Elevational patterns of diversity in ant communities in the Eastern Himalayas

विद्या वाचस्पति की
उपाधि की अपेक्षाओं की आंशिक पूर्ति में प्रस्तुत शोध प्रबंध

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To my late grandmother who I dearly miss.

A woman ahead of her times.

CERTIFICATE

Certified that the work incorporated in the thesis entitled **Elevational patterns of diversity in ant communities in the Eastern Himalayas** submitted by **Netra Kadambi** 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.



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I declare that this written submission represents my idea in my own words and where others' ideas have been included; I have adequately cited and referenced the original sources. I declare that I have acknowledged collaborative work and discussions wherever such work has been included. 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

The work reported in this thesis is the original work done by me under the guidance of Dr.Ramana Athreya



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As I contemplate the last few years, I feel amazed and bewildered in equal measure. Amazed at how far I have come, but bewildered at how I made it this far despite choosing some of the most meandering paths with no end in sight.

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Synopsis

Elevational patterns of diversity in ant communities in the Eastern Himalayas

Montane ecosystems serve as natural laboratories to investigate biodiversity patterns across climatic gradients. Most studies have examined the effect of macroclimatic variables that correlate with elevation, such as temperature, in shaping communities. However, the role of microclimatic variables in modifying elevational responses of communities remains poorly understood. Local topographic factors, such as aspect and inclination, can significantly affect the diversity and composition of communities independent of elevation. This dissertation attempts to address this gap with a comparative study of ant communities (Family: *Formicidae*) on two mountain slopes differing in aspect, inclination and summit height in the eastern Himalayas. However, we recognise that the two mountain slopes, on the northern and southern faces of the same range, differ in multiple ways from each other, and separating their individual contributions is a challenge.

Ground-dwelling terrestrial insects are known to respond more sensitively to microclimatic variation and edaphic factors, both of which can vary from one slope to another in a region. Additionally, the responses of communities on the same slope may vary in different taxa. To evaluate whether distributional patterns are taxon-specific, we compared ant diversity profiles with other taxa—*Sphingidae* (hawkmoths) and *Aves* (birds)—sampled on the same slope across several spatial and taxonomic scales. Eastern Himalayas are highly-folded ranges with steep elevational gradients, providing an excellent system to study the role of different environmental and geographic factors shaping diversity.

We collected individuals spanning 40 genera of ants along three elevational transects on two mountain slopes; inside Eaglenest wildlife sanctuary and near Khupi village. Both mountain slopes are located in West Kameng district of Arunachal Pradesh. Along each transect spanning 1000–2000 m a.s.l., we sampled at intervals of 30 m ground distance, with each sampling location consisting of a set of three quadrats spaced 10 m apart, approximately perpendicular to the local gradient. Following usual practice, we estimated the abundance of a genus as the number of

quadrats in which it occurred, and not by counting the total number of individuals. This yielded 3,090 total genus-quadrat records, split almost evenly between the two mountain slopes (1,577 and 1,513 records, respectively). The hawkmoth and bird dataset used in this thesis was collected by Mansi Mungee and Rohan Pandit along the same transect in Eaglenest.

Elevational profiles of alpha diversity: We investigated the alpha diversity elevational communities of ants in the study region and compared it to those of birds and hawkmoths. We also compared diversity profiles in ant communities on two mountain slopes which differed in climate and topography. Diversity estimates are dependent on the spatial and taxonomic scale of measurement, making associations between diversity and environmental variables also sensitive to measurement scales. We tested taxonomic and spatial scale–dependent variation in diversity profiles of birds and hawkmoths along the same transect (as ants) in Eaglenest. We used generalised additive models (GAMs) to quantify the diversity–elevation relationships under different sampling scenarios. We observed no change in the profiles of hawkmoths and birds when the data was truncated to two-thirds (700–2300 m) of the sampled extent. However, we found an unexpected increase in curvature when we truncated the bird and hawkmoth data to one-third (1100–1900 m) of sampled extent. However, this was likely due to a single outlier at 1100 m. We also demonstrated the convergence of diversity–elevation relationships into simpler linear patterns when biodiversity was measured at higher taxonomic levels or with limited taxonomic coverage. Despite differences in topography, ant communities on the two mountain slopes exhibited similar monotonic decline of diversity with elevation. We note that many studies across the world are limited in taxonomic scale and spatial coverage (<1000 m elevation) for reasons of logistics and resources; their interpretations have to be treated with caution in the light of these results.

Beta diversity across spatial and taxonomic scales: Taxonomic composition of communities changes rapidly along elevational gradients due to environmental filtering and stochastic processes. However, little is known of how elevational profiles of beta diversity are modified by microclimatic variation associated with topographic factors, or how they compare with horizontal (within-elevation) heterogeneity. Furthermore, few studies have examined the extent of congruence in beta diversity profiles of different taxa sampled along the same transect. We observed a doubling in the magnitude of beta diversity change per kilometre of elevational distance in ant communities on the more steeply inclined, north-facing Khupi slope. While turnover dominated on both the slopes, we observed an increase in nestedness in Khupi. This could be due to attrition of communities at higher elevations, since we sampled close to the ridge in Khupi. We also found that incomplete sampling, resulting in an inverse relationship between beta diversity estimates and abundance, may lead to

overestimation of beta diversity. Hawkmoth and bird species exhibit similar beta diversity profiles across elevational spans of ~1000 m that ants were sampled in. However, across the full extent of 200-2800 m, the profile of beta diversity was steeper in birds than in hawkmoths.

Elevational responses of ant functional guilds: Functional composition of communities is dictated by interaction of traits with their environment (abiotic, biotic) and resources, both of which change with elevation. We investigated the effect of small-scale topographic and associated microclimatic drivers in influencing elevational patterns of functional alpha and beta diversity in ant communities. Ants perform a wide range of functions across several dimensions such as thermal niche, trophic position and competitive abilities. We assigned the sampled ant genera to one of many guilds along each of these three dimensions to identify functionality patterns at each elevation. The combination of a flat elevational profile of functional alpha diversity and a decreasing taxonomic diversity profile indicated high functional redundancy in the ant communities. We observed no difference in the composite patterns of functional beta diversity between Eaglenest and Khupi. However, elevational profiles of individual guilds differed between the sites. In other words, the same functional space was occupied by different guilds/genera in the two sites. Seven of the eleven functional guilds showed strong elevational trends in relative abundance and functional beta diversity in Khupi, compared to only two of eleven in south-facing Eaglenest.

In summary, we systematically collected and curated a large dataset of a highly abundant and speciose group of insects from a global biodiversity hotspot with scarce representation. We highlight the need to consider both macroclimatic and microclimatic gradients when analysing elevational diversity patterns, especially in ground-dwelling terrestrial groups with limited dispersal abilities. Our findings reveal the utility of sampling multiple cross-sections of mountain slopes within a region to capture sufficient topographic heterogeneity, which may aid in teasing apart the contributions of macroclimatic and microclimatic variations in the observed diversity patterns.

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Chapter One

Introduction

The spatial distribution of life on Earth is markedly uneven, with certain regions supporting disproportionately higher levels of biodiversity than others (Myers et al., 2000). Tropical regions, for instance, host remarkable diversity in comparison to highly depauperate temperate ecosystems close to the poles (Arita & Vazquez-Domingues, 2008). This gradient in diversity across latitude, a.k.a. Latitudinal Diversity Gradient, is a widely recurring pattern in both terrestrial and marine ecosystems (Hillebrand, 2004). Investigators have tried to determine the key drivers of such broad-scale floral and faunal distributional patterns for more than a century. Multiple hypotheses have been put forth to explain the latitudinal pattern, all of which employ a range of ecological (climate & biotic), evolutionary (net diversification rates), geological (age, orogeny) and geometric (area, mid-domain effect) factors to explain the observed patterns (Willig et al., 2003; Allen & Gillooly, 2006; Fløjgaard & Svenning, 2012; Brown, 2013; Kinlock et al., 2017; Pontarp et al., 2019; Y. Zhang et al., 2022). However, mechanistic links between these drivers and the latitudinal diversity pattern remain elusive, due to their spatial co-occurrence (Mannion, 2020).

Much of our current knowledge on biodiversity patterns comes from examining changes in taxonomic diversity, i.e. species richness, evenness and turnover (Meynard et al., 2011; Stevens et al., 2013). Approaches such as rank-abundance plots or species-sorting models are commonly employed methods among investigators to examine taxonomic (species) diversity patterns (Matthews & Whittaker, 2014). Such analyses treat species as functionally and evolutionarily equivalent, disregarding their differential contributions to ecosystem functioning and any implications of shared ancestry (Tilman, 2001; Swensen, 2011; Arnan et al., 2015). Also, the same taxonomic diversity patterns can emerge from fundamentally different processes — niche-based (e.g. environmental filtering, competition) or stochastic (dispersal, drift) — hindering our ability to determine the primary drivers of observed patterns (Chisholm & Pacala 2010). Recent frameworks that incorporate functional and phylogenetic data alongside taxonomy help disentangle the relative

contributions of niche-based and stochastic processes (Stegen & Hurlbert, 2011; Gianuca et al,. 2017). For instance, similarity in ecology (e.g., diet, body size, thermal tolerance) or phylogeny (degree of relatedness) can shape coexistence patterns driven by environmental filtering and limiting similarity (Kraft et al., 2015). Thus, approaches that move beyond examining just taxonomic diversity patterns, by incorporating functional and/or phylogenetic dimensions of diversity, allow us to form a clearer understanding of how communities assemble.

The nature and magnitude of the processes influencing diversity are scale-dependent (Rahbek, 2005; Tordoni et al., 2024), making it essential to study the various dimensions of diversity (taxonomic, functional, phylogenetic) at both local (alpha diversity) and regional (gamma diversity) spatial scales (Stefanidis et al., 2023; Li et al., 2024). For instance, environmental filtering may result in the significant turnover of mean trait values across a region (beta diversity). These patterns of change across the region may vary across the three diversity dimensions. It is widely accepted (though inadequately tested) that biotic interactions (e.g. competition) drive assembly at local scales, while regional-scale assembly patterns are more influenced by environmental filtering and stochastic processes (Slingsby et al., 2006; Cavender-Bares et al., 2009). Examining both alpha and beta diversity provides complementary information regarding the assembly rules shaping richness and composition of local communities (Bernard-Verdier et al., 2012).

1.1 Elevational Gradients: Opportunities and Challenges

Apart from latitudinal diversity gradients, elevational diversity gradients have been widely studied across the world (Guo et al., 2013). Studies of montane ecosystems have surged, especially with the recognition that they are major biodiversity hotspots. Mountains occupy only about 25% of the terrestrial surface yet harbour approximately 85% of the world's amphibian, bird, and mammal species (Rahbek et al., 2019). However, the mechanisms underlying the exceptional diversity remain poorly understood (Perrigo et al., 2019; Graham et al., 2025). In the context of accelerating climate change, widespread land-use transformations, and the associated loss of biodiversity, it is increasingly urgent to improve our understanding of the ecological and evolutionary processes that generate and sustain these hyper-diverse montane communities.

Montane systems provide unique opportunities to investigate the processes driving the origin and maintenance of diversity for several reasons. The existence of multiple, geographically distinct mountain ranges – each with its own evolutionary and biogeographic history – creates replicated natural laboratories along environmental gradients (Körner, 2007; Rahbek et al., 2019). Comparative analyses across these systems facilitate tests of the generality of mechanisms shaping species distributions (Graham et al., 2025; Rahbek et al., 2019). Elevational gradients are particularly tractable for empirical study. Unlike latitudinal gradients, they extend across relatively short geographic distances, facilitating efficient sampling of speciose communities (Lomolino, 2001; McCain, 2005). Despite their compact spatial scale, elevational gradients may capture nearly a large range of habitat type — from tropical lowland forests to alpine environments — spanning diverse climatic regimes that parallel latitudinal gradients (Colwell et al., 2016; Körner, 2007). Moreover, the temperature gradient across 1000 m of altitude in a tropical mountain is equivalent to that across 1000 km of latitude. This pronounced climatic and resource heterogeneity promotes high regional diversity through rapid species turnover (McCain & Grytnes, 2010; Sundqvist et al., 2013). Additionally, the complex topography of mountains creates a mosaic of microhabitats, enhancing local-scale diversity and generating fine-grained ecological variation (Rahbek et al., 2019; Stein et al., 2014).

Despite significant advancements, our knowledge of the mechanisms structuring biodiversity within montane systems, particularly along their steep elevational gradients and complex topographic relief, remains limited (Elsen & Tingley, 2015; Graham et al., 2025). A major challenge is that biodiversity and its spatial variation are inherently scale-dependent (Gerstner et al., 2024; Peters et al., 2016; Spake et al., 2021). The spatial extent and resolution, along with the taxonomic resolution employed, impact our estimates of biodiversity (Guo et al., 2013; Nogues-Bravo et al., 2008; Peters et al., 2016). Addressing scale dependencies such as these is therefore critical for advancing our understanding of montane biodiversity.

Studies of elevational gradients widely employ interpolated macroclimatic data at coarse scales of 30 arc-second (~1 km at the equator) resolution (Lembrechts et al., 2019). While this approach may be adequate on flat (homogenous) terrain, increased structural complexity characteristic of urbanised or rugged landscapes often results in fine-scale heterogeneity in abiotic conditions

(Lembrechts et al., 2019). For instance, in rugged landscapes such as montane ecosystems, circulating air (dry/wet) and solar radiation interact with topographical features such as aspect, slope inclination and vegetation cover, creating local topoclimates (Dobrowski, 2011; Randin et al., 2009). The vertical dimension, or strata, in forest systems contributes to microclimatic heterogeneity, with sub-canopy temperatures at times 5°C lower than in comparable forest clearings (Chen et al., 1999). Studies have shown that microclimatic differences along the vertical dimension are important in shaping community composition. For instance, at the community level, arboreal ants consistently exhibit higher heat tolerance thresholds (CT_{max}) compared to ground-dwelling ants (Leahy et al., 2022), regardless of phylogenetic relatedness. It is not just that temperatures differ between the sub-canopy and above-canopy layers; the association between them is also partially decoupled, reflecting the different processes regulating ambient temperature in each layer (Schilperoor et al., 2020). Hence, both topographic and microclimatic heterogeneity operating at finer spatial scales, especially in highly rugged montane landscapes, may modify broad-scale effects of macroclimatic variables on assembly patterns (Lippok et al., 2014; Opedal et al., 2015).

