perhaps more optimized towards its primary function - foraging.

Insectivores exhibited a high propensity for migration towards lower elevations in winter - this is possibly because their distribution follows that of the insects that comprise their diet - these are ectotherms and probably prefer the warmer lower elevations, or become dormant and impossible to find at high elevations in winter. Species that forage in the mid canopy and bush, as well as leaf, air and moss dwellers prefer to move to lower elevations in winter, but it is as of yet unclear which among these groups are driven by food availability as opposed to the local microclimate.

The median shift between summer and winter was consistent with no change only for species with plains restricted distributions. Hill residents, hill breeders as well as those with resident distributions in both hills and plains all showed migrations to lower elevations in winter. However, all the plain restricted species had low-mid elevational distributions, with relatively milder winters and lower pressure to migrate. The crested goshawk was the highest among the group, with its mean summer and winter elevations being 1787 and 1450 m respectively.

In contrast to Lugo Ramos et al. (2017), our moderate but significant value of Pagel's λ suggests there is some synchrony in the evolution of altitudinal migration (or lack thereof) between sister species. However, deeper and more focussed investigations (perhaps using traits relevant to migration for phylogenetic reconstruction) could yield more meaningful insights.

Factors such as food limitation, predation and climate that drive long-distance migrations are also likely to apply in case of altitudinal migration. However, it is hypothesized that over short spatial scales, these extrinsic drivers may act synergistically with species-specific requirements, resulting in migratory behaviours that are much more plastic as compared to their long-distance counterparts (Hsiung et al., 2018). As a result, we often see flexible partial migratory syndromes along montane elevational gradients, with a mix of migratory and stationary individuals/populations (Norbu et al., 2013). This probably explains why we see quite a few species that show a smaller (secondary) peak in their winter distribution. There could also be changes in visibility/detection between summer and winter. It would be very interesting to be able to look at these species distributions in more detail to try and better understand partial migrations.

Despite their ubiquity as well as sensitivity to global change, there are very few multi-species studies of altitudinal migration. Several recent studies highlight the fragility of migratory behaviour as they begin disintegrating with the advent of climate change (Crick, 2004; Wilcove & Wikelski, 2008; Wilcove, 2010). More such studies are the call of the hour, especially in tropical mountains that are hyper-diverse as well as particularly vulnerable to habitat fragmentation and global change (Eguiguren-Velepucha et al., 2020).

6 | Conclusion

6.1 Summary

We have demonstrated a recipe for testing theoretical models of the environment-abundance paradigm with field data along elevational gradients. This was possible primarily owing to three characteristics of such landscapes:

1. They are essentially univariate, since biologically relevant factors are tightly correlated with elevation.
2. They are effectively one-dimensional, i.e., the environment changes rapidly along the slope but remains relatively unchanged for large stretches along contours.
3. They significantly reduce the sampling effort required to record the complete distribution for a large number of species.

We have shown that abundance distributions along such gradients are best described as bell-shaped, since the community average profile shape was consistent with gaussian distributions, characterized by the presence of a peak as well as tails. Additionally, community asymmetry was consistent with the Abundant centre hypothesis, since community mean asymmetry was consistent with zero. We also show that distributions get progressively compressed at high and low elevation limits, resulting in a small amount of residual asymmetry that mainly comes from range-edge populations.

Analysis of abundance, extent and RMSD of distributions suggests that summer distributions have soft boundaries and may be at carrying capacity. We failed to establish significant relationships for both cases in winter, which probably suggests that strategies to accommodate growing population densities are more varied in winter.

We also looked at the impact of altitudinal migrations on distributions between summer and winter. We found that species were more likely to move to lower elevations in winter, but range expansions were as common as range contractions. We have also shown that migratory propensity is anti-correlated with body size, but does not depend on flight ability. We found some correlation in certain habitat and dietary preferences as well as phylogenetic relatedness with migratory propensity. However, a more thorough investigation that includes a larger number of species is required for clearer, more definitive patterns.

6.2 Conservation implications

Several aspects of this research can potentially influence conservation policies, especially in the context of climate change.

- In Chapter 2, we describe procedures to estimate the width of species distributions in a reliable and ecologically relevant manner. Reliable estimation of the extent of species ranges are crucial to both determining priority areas for conservation of threatened taxa, as well as monitoring their ranges over time.
- In Chapter 3, we show that abundance distributions along elevational gradients are peaked, with extended tails on either side. We also find that the distributions are symmetric at mid-elevations, but become compressed at both lower and higher elevations. This seems to suggest that both lower and higher elevation habitats are high-stress environments – the former, perhaps related to crowding, and the latter to extremes of environment. This is particularly relevant in the context of global warming, as organisms are expected to move upwards in search of suitable habitats. This is highlights the vulnerability of montane ecosystems in general, and high elevation species in particular to climate change.
- Our findings in Chapter 4 seem to suggest that summers in montane environments find communities at their carrying capacity, and are more conducive to density driven range expansion. We are not quite sure what happens in winter, but a change in patterns between seasons suggests a stark difference in the processes that shape communities. This highlights the need for year-round monitoring of at-risk ecosystems.
- In Chapter 5, we explore elevational (or short distance) migration in the bird community. There are reports from all over the world about short-distance migration is the most vulnerable of all migratory behaviour in the face of climate change, and how it is already changing rapidly with changes in global climatic patterns. We show that most species in Eaglenest migrate to lower elevations in winter, and the fact that this is somewhat correlated with thermoregulation suggests that this may be crucial for survival to the next breeding season.

Overall, these are novel findings from what to the best of our knowledge is the largest systematically collected primary dataset for birds in the eastern Himalayas – the 6th most biodiverse region in the world, second only to the Andes in terms of passerine diversity.

6.3 Global Perspective

6.3.1 The western Himalayas

The eastern Himalayas differ from the western Himalayas in two key aspects which may be relevant.

- climatic regimes – as a result of which they are much more biodiverse
- anthropogenic disturbances are higher in the western Himalayas, which will impact connectivity between habitats, hindering dispersal.

Uninterrupted elevational transects like the one in our study are very rare in the western Himalayas, where the valley floor is often as high as 1200 m. However, if a similar sampling effort could be carried out on a continuous south-facing slope of the western Himalayas while minimizing disturbances, in principle one could expect similar overall patterns, albeit with fewer species in comprising communities.

6.3.2 Other mountain ranges

The east-west orientation of the Himalayas minimizes latitudinal variation in habitat type and connectivity across the range. A handful of ranges in the world have a similar orientation. Ranges such as the Western Ghats, Andes and Appalachian Mountains are north-south oriented, as well as lower than the Himalayas in terms of their elevation. This means that biologically relevant environmental variables change along contours as well, which violates the assumption of a unidimensional system. This is bound to impact the patterns one might observe, but exactly how they will differ from our observations remains an open question.

In conclusion, we suggest that a global network of such studies with a variety of taxa and landscapes can help establish general patterns with respect to species distributions. Anchoring them to analytical frameworks that comprise testable hypotheses is a particularly crucial step towards an understanding of the ecological processes that underlie species distributions. Community-wide studies may also help elucidate the role of biotic interactions in determining distribution shapes. In conclusion, studies such as this not only are a step forward in terms of mechanistic understanding, but also shed light on poorly studied tropical montane ecosystems that are particularly vulnerable in the current era of biodiversity loss and global change.

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