1.2 Motivation for this study

The Himalayas hosts some of the highest terrestrial massifs on earth. The ranges extend for about 2400 km long, from Pakistan in the north-western extreme to China and the border with Myanmar in the far eastern stretches. The Himalayas are wider in the west (400 km in Kashmir) but much narrower in the east (150 km in Arunachal) due to differences in tectonic pressure along their east-west span. These differences in the orogenic formation along its length have resulted in topographical and climatic variation (S. P. Singh et al., 2019). The eastern stretches of the Himalayas are much steeper than the more gradually rising western stretches, forcing rapid ascent and adiabatic cooling of monsoon-bearing winds originating from the Bay of Bengal throughout summer. This leads to more intense and evenly distributed rainfall across all elevational bands (Yadav et al., 2024). On the other hand, monsoonal winds during mid-summer from the Arabian Sea significantly deplete their moisture over western and central India before they reach the western Himalayas. Thereafter, monsoonal winds rise more gradually in the western Himalayan ranges, progressively emptying out at several lower ridges, leading to more moderate and uneven rain across elevation (Yadav et al., 2024). While the western Himalayas receive less summer rainfall

than the eastern stretches, their unique topography facilitates greater winter precipitation (snowfall) compared to the eastern Himalayas (Singh & Kumar, 1997).

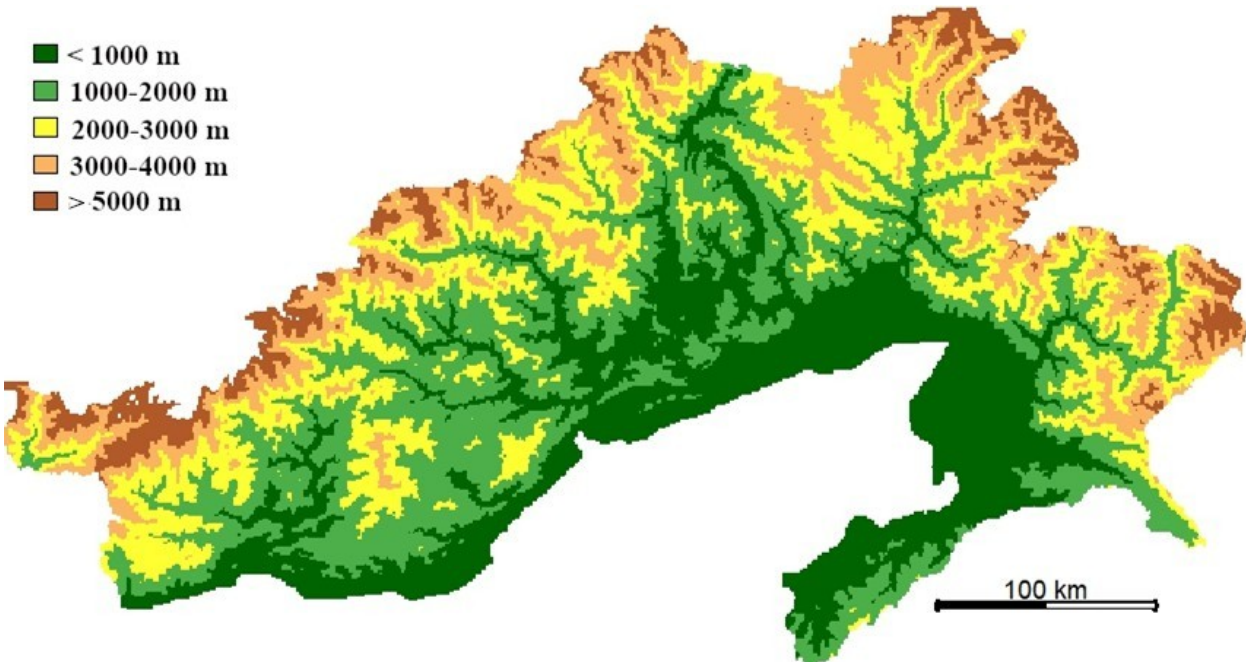


Figure 1.1: Terrain map of Arunachal Pradesh located in Eastern Himalayas showing five distinct elevational bands (< 1000 m, 1000–2000 m, 2000–3000 m, 3000–4000 m, > 5000 m) represented by distinct colours (as shown in the legend). The scale bar indicates aerial distance in kilometres. Data on elevation was obtained from the 30 arc-second (~1 km) SRTM-based DEM and projected to UTM Zone 46N.

We observe more tropical conditions in the lower elevations in the east lowlands but more arid, seasonal temperate climates in the north-west. The tropical-temperate gradients observed across the length and height of the Himalayas are closely associated with turnover in the vegetation type (Leng et al., 2024; Ohsawa, 1993). Along with differences in assemblage composition, structural differences include significant shifts in the position of the tree line, which is much higher in the Eastern Himalayas (3800–4200) compared to the western Himalayas (3300–3600 m) (Peili et al., 2020). This is due to the longer growing season in the east as a consequence of lower latitude (27°–30°N in the east, 28°–37°N in the west), reduced seasonality and higher precipitation (Singh et al. 2019). The eastern Himalayas consist of highly folded mountains, unlike the more widely spaced western Himalayas. This configuration retains more radiative heat within (narrower) valley systems, contributing to the higher tree-line (Joshi et al., 2024; Kattel et al., 2019).

Contemporary climate (warm and wet), complex topography and evolutionary legacy of the eastern Himalayas explain its status as a global biodiversity hotspot. Situated at the junction of Myanmar, China and India, the region exhibits the admixture of Indomalayan, Sino-Japanese and Palearctic elements. Studies from this region are dominated by mammals (22%), followed by angiosperms, birds and arthropods, with very few studies conducted on lower-order taxonomic groups (Basnet et al., 2019). Of the 161 studies on arthropods, most have focused on either species discoveries/descriptions or on fossil discoveries, rather than on biodiversity patterns (Basnet et al. 2019). A search using Web of Science yielded 80 papers that examined elevational diversity patterns of insects in the Himalayas. Only 13 of these investigated both alpha and beta diversity. Functional and/or phylogenetic studies are less numerous than taxonomic ones.

In spite of their exceptional biodiversity, the Himalayas are grossly under-represented in terms of the number of ecological studies and datasets. Our study contributes to this growing body of research by investigating community assembly patterns. We also highlight the influence of spatial and taxonomic scales in shaping our inferences about diversity patterns by conducting comparative analyses across distinct taxa (ants, hawkmoths, birds) sampled from the same mountain slope but with widely differing life-history strategies. Such multi-taxon approaches facilitate the separation of taxon- and environment-specific factors driving distributional patterns.

We sampled ant communities along two mountain slopes differing in slope aspect, inclination and height of the local massif. This sampling strategy allowed us to assess the contributions of small-scale microclimatic and broad-scale elevational effects on community assembly. We examined both taxonomic and functional assembly patterns to first quantify elevational and slope-specific shifts in taxonomic richness and community composition, and to evaluate whether these shifts are accompanied by changes in ecological strategies.

Ants (Family: Formicidae) are an excellent system to address these questions. The local diversity and biomass of ants in most biomes (forests to deserts) far exceed those of other insect groups (Rosenberg et al., 2023). Ants span a broad thermal niche, dominate across a wide range of feeding niches, and occupy the vertical stratum from subterranean to canopy spaces (Leahy et al. 2021).

They span multiple orders of trophic levels; from sap-feeders and aphid tenders to seed harvesters and predators (Drager et al., 2023), although most ant species are omnivorous (Uhey et al., 2019). Ant species are known to have a narrow tolerance to soil moisture (Dahmns et al., 2005; Dauber et al., 2005; Heuss et al., 2019; Seifert, 2017) with moisture availability and variation strongly influencing their elevational distributions (Pérez-Sánchez et al., 2023). One study from the Australian Wet Tropics reported a strong shift in elevational composition of ant communities coinciding with the orographic layer, suggesting effects of seasonal stability in moisture availability as the driver of this pattern (Nowrouzia et al., 2016). It is known that resource utilisation by ants is dependent on both environmental variables (like temperature; Dunn et al., 2010) and their own idiosyncratic life histories (like nest size; Law & Parr, 2020).

Ants are eusocial, unlike many other insect families (e.g., hawkmoths) that are solitary. For eusocial insects, traits under selection are often at the level of the colony and not individuals (Wilson & Hölldobler, 2005). For instance, colony size shapes competitive ability, resource acquisition and stress tolerance (Gibb et al., 2023). In contrast, traits at the individual level (such as body size) determine fitness in solitary insects. Despite being ectotherms, solitary and eusocial insects may employ different strategies to thermoregulate (Perez & Aron (2020). Birds, on the other hand, can internally regulate body temperature and have a greater dispersal ability than ants. These differences in life-history are likely to impact assembly patterns for the three taxa experiencing the same environmental pressures. Therefore, we compared the diversity profiles of ants (determined in this thesis) with previous work from the same area on birds and hawkmoths.

In many terrestrial habitats, ants are the primary predators of other insects and soil invertebrates (Cerdá & Dejean, 2011). Species of *Oecophylla* in the Old World compete with insectivorous birds in the lowlands of montane ecosystems, resulting in mid-elevation peaks in bird diversity (Supriya et al., 2020; Srinivasan et al., 2024). Species of *Atta* and *Acromyrmex* genera are the primary herbivores in Central and South American forests (Swanson et al., 2019) *Pogonomyrmex* species compete with rodents and birds for seeds in desert biomes (Davidson, 1980). Ants are known to move comparable amounts of soil as earthworms, aiding in seed dispersal and influencing edaphic properties that exert bottom-up effects on plant communities (Cammeraat & Risch, 2008; Rocha et al., 2024). In summary, the abundance and distributional patterns of ant communities are

determined by both microclimatic and macroclimatic factors, helping us to separate the contributions of processes operating at different scales.

This thesis investigates elevational patterns of diversity of ant communities. It examines the way conclusions may be modified by methodological issues and biological factors beyond elevation (including sampling scale, taxon-specific life histories, microclimate and topography).

In Chapter Two, we provide a detailed summary of the study sites, along with the sampling methodology. We describe the ant dataset generated in this thesis and briefly outline the hawkmoth and bird datasets obtained by collaborators from the same area.

In Chapter Three, we examine spatial- and taxonomic-scale-dependent variation in taxonomic alpha diversity patterns across two invertebrate taxa (ants, hawkmoths) and one vertebrate taxon (birds). We also present the dependence of alpha diversity patterns on slopes differing in aspect, inclination, local elevational limit and possibly anthropogenic disturbance. While this study investigated the difference in communities between two slopes in the same region ascribing the differences to the individual factors was beyond the scope of this work.

In Chapter Four, we investigate elevational patterns of taxonomic beta diversity in ant, bird and hawkmoth communities sampled along the same mountain slope. For ant communities, we examine beta diversity patterns within and across elevational bands to assess the contributions of underlying macro- and microclimatic factors.

In Chapter Five, we focus on functional guild patterns (alpha and beta) in ant communities. We examine the role of elevation and local (slope-specific) factors in determining the relative abundance and the turn-over of different (functional) guilds in ants.

The references are all listed at the end of the thesis, along with an appendix containing the local taxonomic key to subfamilies and genera of Arunachal Pradesh. Finally, I provide a synthesis of my thesis along with possible future directions inspired by our results.

Chapter 2

Methods and Data

2.1 Study Area

Data from the present study was collected from Eaglenest Wildlife Sanctuary (27º02´–09´N 92º18´–35´E; 200–3,200 m) and Khupi Model Village (27º11´–27º12´N 92º38´–39´E). Both locations are in West Kameng district of Arunachal Pradesh **(Figure 2.1)**. Eaglenest Wildlife Sanctuary has been under protection since 1989 while forests around Khupi Model Village remain unprotected with a major national highway (NH13) passing through the region. Southern slopes in the region, such as Eaglenest Wildlife Sanctuary, receive almost twice as much rainfall annually (> 3000 mm) compared to northern slopes (< 1500 mm), such as Khupi Model Village (Choudhury, 2003). However southern slopes also experience longer periods of solar irradiation annually compared to northern slopes. Hence, moisture availability would depend on the balance between precipitation and evaporation cycles, and may differ across slopes. While there is occasional snowfall in the winter months above 2000 m in the southern slopes of Eaglenest Wildlife Sanctuary, it seems to occur as low as around 1750 m in Khupi (Choudhury, 2017).

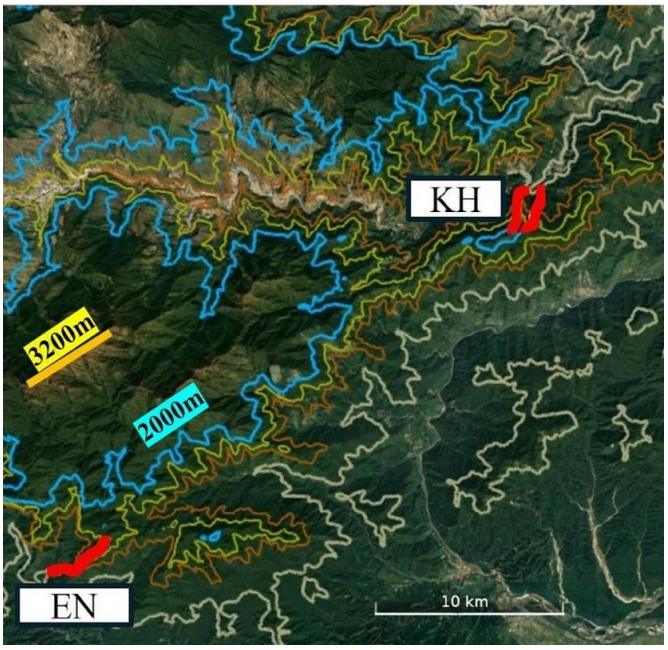


Figure 2.1: A contour map showing Eaglenest Wildife Sanctuary (EN) and Khupi Model village (KH). The map shows four contour lines spaced 250 m apart in elevation (1000 m a.s.l.– cream, 1250 m a.s.l.– brown, 1750 m a.s.l.– mustard, 2000 m a.s.l. – blue). Thick red lines represents the three elevational transects: one in Eaglenest (EN: 950 m–1850 m a.s.l.) and two in Khupi (KH1: 1150–2100 m a.s.l.; KH2: 1050–1950 m a.s.l.). The yellow bar represents the ridge located at 3200 m in Eaglenest. Note that the transects at Khupi (KH = KH1 & KH2) terminate at the local ridge (2100 m a.s.l.) just above the 2000 m blue contour line.

2.1.1 Eaglenest Wildlife Sanctuary

Eaglenest Wildlife Sanctuary is a small sanctuary covering area of 218 km^2 in the western part of Arunachal Pradesh. The Eaglenest Ridge (3200 m asl) towers its northern boundary beyond which lies the Bugun community reserve forest on the northern aspect. Most of the sanctuary lies on the southern aspect of the ridge. Towards its eastern edge lies the Tippi river which joins the Kameng river downstream, forming a natural boundary between the sanctuary, and Sessa as well as Pakke Tiger Reserve, found on the eastern banks of Kameng.

The sanctuary itself consists of largely intact forest across most of its elevational span with some disturbance (< 500 m) below its lower boundary. A unique feature of the sanctuary is the accessibility to its large elevational gradient via a dirt track passing from the lowlands (200 m asl) up to the Eaglenest Pass (2800 m asl). The dirt track was built for mobilisation of the 'Red Eagles' division of the Indian army and subsequently used by the Dalai lama in the 1950s in his escape from Tibet.

In the summer months (May-June), temperatures can rise above 25ºC in the lowlands with the higher reaches remaining cooler (10–20ºC). The vegetation across this large temperature gradient forms distinguishable zones with the tropical wet evergreen forests (< 900 m) in the upper reaches of Assam, the moist temperate forests (1500–2600 m) in the middle, transitioning into the moist deciduous forests above 2800 m (Champion & Seth, 1968).

While there are few ecological studies from the region, there has been a surge in both floral and faunal checklists over the past two decades. Birds, reptiles and mammals have been widely surveyed with very few checklists for insects and other arthropods, with the exception of Lepidopterans. A single study of ants from the region continues to yield several recent papers of newly discovered species (Aswaj et al., 2021, 2023; Marathe et al., 2021). However, very little is known of arthropod diversity from the region.

2.1.2 Khupi Model Village

Khupi Model Village is located approximately 25 km north-east of Eaglenest Wildlife Sanctuary in the West Kameng district of Arunachal Pradesh. The village is located close to the Trans-Arunachal

highway (NH13) on a north-facing slope at 1650–1750 m asl. The ridge lies at 2100 m compared to a much higher ridge (3200 m asl) at Eaglenest. Two rivers run on either side of the ridge at Khupi, namely Tenga river (900 m asl) below the north-facing slopes and Kameng river (400 m asl) below the south-facing slopes. There is continual human activity contributing to substantial disturbance in the proximity of the highway.

2.2 Ant Data

2.2.1. Field sampling and curation

Many studies sample different sections of the elevational gradient from different mountain slopes. This approach conflates elevation effects with microhabitat and topographical differences from the different slopes. This approach circumvents the issue of limited accessibility within a single slope to



Figure 2.2: Dirt track (left) and highway (right) at Eaglenest Wildlife Sanctuary and at Khupi respectively. The dirt track starts at Khelong camp site (700 m a.s.l.) to Eaglenest pass (2800 m a.s.l.). Below Khelong camp site, there is a tarmac road leading to the Kamengbari in Assam-Arunachal border via Doimara village (200 m a.s.l.). Beyond Eaglenest pass, the road leads to the Bugun Community reserve and Tenga valley along the north-facing slopes. At Khupi, sampling sites are below and above the Trans-Arunachal highway (1650 m). There is substantial human-induced disturbance close to the highway. The dirt track in Eaglenest is relatively less disturbed compared to the highway at Khupi.

all elevations. In our case, both the field sites provided access to all elevations via a dirt track in Eaglenest and a highway at Khupi **(Figure 2.2)**. Therefore, we could sample steep and geographically compact elevational transects at both sites.

We had a single local transect (900–1850 m) at Eaglenest and two local transects (1050–2100 m) at Khupi that were not more than 1.8 km apart. All three transects spanned comparable elevational extents. Apart from the highway interrupting at 1600–1700 m along the two elevational transects at Khupi, there were no apparent dispersal barriers along the full length of the three elevational transects. The local transects chosen were along slopes with largely undisturbed forests. All sampling was carried out in the monsoon season (May-August of 2021) when arthropod availability is at its peak. Before sampling, we created narrow trails that provided access to all sampling sites between 1000–2000 m asl. We cleared just enough understory vegetation for single file movement along the trails. We waited for at least a week after clearing the vegetation to ensure no effects of recent disturbance impacts ant communitieswe sampled.

The trail at Eaglenest (5.6 km in length) was created just below and above New Khelong, a site adjacent to Sessni found at approximately 1150 m asl. Below New Khelong, the trail terminated at the river located at 900 m. Above New Khelong, it terminated at a local peak (1850 m) substantially far from Eaglenest ridge (3200 m). At Khupi, we created two trails (KH1 & KH2) for the two transects below and above the highway (1600–1700 m). Like Eaglenest, the transects at Khupi terminated at the river (1050 m) below. However at higher elevations, the transects terminated within a short walking distance (few tens of metres) from the ridge at Khupi. While transects at both sites span a similar elevational gradient, transects at Khupi were much steeper than the one in Eaglenest; spanning just 2.9 km (KH1) and 3.6 km (KH2) compared to 5.6 km in the latter **(Figure 2.3)**. Differences of note between the two sites, Eaglenest and Khupi, are listed in **Table 2.1**.

Along each transect, we sampled in units of three $1m^2$ quadrats spaced approximately 10 m apart from each other **(Figure 2.4)**. We placed quadrats in sites with a fair amount of leaf litter, avoiding sites with decaying logs or rocky substratum. We sampled in sets of three quadrats across intervals of 30 m of geographic distance along the length of each elevational transect. In Eaglenest, we had 188 sets with 564 quadrats. At Khupi, KH1 yielded 97 sets with 291 quadrats while KH2 yielded 120 sets with 360 quadrats **(Table 2.2A & B).** We sampled not more than 16 sets with 48 quadrats per day to ensure no back log in subsequent specimen processing.

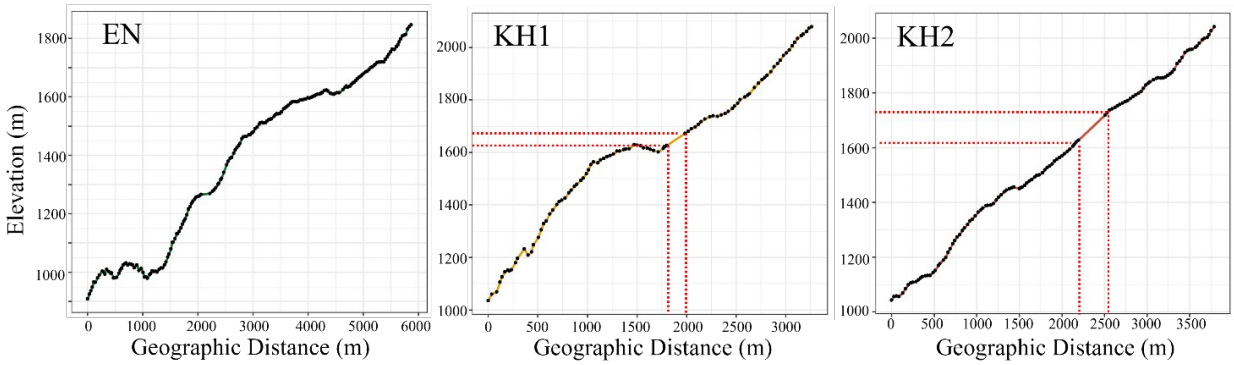


Figure 2.3: Change in elevation (m) with geographic distance (m) in 3 elevational transects. Solid black circles represent sampling locations/nodes. The 3 transects include 1 from Eaglenest Wildlife Sanctuary (EN: 5.6 km) and 2 from Khupi (KH1: 2.9 km) and KH2 (3.6 km). The red dashed lines shows the sampling gap (KH1 & KH2) due to the highway.

Features	**Khupi**	**Eaglenest**
Aspect (Climate)	North-facing (cooler)	South-facing (warmer)
Transect Terminus (Geography)	At the ridge	1400 m below the ridge
Highway (Disturbance)	Yes	No

Table 2.1: Notable differences between the two slopes (Eaglenest and Khupi) sampled

All sampling was carried out in the morning within a span of 3–4 hours. However, on rare occasions we had to sample in the afternoon when there was heavy downpour in the morning. In the following section, I will describe the standardized protocol we used for sampling litter ant fauna.

Table 2.2: Details of the sampling in Eaglenest and Khupi. The columns are Commun. = Sequence number of elevational community, Mean_Elev = mean elevation of the quadrats in the community, SD_Elev = standard deviation of the quadrat elevations, Nquad = number of quadrats pooled, and Abund = generic abundance.

2.2a	Khupi 1 (KH1)			
Commun.	**Mean_Elev**	**SD_Elev**	**Nquad**	**Abund.**
1	1145	61	14	100
2	1384	72	15	95
3	1574	40	18	93
4	1646	40	16	103
5	1786	48	17	95
6	1989	64	17	98
		Total	97	584

2.2b	Khupi 1 (KH1)			
Commun.	**Mean_Elev**	**SD_Elev**	**Nquad**	**Abund.**
1	1079	26	10	110
2	1133	11	8	100
3	1225	41	10	100
4	1356	34	13	102
5	1442	16	11	101
6	1498	23	11	100
7	1584	28	12	111
8	1778	37	19	102
9	1931	63	26	103
		Total	120	929

2.2 c	Eaglenest (EN)			
Commun.	**Mean_Elev**	**SD_Elev**	**Nquad**	**Abund.**
1	974	33	14	145
2	1012	18	17	146
3	1004	15	16	146
4	1166	66	21	141
5	1318	47	15	144
6	1457	27	15	139
7	1528	16	16	141
8	1588	12	19	144
9	1623	13	21	143
10	1694	22	18	143
11	1786	37	16	145
		Total	188	1577

2.2 d	Khupi (KH = KH1 + KH2)			
Commun.	**Mean_Elev**	**SD_Elev**	**Nquad**	**Abund.**
1	1081	29	16	156
2	1146	15	13	148
3	1247	43	19	149
4	1380	31	20	147
5	1460	17	18	152
6	1535	26	19	152
7	1608	16	27	153
8	1727	25	20	149
9	1828	39	34	153
10	1987	49	31	154
		Total	217	1513

Sampling protocol: Ants of the Leaf Litter

ALL or Ants of the Leaf Litter Protocol (Agosti et al., 2000) is a standardized method of collecting ground-dwelling ants. It largely involves passive sampling using winkler and pitfall traps with optional active searches. According to the protocol, twenty winkler-pitfall trap pairs spaced 10 m apart on either side of a 200–250 m transect, is sufficient to capture 70% of the ant fauna of a given site. Towards the higher limit, the protocol recommends not more than 50 paired traps per site, with quadrats covering 1 m^2 in area and spaced 5 m apart. Occurrence is measured at the quadrat or trap level. Some of the detailed specifications outlined by the protocol include dimensions of transects and quadrats, the spacing of pitfall traps from leaf litter collection quadrats, labelling of samples

and ecological parameters that need to be measured for each site. These specifications allow for reliable comparison of datasets collected by different research groups in different habitats.

We re-adapted this method, employing only winkler traps without pitfall traps, to sample ant fauna along our three elevational transects at Eaglenest (EN) and Khupi (KH1 & KH2). Our initial objective was to measure intraspecific genetic divergence across elevation for which we needed few elevationally widely occurring ant species. Therefore winkler traps were sufficient since we needed a large number of individuals of a widely occurring species. Studies comparing both methods had shown greater efficiency of winklers compared to pitfalls. (Olson, 1991). Furthermore, previous work in Eaglenest by Marathe revealed similar accumulation curves with increasing sampling effort for both pitfalls and winklers. While both methods may sample slightly different ant communities, with pitfalls capturing larger insects in more open habitats and winklers more suited for habitats with deep litter layers, one method was sufficient for our initial objectives. Hence we chose the more efficient of the two methods i.e. winkler extraction.

Sampling using winkler traps involves collecting leaf-litter present at the site defined by a quadrat of fixed dimensions **(Figure 2.4)**. The collected litter is sifted on site using a sifting apparatus to remove large debris and twigs. Siftate is placed in a cloth bag with a quadrat label containing quadrat unique identifier, GPS coordinates, date and time of collection, name of the collector and special remarks, if any. All quadrat labels are also imaged on site along with the collection bag using a time-calibrated camera. At the field station, the siftate from each quadrat is emptied into a separate mesh bag and placed within a winkler sack for 48 hours. Each winkler sack is a large cloth bag with a rigid metallic frame and a single opening at the bottom. All small invertebrates from the sifted leaf litter come out of the mesh bag due to disturbance and changes in their immediate environment, falling into a labelled plastic cup containing absolute ethanol as the fixative. Each cup was fastened to the bottom opening of the Winkler sack.

Specimen curation and preservation

After completion of 48 hours, contents of each cup are emptied into a transparent petri dish one after the other. At a given time, contents from only one cup (corresponding to one quadrat) is emptied **(Figure 2.5)**. Ants are separated from other small invertebrates and carefully placed in a

clean petri dish. Soil and other debris is removed by gently washing each specimen in absolute ethanol. Each ant is subsequently placed in a single labelled 0.6 ml vial filled with approximately 0.5 ml absolute ethanol. Ethanol in each vial was replaced after a week to ensure complete dehydration of specimens. All vials are doubly labeled with a unique specimen identifier also placed inside the vial. Specimens from each quadrat represented as a series of 0.6 ml uniquely labelled vials are photographed alongside the quadrat label. The first and last vial in the vial series is noted alongside the unique quadrat ID, date and time of sorting and name of the sorter in a field notebook. The collection strategy allowed us to trace each specimen to a GPS location via multiple replicate formats of raw data in the form of field notebooks and images.

For quadrats in which specimens of any single morphotype exceeded ten individuals, I used either 2.0 ml, 15.0 ml or 50.0 ml doubly labelled containers to store the individuals. This threshold is arbitrary and was largely governed by availability of plastic-ware in the field. For each large container that I used, I kept a corresponding empty 0.6 ml vial with labelled information on the nature and whereabouts of the larger container with the specimens. For each quadrat, we also kept the other arthropods we found in a 2.0 ml vial with absolute ethanol as a fixative.

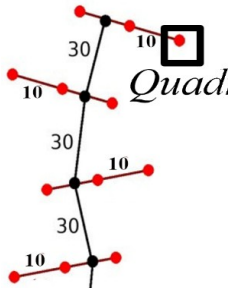
We collected 22577 ant specimens from all three elevational transects. All specimens were transported from the field site at room temperature and stored at -20℃ in the laboratory. All ant specimens were identified using Radical Scientific RSM-9A.

2.2.2 Specimen Identification

In the field, I had to quickly sort ant specimens (Family: Formicidae) from the remaining arthropods. I used the following diagnostic features for worker castes and queens:

- **a)** Head prognathous.
- **b)** Antenna geniculate between a basal (scape) segment and 4–12 funicular segments.
- **c)** Abdominal segment II highly reduced (petiole), usually nodular and isolated from the mesosoma and the remaining abdominal segments.
- **d)** In some ants, abdominal segment III is also highly reduced and isolated from the remaining segments (post-petiole).

Queens usually have massive mesosomal tissue with wing scars on the mesothoracic segments.



■ Sets of three quadrats (1 by 1 m^2) were placed at suitable sites, comprising a single sampling location/nodes.

■ Adjacent quadrats: 10 m apart; outermost quadrats: ~ 20 m apart.

■ Sampling locations along elevation were 30 m apart in geographic distance.



■ Leaf litter was collected within the bounds of the quadrat using industrial gloves and placed inside a sifting apparatus.

■ The apparatus was shaken using a handle to force small materials to pass through a metallic mesh.

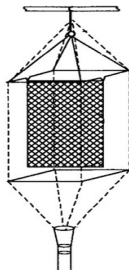
■ The remaining litter was emptied back to the quadrat.



■ Soil-dwelling arthropods and physical debris in the siftate was collected and placed in a cloth bag with the location label.

■ Location label contained the unique identifier, GPS coordinates, collector name and time of collection. Label was imaged on site.

■ In a single day, we sampled litter fauna from a maximum of 50 quadrats.



■ Litter from each quadrat was emptied into an inlet sack with of 4 mm grid size and placed inside a separate Winkler apparatus.

■ A plastic cup with 100% ethanol was fastened at the bottom of the Winkler apparatus with a label containing a quadrat unique identifier. Cups are left in the apparatus for 48 hours.

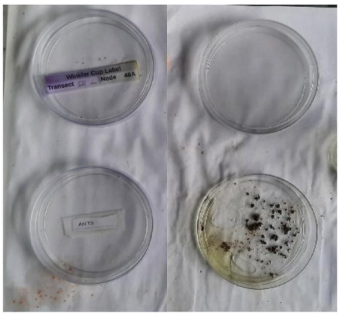
Figure 2.4: Field sampling of ground-dwelling ant communities using a passive technique of Winkler extraction. The sampling technique employed was consistent across all three (EN, KH1, KH2) elevational transects.



■ Sets of three quadrats (1 by 1 m^2) were placed at suitable sites, comprising a single sampling location/nodes.

■ Adjacent quadrats: 10 m apart; outermost quadrats: ~ 20 m apart.

■ Sampling locations along elevation were 30 m apart in geographic distance.



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■ The remaining litter was emptied back to the quadrat.



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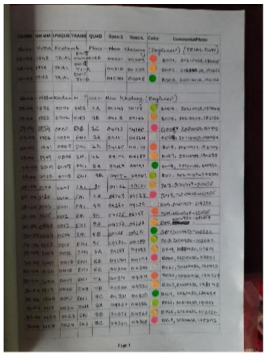
■ In a single day, we sampled litter fauna from a maximum of 50 quadrats.



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■ A plastic cup with 100% ethanol was fastened at the bottom of the Winkler apparatus with a label containing a quadrat unique identifier. Cups are left in the apparatus for 48 hours.

Figure 2.5: Procedure followed for curation of ant specimens collected from three elevational transects in Eaglenest (EN) and Khupi (KH1 & KH2).

Key to ant subfamilies of Arunachal Pradesh

Ants of India belong to 10 out of 17 extant ant subfamilies reported globally. Nine of the ten subfamilies are found in Arunachal Pradesh. The only subfamily with no records so far in Arunachal Pradesh is the largely subterranean subfamily of *Leptanillinae*. However, it has been found in the neighbouring Yunnan province of China and has also been recently reported in Mizoram state of India (Aswaj et al., 2020). Our dataset reports eight of the nine subfamilies known from Arunachal Pradesh. Previous work in Eaglenest has reported all nine subfamilies (Marathe et al., 2020, 2021). The key used to identify ants of Arunachal to subfamily and generic level is provided in the appendix. All ants were identified at the genus level due to difficulty in ascertaining species in the given timeframe. We are in the process of identifying all specimens to the level of morphospecies.

2.2.3 Ant elevational data

As discussed earlier, the sampling design was identical for all three transects and involved collecting consecutive sets of three quadrats spaced 10 m from each other, with each set spaced 30 m apart along ground distance **(Figure 2.4)**. We quantified abundance at the genus level. Occurrence was recorded at the quadrat level as per standard practice (Agosti et al. 2000). The abundance of a genus in a transect was the total number of quadrats in which it occurred along the transect. The transect at Eaglenest recorded the highest total abundance of ant genera (EN = 1577) with comparatively lower abundances at KH1 (584) and KH2 (929). Given our sampling design, we expected these differences in abundances. Shorter, steeper transects (KH1=291; KH2=360) naturally contain fewer quadrats compared to the longer transect (EN = 561) as shown in **Table 2.2C & D.**

Table 2.3: Number of genera identified across 8 ant subfamilies in this dataset. Note than there are 40 genera across both sites (EN = 35 genera, Khupi = 34 genera)

Subfamily	Genera
Myrmicinae	16
Ponerinae	12
Formicinae	6
Dolichoderinae	2
Dorylinae	2
Proceratiinae	2
Amblyoponinae	2
Ectatomminae	1

To examine elevational patterns of diversity, we had to first define limits of ant elevational communities. Standard practices consider all traps within 100–200 m grid as a single community (Agosti et al. 2000) with replicate plots of similar habitat > 300 m in geographic distance to avoid pseudoreplication (Marathe et al., 2020; Munyai & Foord, 2012). Since we did not have line transects within each elevation, we pooled neighbouring quadrats within elevational bands to obtain non-overlapping communities with approximately equal abundance at each elevation to standardise for sampling effort. The number of quadrats pooled in each community is shown in **Tables 2.2a-d**. The abundance of the ant communities and their mean elevation and elevational dispersion within the three transects (EN, KH1 and KH2) are shown in **Figure 2.6**.

To compare diversity patterns between the two mountain slopes, we pooled quadrats within each elevational band from the two transects (KH1 & KH2) at Khupi to obtain a single transect, KH. These two transects (KH1 & KH2) may be treated as independent elevational replicates since they are >300 m apart (Marathe et al., 2020; Munyai & Foord, 2012). We recognise that pooling independent transects at Khupi introduces differences in the horizontal spatial extent sampled between the slopes. Moreover, ant communities can exhibit differences at microhabitat scales of a few tens of metres (Barton et al., 2024; M. Luque & Reyes López, 2007). However, our main objective was to investigate slope-specific differences in richness and composition. Given that the separation between KH1 and KH2 along the contour is 2 orders of magnitude smaller than between

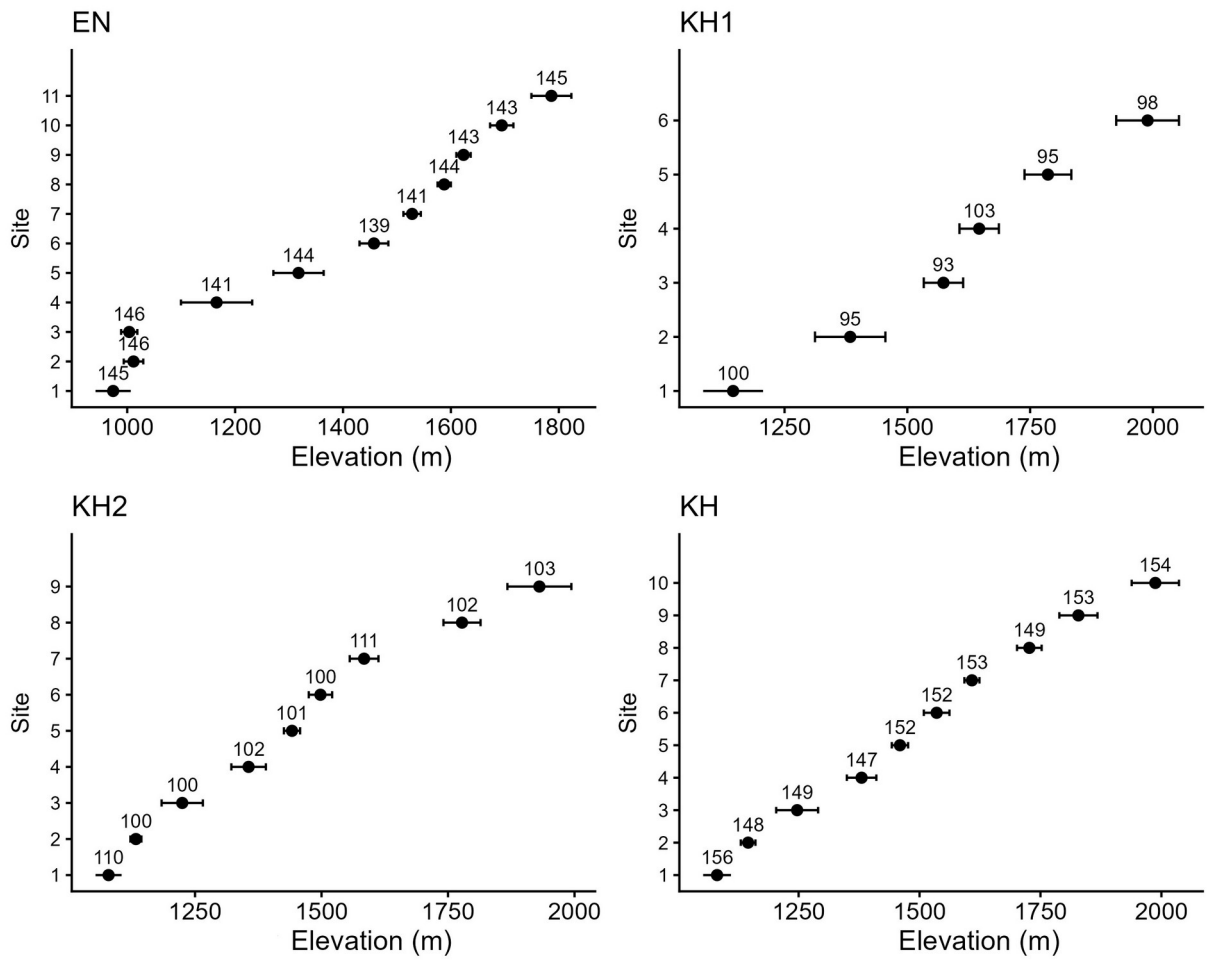


Figure 2.6: Ant elevational communities in Eaglenest (EN) and Khupi (KH1, KH2, KH=KH1+KH2). The mean elevation of each community (set of pooled quadrats) is represented by a solid black circle and its 1 SD spread by the horizontal bars. The community index is listed along the y-axis. The abundance of each community is listed above the corresponding data point.

EN and KH we ignored the spatial separation between the two Khupi transects to create a single elevational profile for comparison with Eaglenest. This decision was also based on the desire to match the abundance in the Eaglenest and Khupi transects since many statistical tests implicitly or explicitly require similarity of sample size for optimal inference.

We report 40 ant genera across the three elevational transects **(Table 2.3)**, of which five genera contribute to 60% of the total abundance: *Pheidole*, *Tetramorium*, *Carebara*, *Brachyponera* and *Myrmecina.*

2.3 Other Taxa: Hawkmoths and Birds

Both hawkmoths and birds were sampled along a single local transect in Eaglenest Wildlife Sanctuary without pooling communities from multiple slopes. However, the lowest elevation (200 m) could not be sampled inside Eaglenest due to security reasons. Therefore, hawkmoths and birds at 200 m elevation had to be sampled in the adjoining Pakke Tiger Reserve about 20 km from the lowest elevation (500 m) inside Eaglenest. The hawkmoth and bird dataset employed in Chapter 3 and Chapter 4 of this thesis is further described below.

Hawkmoth species were sampled between April–July of 2014 by Mansi Mungee. Moth screens were placed at 13 elevations separated by approximately 200 m in elevation, between 200 m and 2800 m. All sampling was carried out within five days before and after the new moon. Sampling was standardized by equalizing the number of individuals collected at each elevation instead of sampling the same number of days at each elevation due to daily random fluctuations in the number of moths; anywhere from 5 to 3000 individuals (Mungee & Athreya, 2021). A total of 4731 individuals of hawkmoths were imaged with leg tissue collected before identifying all specimens to the species level. The dataset consists of 80 hawkmoth species belonging to 30 genera and 3 subfamilies. The summary of the dataset is in **Table 2.4** & **Figure 2.7**.

Bird counts were conducted by Rohan Pandit along the same elevational gradient (200–2800 m) but at a finer elevational resolution of 50 m, yielding 49 elevations. Each elevational community was sampled along a 200 m line transect using both visual and aural cues within a 2 hour period between 0600-1200 hrs in April–June between 2012–2014. There were 12 replicates for each elevation spread out across 12 separate days and randomized across early (0600–0800 hr), mid (0800–1000 hr) and late (1000-1200 hr) morning slots. Therefore, for each elevation, replicates were equally distributed across these three slots to prevent bias due to differences in bird activity. Birds were sampled from the same elevations in winter of 2012–2013 (January–February) in a similar manner (Mungee et al., 2021). However, all analyses in this theses will be restricted to the summer bird dataset. A total of 15867 birds were counted in the summer; belonging to 245 species across 145 genera, 49 families and 13 orders **(Table 2.4)**.

Level	Hawkmoths	Birds
Individuals	4731	15867
Species	80	245
Genera	30	145
Families	NA	49
Orders	NA	13

Table 2.4: Total hawkmoth and bird counts across all elevations sampled, at the individual and higher taxonomic levels. Hawkmoths (Family: Sphingidae) sampled belonged to 3 subfamilies, 30 genera and 80 species. Bird (Class: Aves) counts in the summer spanned 13 orders, 49 families, 145 genera and 245 species.

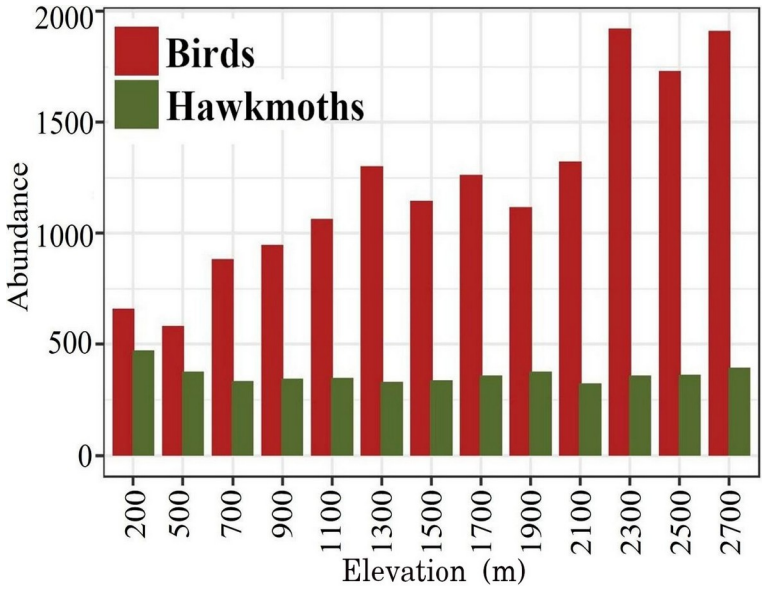


Figure 2.7: Number of individuals of hawkmoths sampled and birds counted the summer months at Eaglenest Wildlife Sanctuary across 200–2700 m. Dataset for hawkmoths and birds was collected by Mansi Mungee and Rohan Pandit. Both datasets were curated by Mansi Mungee.

2.4 Standardization of sampling effort

Sampling more individuals in a community invariably leads to an increase in the observed species richness. Rarefaction allows us to compare biodiversity among different sites varying in the number of individuals sampled. Given an observed species richness of S and total abundance of N in a community, rarefaction involves subsampling a set of predetermined number of individuals (without replacement) multiple times and estimating the average number of species across all subsamples. Each subsampling event involves choosing a fixed number of randomly ordered individuals from the total pool of individuals in the community, ensuring that the order in which species are discovered is randomized across multiple subsampling events. All rarefactions were conducted using the R package '*vegan' v 2.7.1* (Oksanen et al., 2001).

The standard practice is to subsample with a rarefaction size of the smallest community (N_{min}) within each community matrix (N_{total}). Instead of this, we rarefied with a depth of two individuals fewer than the minimum (N_{min} - 2) to avoid redundancy in replicate communities. The mean and standard deviation of multiple richness metrics, discussed in greater detail in Chapter 3, was obtained from rarefied bird and hawkmoth elevational communities across 800 iterations. Rarefaction was not carried out for ant communities since, as explained earlier, we pooled quadrats within each transect to approximately equalise the abundance i.e. sampling effort at each elevation.

Chapter 3

Elevational profiles of alpha diversity

3.1 Introduction

As discussed in Chapter 1, elevational gradients offer some logistical and ecological advantages over latitudinal gradients. Consequently, they have been widely investigated across a broad range of taxa (Beck et al., 2017; McCain, 2005, 2010; Zu et al., 2024). These studies consistently reveal a set of four recurring richness patterns: (i) a monotonic decline with elevation, (ii) a low-elevation plateau followed by decline, (iii) a low-elevation plateau with a low-elevation peak, and (iv) a mid-elevation peak (McCain, 2009). Less frequently, studies have documented increasing richness with elevation (Grytnes et al., 2006; Wiens et al., 2007) or no clear elevational pattern (Kessler et al., 2011). Importantly, no single richness pattern emerges as universal across the tree of life. Rather, multiple global meta-analyses spanning birds, reptiles, mammals, insects, and plants highlight considerable variation in elevational richness responses (Beck et al., 2017; McCain, 2005, 2009, 2010; Zu et al., 2024). For instance, bird communities exhibit nearly equal frequencies of all four major patterns (McCain 2009), while insects such as moths and ants display predominantly hump-shaped distributions in approximately 50–75% of studies (Beck et al., 2017; Szewczyk & McCain, 2016). Plant assemblages show near-equal proportions of hump-shaped and declining trends (Zu et al., 2024), whereas reptiles are dominated by declining distributions (54%), with hump-shaped patterns observed in roughly 20% of cases (McCain 2010).

These, and many more studies, have substantially advanced our understanding of the mechanisms underlying the variation in elevational diversity patterns across taxa. These mechanisms can be broadly categorized into two classes: environmental drivers and geometric constraints (Herrera-Alsina et al., 2025; Rahbek, 1997). Environmental drivers encompass abiotic factors, such as temperature, precipitation, and solar radiation, as well as biotic processes, including resource availability, species interactions, and host–parasite dynamics (Dolson & Kharouba, 2024; Uhey et al., 2022). Their influence may operate independently or through complex interactions, and their

relative importance often depends on the ecological strategies and life-history traits of the taxa under consideration (Alexander et al., 2016; Kissling & Schleuning, 2015; Wiens et al., 2007). For example, moths, which are primarily herbivorous, are strongly shaped by the elevational distribution of their host plants (Jahner et al., 2017), whereas omnivorous arthropods such as ground-dwelling ants are more closely tied to abiotic gradients, particularly temperature and precipitation (Hodkinson, 2005; Uhey et al., 2022). Parasitoid wasps and flies, by contrast, may respond primarily to the availability and abundance of arthropod hosts, thereby linking their distributions only indirectly to abiotic conditions (Dolson & Kharouba, 2024; Maunsell et al., 2015).

In contrast, geometric constraints are more agnostic to species identities, related as they are to the available elevational range and elevational profile of available area in the region. These factors have been implicated in patterns such as the Mid-Domain effect (Colwell et al., 2000; Currie & Kerr (2008); Gao et al., 2021). Nevertheless, they are not wholly decoupled from ecological context. For instance, the Mid-Domain Effect also depends on the absolute elevational ranges of individual taxa with small-ranged species frequently deviating from the prediction (McCain, 2005; Sun et al., 2020). The elevational profile of diversity may be related to availability of niches and diversification rates of particular clades (Herrera-Alsina et al., 2025).

A common framework for identifying the processes that generate elevational diversity patterns involves replicating transects or compiling species inventories across multiple montane systems and then examining generalities in how environmental drivers and geometric constraints shape diversity (Colwell et al., 2004; Montaño-Centellas & Jones, 2021; Rahbek, 2005). However, such comparative approaches rarely account for the substantial variation in spatial and taxonomic scale across studies (Barczyk et al., 2024; McCain & Knight, 2013). Even across similar spatial and taxonomic scales, sampling along different mountain slopes within a region with shared evolutionary history could still yield different patterns. This could be due to subtle differences—along similar climatic gradients— in microclimate and physical topography. In the following section, I will discuss some of these issues with a few studies that explicitly test the dependency of spatial, taxonomic and topographic factors on elevational diversity patterns.

3.1.1 State of the field

Various properties of ecological communities—such as diversity or function— are subject to change across geographical space. Our interpretation of spatial diversity patterns is contingent on taxonomic and spatial scales, as well as on the specific summary index employed for quantification. Furthermore, accounting for differences in sampling effort and area is essential to prevent misleading inferences of diversity patterns (Rahbek, 2005). Existing studies are replete with such methodological inconsistencies that introduce substantial variation in observed patterns, independent of the underlying ecological processes.

However, even after accounting for methodological issues, elevational diversity patterns for the same taxon may not be comparable along similar elevational gradients. Subtle differences in physical topography—even between neighboring slopes with shared evolutionary histories and broadly similar contemporary climatic regimes—may potentially influence diversity-elevation relationships (Bennie et al., 2006; De Frenne et al., 2013). Features such as ridgelines, saddles, terrain ruggedness and aspect of the slope generate substantial microclimatic variability within a single mountain, modifying precipitation and solar radiation regimes and thereby influencing species distributions and elevational ranges (Guo et al., 2013; Svenning et al., 2010). While it was previously assumed that tropical mountains near the equator receive relatively uniform solar incidence across slopes—unlike their mid-latitude counterparts (Gallardo-Cruz et al., 2009; Shuai et al., 2017; Singh, 2018)—recent work demonstrates that even mountains as close to the equator as 8° latitude can exhibit marked aspect-dependent asymmetries in solar incidence, with corresponding shifts in vegetation structure (Maheshwori et al., 2025).

In the Western Ghats of peninsular India, for example, slope aspect interacts strongly with monsoonal dynamics to produce pronounced ecological contrasts. South-facing slopes in the northern hemisphere are generally warmer than north-facing ones due to more intense solar incidence. However they may or may not be drier depending on the balance between directional rain-bearing wind patterns (e.g. the monsoons) and evapo-transpiration (Champion & Seth, 1968; Gadgil, 2003). In the Western Ghats, these gradients drive differences in soil moisture, plant productivity, and forest structure: canopy height and tree cover are consistently greater on northern and western slopes compared with southern and eastern slopes, with steep slopes further

accentuating these contrasts (Maheshwori et al., 2025). Such fine-scale heterogeneity underscores the importance of accounting for topographic context when interpreting elevational diversity patterns. Comparative studies overlooking slope aspect risk misattributing richness patterns to climatic or geometric factors, rather than to underlying interaction between topography and climate or geometry.

While several variables interact with elevation to shape diversity patterns, the sampled extent of elevation can singularly determine the patterns observed. The extent of elevational gradients captures a range of multiple environmental variables, each of which may vary in strength along the gradient. For example, in arid montane systems of Colorado ranges, precipitation limits diversity in ground-dwelling arthropods at lower elevations. However, temperature becomes a limiting variable at higher elevations (Irungbam et al., 2025; Uhey et al., 2022). Such differential effects on community assembly are obscured in shorter elevational extents that omit certain sections of the gradient and therefore insufficiently capture the full range of all environmental variables that influence richness and diversity patterns of communities.

Nogués-Bravo et al. (2008) demonstrated that both the extent of spatial scale (i.e., the proportion of the elevational gradient sampled) and the resolution of sampling (grain size) can alter richness patterns in floristic communities of the Pyrenees. Recent global meta-analyses have reinforced this point, showing a shift from more complex cubic or parabolic relationships to simpler linear or declining trends when the sampled elevational range is reduced from >3000 m to ~1000 m (Costa et al., 2023; Irungbam et al., 2025). In a synthesis of 182 elevational gradients worldwide spanning plants, invertebrates, and vertebrates, Costa et al. (2023) found that progressively omitting the lower portion of the elevational gradient consistently flattened richness–elevation relationships. Incomplete sampling of gradients (e.g., ~1000 m rather than ~3000 m) restricts the observed profile of species turnover, thereby obscuring true diversity patterns (Nogués-Bravo et al., 2008; Costa et al., 2023).

Put simply, omitting lower and/or upper elevational edges of gradients tends to linearize richness patterns irrespective of environmental or geometric mechanisms (Costa et al., 2023; Irungbam et al., 2025). However, this tendency does not imply that all linear richness patterns are invariably a consequence of incomplete sampling of the gradient. Certain forms of life are limited by their

biology in their distribution towards higher or lower elevations, yielding actual monotonic (linear) diversity patterns along the gradient. On the other hand, unimodal patterns obtained across even a completely sampled gradient can be explained under a purely geometric framework (Mid-Domain Effect) without invoking any biological mechanisms. Therefore, spatial invariance can substantially complicate the inferences regarding the mechanisms underlying elevational diversity patterns.

Despite increasing recognition of this issue, surprisingly few empirical studies encompass the full elevational extent of environmental gradients, even as calls for scale-explicit analyses have intensified (Lomolino, 2001; Rahbek, 2005; Willis & Whittaker, 2002). Practical constraints, including anthropogenic disturbance at low elevations, inaccessibility of high-elevation terrain, and limitations of funding and logistics, continue to curtail spatial coverage (Guo et al., 2013).

In addition to spatial scale, the taxonomic scale at which biodiversity is measured can profoundly influence both the form of elevational richness patterns and the processes inferred to underlie them (Guo et al., 2013; Peters et al., 2016; Weiser et al., 2018). For example, Peters et al. (2016) conducted parallel sampling of 25 major plant and animal taxa along Mt. Kilimanjaro and demonstrated that richness patterns differ markedly depending on taxonomic resolution. At lower ranks (e.g., species or genus), richness responses were complex and often varied, whereas aggregating to higher ranks (e.g., family and orders) yielded smoother, monotonic declines in richness that were strongly associated with temperature. In general, higher taxonomic ranks tend to exhibit consistent monotonic declines with elevation, while species-level analyses reveal greater site-to-site variability (Peters et al., 2016; Guo et al., 2013), however this has rarely been tested for other mountain systems.

This discrepancy is often attributed to differences in niche conservatism. Recently diverged, lower-rank taxa typically exhibit narrower ecological tolerances, producing more variable and localized richness peaks, whereas older, higher-rank clades have had longer evolutionary time to expand their niches, thereby occupying broader elevational and climatic ranges (Wang et al., 2025; Weiser et al., 2018). Although taxonomic rank often correlates with evolutionary age, comparisons across disparate groups are not straightforward. Different proxies for phylogenetic scale, whether

taxonomic rank, clade age, or phylogenetic depth, can substantially alter the inferred relationship between diversity and environment (Hoorn et al., 2018).

One way forward is to adopt comparative frameworks that explicitly evaluate richness patterns across multiple levels of taxonomic resolution within the same lineage, or across equivalent ranks in distantly related lineages (Weiser et al., 2018; Wang et al., 2025). Such approaches allow researchers to disentangle whether observed patterns arise from intrinsic evolutionary history (e.g., age or diversification of a clade) or from methodological artefacts of taxonomic aggregation. In doing so, they provide a more mechanistic understanding of how biodiversity patterns scale phylogenetically, and why generalizations across taxa may or may not hold.

Despite decades of research, a major limitation in studies of elevational diversity is the limited attention given to spatial and taxonomic scale. Most work continues to emphasize environmental and geometric explanations (Katuwal et al., 2016; Longino et al., 2019; Manish et al., 2017; Schowalter et al., 2025), while scale-dependent variation remains rarely examined. As a result, meta-analyses across multiple taxa have struggled to identify consistent generalities, with even well-studied groups such as birds and plants showing high variability in reported patterns and processes. This stagnation reflects a broader gap: without explicitly incorporating factors such as spatial extent, sampling grain, taxonomic rank, and topographic heterogeneity, comparative studies risk obscuring the actual drivers of biodiversity distribution. Addressing these overlooked dimensions is therefore essential for moving beyond descriptive pattern cataloguing toward a mechanistic understanding of elevational diversity.

In this chapter, I addressed the challenges outlined above by comparing elevational diversity profiles of three taxonomic groups (birds, hawkmoths, and ants) across varying spatial extents, taxonomic ranks, and topography. All three groups were sampled along the same mountain in Eaglenest Wildlife Sanctuary (EWS), Eastern Himalayas, spanning a common elevational range of 950–2000 m. Ants were additionally sampled at Khupi Model Village, located ~25 km from EWS, while hawkmoths and birds were surveyed over broader elevational extents of 200–2800 m. Sampling multiple taxa along the same slope allows scale–dependencies to be explicitly tested: by fixing one scale (spatial or taxonomic) while varying the other, it becomes possible to disentangle

their relative contributions to elevational diversity profiles. Moreover, because elevational area and slope aspect remain constant across transects, confounding effects of topography are minimized (Peters et al., 2016).

3.1.2 Objectives and Hypotheses

We examined how elevational diversity profiles vary with slope aspect, spatial extent, taxonomic scale.

a) **Aspect Hypothesis (only ant data, EN v/s KH):** We investigated whether diversity significantly changes across elevation within a slope and if elevational diversity trends significantly differ between slopes. We hypothesize that microclimatic differences along the two slopes will significantly influence elevational diversity profiles of ants, with southern slopes supporting higher diversity than northern slopes. This is due to various slope-specific differences such as aspect-driven differences in solar radiation and moisture regimes in the eastern Himalayas: southern slopes are warmer and receive higher rainfall than northern slopes (Choudhury, 2003). These environmental contrasts influence the availability of resources, nesting sites, and microhabitats for ants. Given that ants are thermophilic, the warmer southern slopes are likely to provide more favorable conditions, supporting greater diversity. Moreover, diversity on southern slopes may extend across a broader elevational range, as thermal limits occur at higher elevations. In contrast, on the cooler northern slopes, thermal constraints are reached earlier, resulting in lower-elevation diversity peaks. Southern slopes may have higher plant productivity, owing to greater rainfall. Hence, we expect greater overall diversity in southern slopes compared to northern slopes.

b) **Spatial extent (Hawkmoths & Birds, EN only):** Many studies are limited in the elevational range they can sample due to logistical constraints and anthropogenic influence, especially in the lowlands. We hypothesize that such truncated sampling, involving exclusion of lower and/or higher elevations, will reduce their complexity and linearize diversity–elevation relationships. This is because shorter spans reduce the ability to detect non-linearity. For example, fitting a quadratic or cubic model to 1000 m of range (instead of 3000 m) often lacks sufficient data spread to fit higher-order terms. As a result, the “best fit” simplifies to a linear model, even if the underlying ecological process is non-linear.

c) **Taxonomic scale (Hawkmoth & Birds at familial-, generic-, and species-level, EN only):** We hypothesize that elevational richness profiles will become progressively simplified at increasingly higher taxonomic scales, shifting from variable patterns at the species level to smoother monotonic declines at higher ranks (e.g., genus, family, order). Mechanistically, this results from differences in ecological niche breadth and evolutionary history. Recently diverged species often exhibit narrow ecological tolerances and restricted ranges, producing localized richness peaks and higher site-to-site variability. In contrast, higher taxonomic ranks aggregate across multiple species, many of which occupy distinct but overlapping ranges, thereby averaging out variability and producing broader, more predictable declines with elevation (Peters et al., 2016). Thus, scaling up taxonomic rank is expected to reduce noise and reveal stronger associations with broad-scale abiotic gradients such as temperature.

d) **Comparing diversity profiles of two insect families: Hawkmoths (Family: Sphingidae) and Ants (Family: Formicidae):**

We expect differential responses from ground-dwelling arthropods such as ants compared to flying arthropods such as moths. Ants are predominantly omnivorous in habit (Uhey et al. 2021) and would therefore respond more sensitively to arthropod prey abundances across elevation. Moth richness and distribution may be more tightly linked to distribution of associated host plants (Tyler et al., 2020). Additionally hawkmoths are known to be conditional endotherms (Heinrich, 1993), unlike ants which are completely ectothermic (Kadochová & Frouz, 2014). Therefore, we expected ant and moth richness response to be driven by taxon-specific resource requirements and thermal tolerances rather than shared environmental drivers.

3.2 Materials and Methods

We used data for three taxa in Eaglenest Wildlife Sanctuary (ants, hawkmoths and birds) and for one taxon in Khupi Model Village (ants) in Arunachal Pradesh. The data for all three taxa is described in detail in Chapter 2 and briefly summarized in **Table 3.1.** (also refer to Marathe et al., 2021 & Mungee et al., 2021 for a detailed description).

Table 3.1: Elevational datasets for birds, hawkmoths and ants describing sampling extents and taxonomic coverage. Birds and hawkmoths were sampled at Eaglenest Wildlife Sanctuary while ants were sampled at both Eaglenest and Khupi. The table contains the minimum and maximum elevations sampled, sampling resolution, taxonomic ranks examined (observed richness in parentheses) and slope aspect of the study region.

Dataset	Lowest Elevation (m)	Highest Elevation (m)	Sampling Resolution (m)	Taxonomic Ranks	Slope Aspect	Region
Birds	200	2725	210	Species (245); Genus (149); Family (49); Order (13)	South	Eaglenest
Hawkmoths	200	2700	200	Species (80); Genus (30);	South	Eaglenest
Ants	974	1786	80	Genus (35)	South	Eaglenest
Ants	1081	1987	100	Genus (34)	North	Khupi

We calculated multiple metrics of richness and diversity for each community within defined elevational bands (200 m for birds and hawkmoths; ~100 m for ants; **Table 3.1**). These included rarefied richness (Hurlebert, 1971), Chao's richness estimator (Chao et al., 2000), the Abundance-based Coverage Estimator (ACE; Chao & Lee, 1992). Fisher's diversity index (Fisher's alpha; Fisher 1943) and the Chao-corrected Simpson index (Chao et al., 2013; Hsieh et al., 2016). (**Table 3.2**), hereafter referred to, at times, as Simpson's D for simplicity. We employed these metrics to test whether the emergent elevational diversity profiles—and their variation across spatial and taxonomic scales—were consistent across different measures of richness and diversity. We evaluated the relationship between the different metrics using pairwise Pearson correlation coefficients. A more thorough evaluation of the sensitivity and accuracy of these metrics is beyond the scope of this thesis.

To account for differences in sampling effort across communities, all samples within each elevational band (200 m for birds and hawkmoths; ~100 m for ants) were rarefied to an equal number of individuals, as outlined in Chapter 2 **(see page 26)**. These rarefied communities were then used to calculate all richness and diversity metrics.

Table 3.2: Description of alpha diversity metrics used in this chapter. Metrics include rarefaction-based richness, richness estimators (Chao and ACE) based on extrapolation, log-series–based Fisher's alpha, and Simpson's D corrected for unseen species (Chao-corrected Simpson's D). Metrics generally vary in the degree to which common and rare species contribute to the estimated diversity.

Metric	Type	Description	References
Rarefied Richness	non-parametric	• Assumes species richness is a function of sample size. • Down-samples communities to equal number of individuals,	Hulbert (1971); Heck et al. (1975)
Chao Richness	non-parametric	• Assumes all samples have unseen species. • Inflates richness based on singleton and doubleton frequencies	Chao (1984)
ACE Richness	non-parametric	• Assumes all samples have unseen species. • Inflates richness based on frequency of species < 10 individuals	Chao & Lee (1992)
Fisher's α Diversity	parametric	• Assumes species abundances follow a log-series distribution. • Fits a log-series distribution to estimate diversity.	Fisher et al. (1943)
Chao-corrected Simpson's D	non-parametric	• Assigns greater weights to common species. • Corrects for bias using frequency of rare species	Chao et al. (2013)

3.2.1 Generalized Additive Models

To assess changes in the elevation-diversity relationship with changing elevational extent, we used Generalised Additive Models (Hastie & Tibshirani, 1990). GAMs are a modeling technique where the effect of the predictor (elevation) is captured through additive, non-linear smoothing functions using the general form: $g(\mu)=\beta+\Sigma_{(j=1)}^{n} f_j(x_j)$, where the mean response (μ; i.e. diversity) is related to the predictor variables (x_1,….,x_n) by the identity link function $g(\mu)$ which defines the relationship between the response and 'n' additive predictors. β represents the intercept term, and f_j is a smoothing function for the predictor x_j. We used Gaussian error distributions to model the estimated diversity. All GAMs were fitted using the R package '*mgcv'v.1.9.3 (Wood S.N., 2004).*

Since GAMs highlight local variation in the data, such as peaks and troughs, it makes them well suited for comparing subtle differences across multiple fitted profiles. Hence, a higher 'goodness-of-fit' for a GAM, relative to a linear model (e.g., Generalised Linear Model; GLM) can be attributed to a more complex relationship between the predictor and response variable.

We obtained the goodness of fit as 'Deviance Explained (%)' (Dev.Exp.) using the *mgcv* function gam.summary(). In *mgcv*, this statistic represents the proportion of total deviance in the response explained by GAM relative to an intercept-only null model. An intercept-only null model would predict the same richness across all elevational communities, assuming no elevational variation. Similarly, we also obtained the Dev.Exp. (%) for a linear GLM, and then derived model complexity (C) as:

$$C = \frac{\left(\exp.Dev._{GAM} - \exp.Dev._{GLM}\right)}{\exp.Dev._{GAM}}$$

Higher values of C represent a higher degree of non-linearity (i.e., higher-order polynomial) in the fitted GAM, and therefore in the modeled relationship between the response and the predictor.

Finally, to evaluate the effect of varying elevational extents across the different truncation schemes; 2/3 FP, 1/3 FP, LT, MT and HT profiles, we calculated Δ_P which reflects a change in the elevation of diversity-peak position, for the predicted GAM model between the full and truncated extents:

$$\Delta_P = ElePeak_{Full} - ElePeak_{Trunc}$$

$ElePeak_{Full}$ is the elevation of the maximum diversity of the GAM fitted to the data spanning the complete elevational extent, and $ElePeak_{Trunc}$ is the elevation of the maximum diversity for the GAM fitted to the different truncated profiles. We fit GAMs to test the second and third hypothesis. However, since GAMs gave poor fits for ant communities, we fit linear models to test the first hypothesis.

Slope-specific elevational diversity profiles of Ants

Analyses were restricted to ant communities since we did not have data across different slopes for birds and hawkmoths. Ants were sampled from the southern and northern slopes as described in Chapter 2 **(refer to Table 2.2)**. We tested the differences in the diversity-elevation relationship between the two slopes differing in aspect., Khupi Model Village (north-facing; cooler) and

Eaglenest (south-facing; warmer), using GLMs instead of GAMs. First, we fitted linear models to examine how diversity changed with elevation within each transect. Second, we investigated whether diversity–elevation patterns differed significantly between north and south facing slopes by fitting a model with an elevation × transect interaction.

Impact of spatial extent on observed diversity profiles: Birds and Hawkmoths

For our second objective, we first truncated the bird and hawkmoth dataset to different spatial (elevational) extents by sequentially removing the lowest and highest elevation communities. Secondly, we compared equal elevational extents of approximately 800 m but across separate segments of the elevational gradient (lower, middle and upper elevations) using a shifting window approach. The first approach allowed comparison of successively shrinking elevational extents while the second approach tested bias in diversity estimates when certain portions of the gradient are systematically omitted. Details regarding both the approaches are described below (see **Table 3.3** and **Figure 3.1)**.

Approach 1: Low and high elevation truncation

Simultaneous exclusion of lower and higher elevation communities from each edge:

1. 2/3 FP: communities found 800 m below and above 1500–1525 m i.e. 66% of the gradient is retained.

b) Birds: 200–550 m and 2525–2725 m excluded; dataset truncated to 725–2325 m.

c) Birds: 200–500 m and 2505–2700 m excluded; dataset truncated to 700–2300 m.

2. 1/3 FP: communities found 400 m below and above 1500–1525 m i.e. 33% of the gradient is retained:

a) Birds: 200–925 m and 2125–2725 m excluded; dataset truncated to 1125–1925 m.

b) Hawkmoths: 200–900 m and 2000–2700 m excluded; dataset truncated to 1100–1900 m.

Table 3.3: Spatial extents employed in this chapter to examine scale-dependent elevational diversity patterns in Eaglenest Wildlife Sanctuary. The table contains each spatial scale, its acronym, along with the elevational ranges (in meters) analysed for hawkmoths and birds. Both hawkmoth and bird datasets are progressively truncated at the lowest and highest extents to yield 66% (2/3 FP) and 33% (1/3 FP) of the full gradient (FP) centred at 1500 m. Scales examined also include a shifting 800 m elevational window representing the lower (LS1), mid (MS1) and higher (HS1) elevations. The ant dataset was not subjected to truncation owing to its short elevational extent (1000 m).

Spatial scale/extent	Acronym	Hawkmoths	Birds
Full Elevational Extent (m)	FP	1500 ± 1300 OR 200–2700	1500 ± 1300 OR 200–2725
Lowest and Highest elevations Truncated (m)	2/3 FP	1500 ± 800	1500 ± 800
	1/3 FP	1500 ± 400	1500 ± 400
Elevational Shift (800 m extent)	LS1	200–900	200–925
	MS1	1100–1900	1125–1925
	HS1	1900–2700	1925–2725

Approach 2: Low or mid or high elevation truncation (LS; MS; HS):

Inclusion of only one of three (low, mid or high) sections of the gradient at a time.

1. Low-elevation span (LS1): Mid- and high elevations excluded:

a) Birds: ~ 800 m of lower elevations considered; dataset truncated to 200–925 m.

b) Hawkmoths: ~ 800 m of lower elevation considered; dataset truncated to 200–900 m.

ii. Mid-elevation span (MS1): lower and higher elevations excluded:

a) Birds: 800 m of the mid-elevation section considered; dataset truncated to 1125–1925 m.

b) Hawkmoths: 800 m of the mid-elevation portion of the gradient considered; dataset truncated to 1100–1900 m.

iii. High-elevation span (HS1): lower and mid-elevations sections excluded:

a) Birds: 800 m of the high-elevation portion of the gradient considered; dataset truncated to 1925–2725 m.

b) Hawkmoths: 800 m of the high-elevation portion of the gradient considered; dataset truncated to 1900–2700 m.

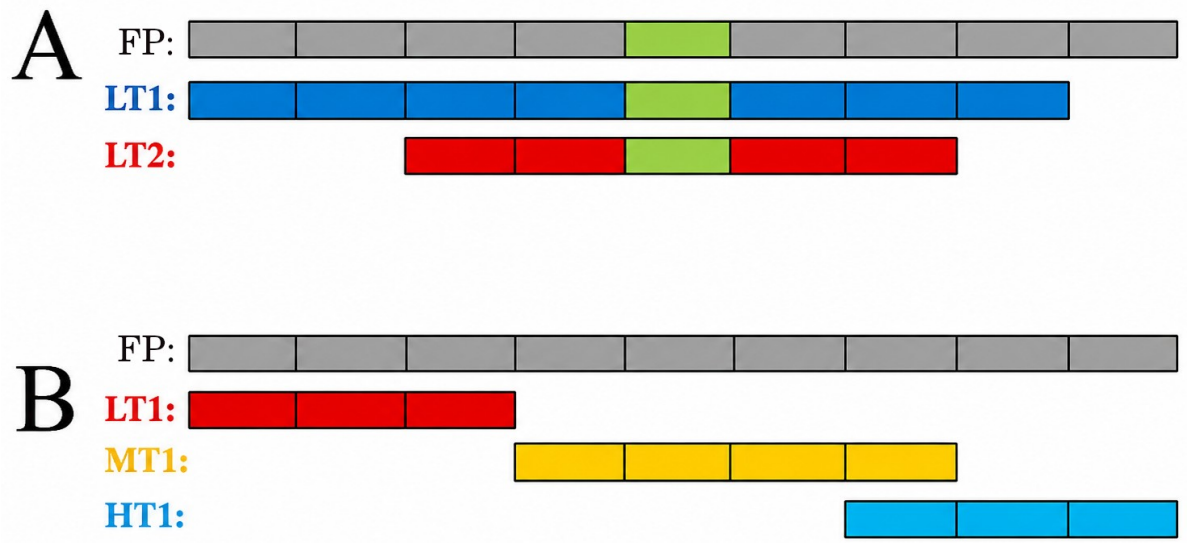


Figure 3.1: Truncation scheme applied to hawkmoth and bird elevational datasets. A and B refer to the two approaches adopted to test scale-dependent effect on diversity. Each rectangular bar (split further into multiple rectangular cells) corresponds to the elevational extents across which Generalized Additive Models were fitted to obtain diversity–elevation profiles. Each cell within each rectangular bar spans 200 m of elevation and represents a single elevation community. The bar labelled as FP represents the full (non-truncated) elevational extent sampled while the other bars represent the truncation (2/3 FP, 1/3 FP) and shift (LS1, MS1, HS1) schemes. A: The green cell in FP, 2/3 FP, 1/3 FP represents the centre of the sampled gradient (1500 m). Elevational communities are progressively dropped at both lower and higher elevations (2/3 FP: 1500 ± 800 m; 1/3 FP: 1500 ± 400 m) to yield truncated datasets encompassing 66% and 33% of the sampled extent respectively. B: shifting window approach is adopted in which a fixed extent of 800 m is either predominantly from the lower elevations (LS1: 200–900), mid-elevations (MS1: 1100–1900) or higher elevations (HS1: 1900–2700).

Impact of taxonomic scale on the observed profiles: Birds and Hawkmoths

We applied a similar analytical approach for our third objective, which was to test the effect of varying taxonomic scale on the shape of the richness–elevation relationship. Depending on the dataset, different taxonomic ranks were considered as units of observation for comparative analyses across taxonomic scales. For birds, we compared diversity–elevation relationships across three taxonomic resolutions in ascending order: species, genus and family (see **Table 3.1**), while only species and genus were used for hawkmoths. All ant datasets were excluded from this analysis due

to only genus-level identifications. All other statistical procedures and performance measures were conducted in the same manner as the second objective.

Comparison of diversity profiles of two insect families at the same location: Ants (Family: Formicidae) v/s Hawkmoths (Family: Sphingidae)

Hawkmoth data, spanning 200–2700 m, was truncated to 900–1900 m to make it comparable to the full elevational extent sampled for ant communities. Since we did not identify ants to the level of species, we compared generic profiles of both insect families. We specifically fitted a linear model to each of five alpha metrics **(Table 3.2)** and quantified differences in the slope, if any, between hawkmoth and ant generic profiles.

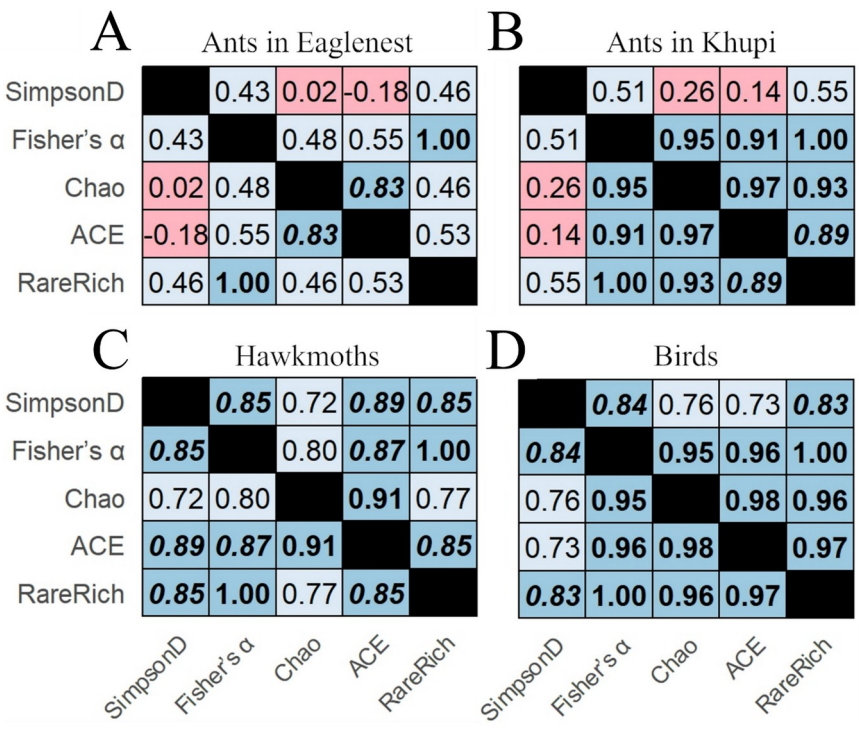


Figure 3.2: Pearson Correlation Coefficients for five diversity metrics used in this Chapter to assess diversity–elevation profiles. The top row are matrices for ant communities at Eaglenest (A) and Khupi (B). The bottom row are the matrices for hawkmoths (C) and birds (D) from Eaglenest. Blue = positive correlation and pink = negative correlation

3.3 Results

Across all taxa, we found a moderate to strong correlation (≥ 0.50) between all pairs of alpha metrics, except for Chao-corrected Simpson's D **(Figure 3.2)**. Bird communities exhibit the strongest pairwise correlations (≥ 0.93), compared to hawkmoth and ant communities. Pairwise correlations between Chao-corrected Simpson's D and the other four metrics were slightly lower, ranging from 0.73–0.84 in birds **(Figure 3.2)**, but dropping to between −0.12–0.55 in ants **(Figure3.2A & B)**. Due to the high concordance among metrics, subsequent analyses were conducted using rarefied richness and Chao-corrected Simpson's D.

3.3.1 Slope-specific elevational diversity profiles of Ants

Alpha diversity of the ant community largely exhibited a monotonic decline with elevation on both slopes i.e. Eaglenest and Khupi, although the magnitude and significance of this pattern varied across metrics **(Figure 3.3**). Rarefied generic richness declined significantly with elevation in both Eaglenest (slope = -4.69 genera/km; p = 0.039) and Khupi (slope = -6.85 genera/km; p = 0.067) **(Table 3.4)**. Fisher's alpha similarly exhibited a significantly declining pattern of diversity at Eaglenest (slope = -1.98/km; p = 0.051) with moderate significance at Khupi (slope = -2.96/km; p = 0.081). Richness extrapolation estimators, such as Chao and ACE, did not significantly change across elevation in both Eaglenest and Khupi (p > 0.1; R2 ≤ 0.20). However, Simpson's D (Chao-corrected) declined significantly across elevation at both Eaglenest (slope = 0.052/km; R^2 = 0.66, p = 0.002) and Khupi (slope = -0.106/km, R^2 = 0.55, p = 0.015) **(Table 3.4; also see Figure 3.3)**.
Elevation × Transect interaction terms were not significant (p > 0.1) for any of the five alpha diversity measures examined**.**

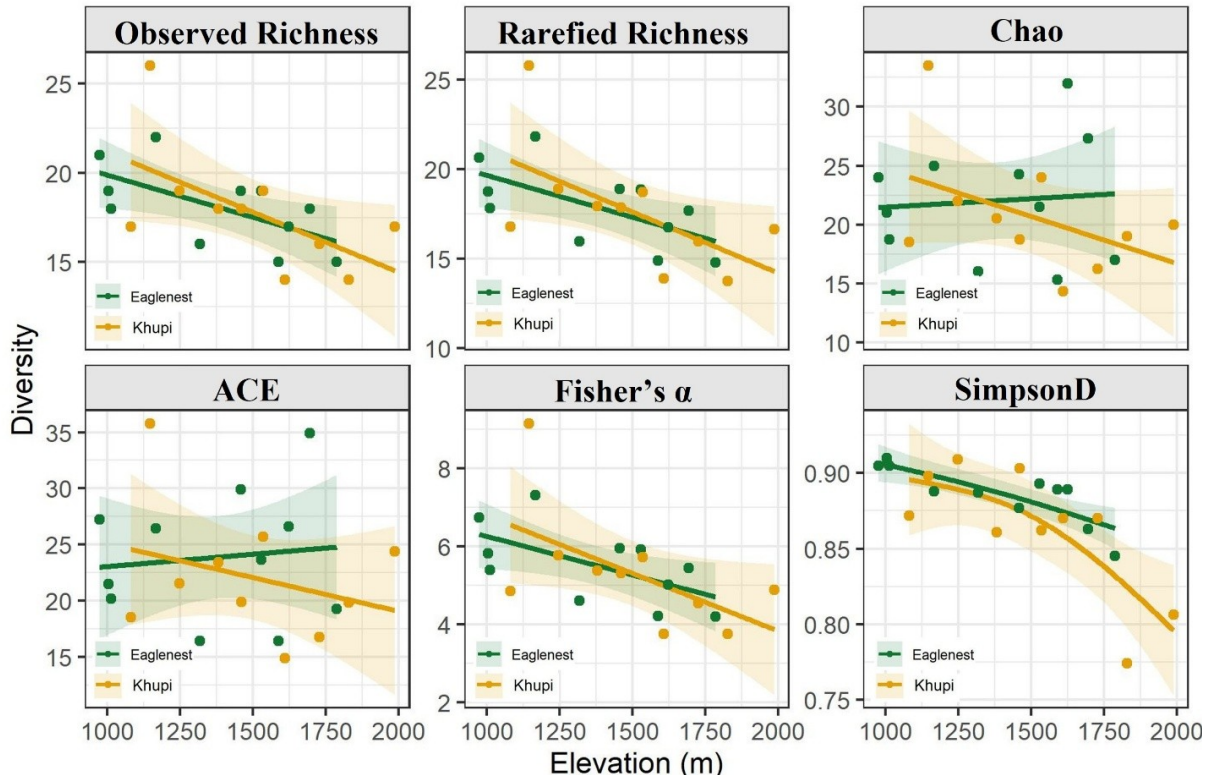


Figure 3.3: Relationships between elevation and six alpha-diversity metrics, including observed (raw) richness, for ant communities in Eaglenest and Khupi across 1000–2000 m. Solid points represent the elevational communities (green = Eaglenest; yellow = Khupi), and solid lines represent the fitted GAMs for each transect (green = Eaglenest; yellow = Khupi). Eaglenest has 11 elevational communities while Khupi (KH1 + KH2) has 10 elevational communities.

3.3.2 Impact of spatial extent on observed diversity profiles: Birds and Hawkmoths

Across the full elevational extent (FP) sampled, hawkmoth (Figure 3.4) and bird (Figure 3.5) species differed substantially in their richness/diversity profiles. Hawkmoth rarefied species profile exhibited slight curvature, corroborated by slightly higher explained deviance of 0.51 explained by GAMs compared to 0.41 by GLMs (Table 3.5). Elevational change in Chao-corrected Simpson's D also exhibits slight curvature with marginal improvement in GAM fit compared to GLM fit. Qualitatively, hawkmoth species profiles across the full extent for both metrics resemble a low-elevation plateau followed by a declining richness.

Table 3.4: Summary of linear model fits between elevation and five alpha diversity metrics for ant communities in the Eaglenest Wildlife Sanctuary (EN) and Khupi (KH) transects. For each transect, the table shows the slope (± SE) per km increase in elevation, associated p-values and model R^2. The Elevation × Transect interaction tests whether elevational relationships differ significantly between transects. Asterisks denote significance levels (*p < 0.1, **p < 0.05).

Metric	Transect	Slope ± SE per km	p	Adj.R^2	F (Elev × Transect)	p (Elev × Transect)
Rarefied Richness	EN	-4.69 ± 1.95**	0.04	0.39	0.34	0.57
	KH	-6.85 ± 3.24*	0.07	0.36	0.34	0.57
Chao	EN	1.44 ± 5.74	0.81	0.01	1.37	0.26
	KH	-8.00 ± 5.60	0.19	0.20	1.37	0.26
ACE	EN	2.20 ± 6.45	0.74	0.01	0.78	0.39
	KH	-6.00 ± 6.68	0.39	0.09	0.78	0.39
Fisher's α	EN	-1.98 ± 0.88*	0.05	0.36	0.34	0.57
	KH	-2.96 ± 1.49*	0.08	0.33	0.34	0.57
Simpson's D	EN	-0.05 ± 0.01**	0.00	0.66	2.37	0.14
	KH	-0.11 ± 0.03**	0.01	0.55	2.37	0.14

At the species level, 2/3 FP (66% of FP) and 1/3 FP (33% of FP) patterns appear largely similar to FP for rarefied richness, with GAMs not adding substantially to GLM fits. However, Chao-corrected Simpson's D along 1/3 FP (33% of FP) yields an upward parabola dominated by noise around 900–1100 m**,** associated with a significant improvement in GAM fit ($exp.Dev_{GAM}$ = 0.72) over GLM fit ($exp.Dev_{GLM}$ = 0.03). Hawkmoth species peak in diversity, across both metrics, at the lowest elevation. Across both 2/3 FP and 1/3 FP, diversity peak systematically shifts to occupy the lowest elevation included in the truncated dataset.

For bird species across the full extent (FP), rarefied richness, peaking at 1456 m, exhibited the strongest non-linear response across elevation **(Figure 3.5 & Table 3.5)**. GLM fits for FP were poor, explaining just 1% of the deviance, with GAMs explaining 78% of the deviance. Under 2/3 FP, GAMs still accounted for a large proportion of the deviance. However, there was a marginal reduction in non-linearity ($exp.Dev_{GAM}$ = 0.64; $exp.Dev_{GLM}$ = 0.27) accompanied by a downslope shift of 112 m in the peak. Under 1/3 FP, elevational richness reverted to a strong non-linear pattern ($exp.Dev_{GAM}$ = 0.99; $exp.Dev_{GLM}$ = 0.03), with an upslope shift of 87 m in the peak compared to FP. In the case of bird communities, Simpson's D was largely in agreement with findings from rarefied richness profiles, with some exceptions. Firstly, diversity peaks were stabler under the 2/3 FP scheme (ΔP ≤ 103 m)compared to the richness peaks. Secondly, the familial diversity profile was

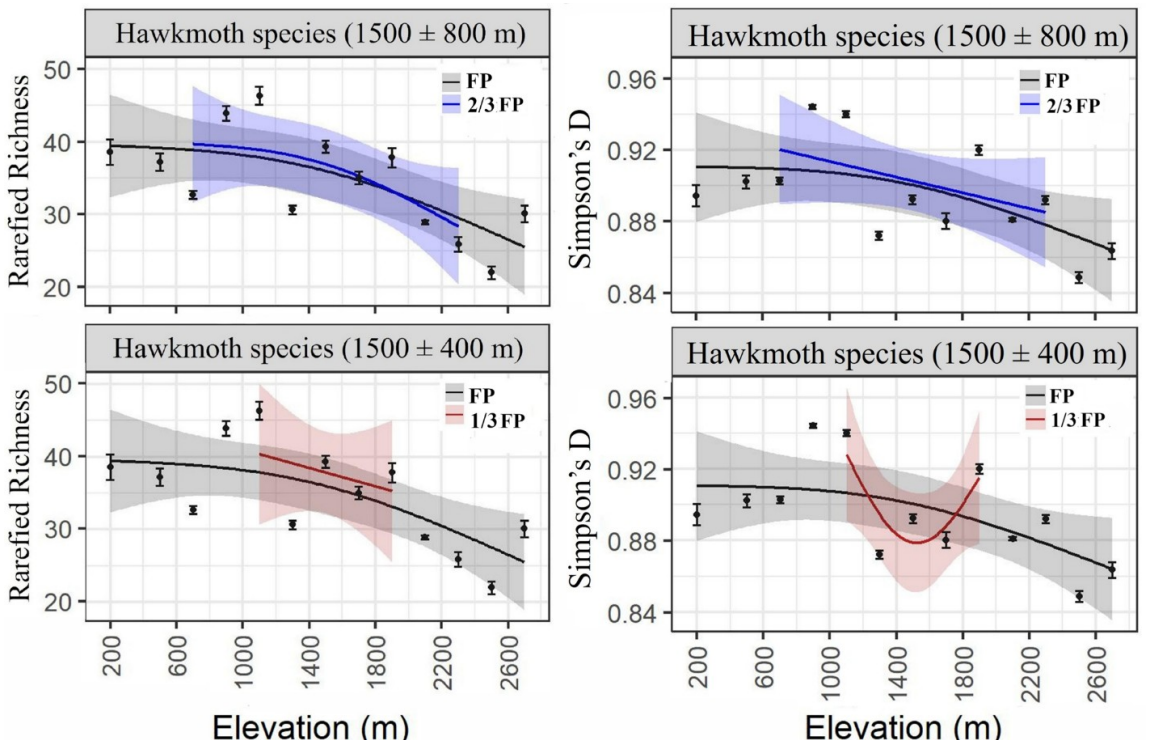


Figure 3.4: Hawkmoth species rarefied richness (left column) and Chao-corrected Simpson's Diversity (right columns) across differing elevational extents. Generalised linear models (GAMs) are used to fit the relationship of richness and diversity with elevation. Solid black points represent raw richness and diversity values at a given elevation with black fitted curves representing the GAM fit for the complete/untruncated (FP: 1500 ± 1200 m) gradient. Blue (left) and red (right) curves represent GAM fit for when 66% (2/3 FP: 1500 ± 800 m) and 33% of the gradient (1/3 FP: 1500 ± 400 m) is examined,, respectively.

flatter relative ($exp.Dev_{GAM}$ = 0.15; $exp.Dev_{GLM}$ = 0.15) to the familial richness profile ($exp.Dev_{GAM}$ = 0.83; $exp.Dev_{GLM}$ = 0.68).

Across limited but fixed spans covering lower (LS1), middle (MS1) and higher (HS1) elevations, GAM fits were dominated by noise and appeared widely different compared to the full profile in both hawkmoths **(Figure 3.6 & Table 3.6)** and birds **(Figure 3.7 & Table 3.6).**

Summary statistics for the GAM models described in this section are provided in **Table 3.7.**

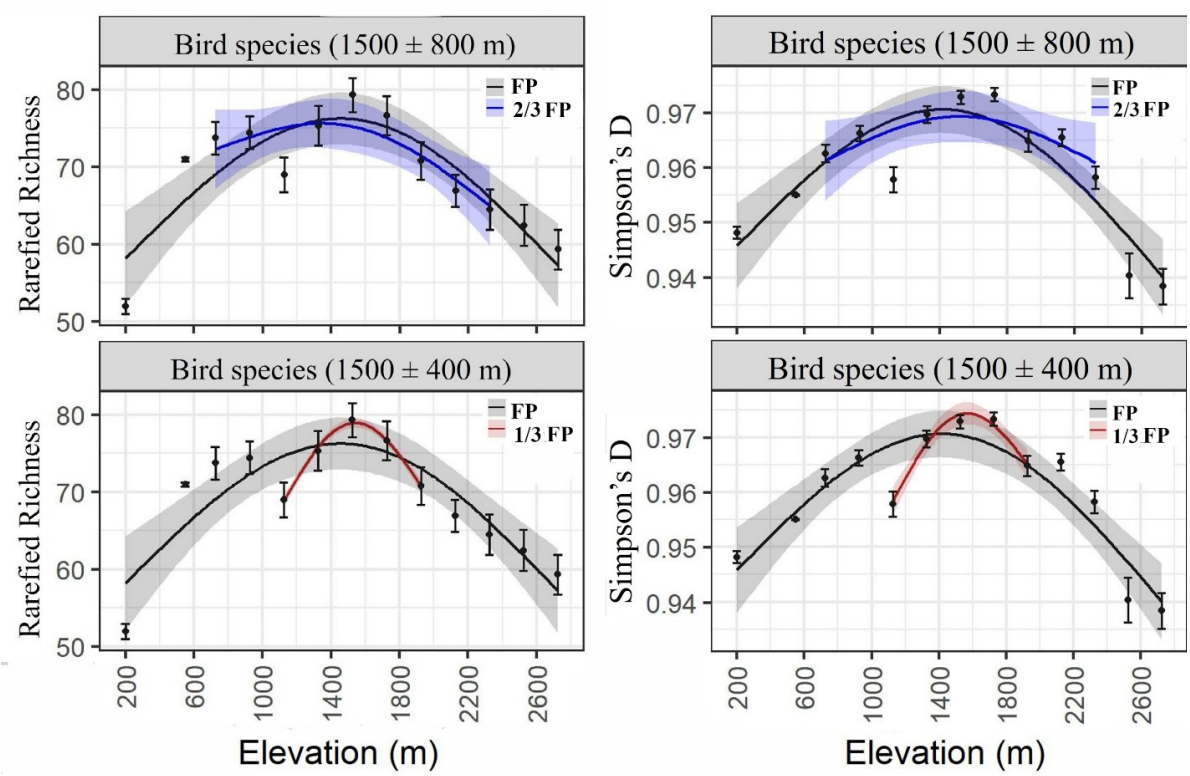


Figure 3.5: Bird species rarefied richness (left) and Chao-corrected Simpson's Diversity (right) across differing elevational extents. Generalised linear models (GAMs) are used to fit the relationship of richness and diversity with elevation. Solid black points represent raw richness and diversity values at a given elevation with black fitted curves representing the GAM fit for the complete/untruncated (FP: 1500 ± 1200 m) gradient. Blue (left) and red (right) curves represent GAM fits for when 66% (2/3 FP: 1500 ± 800 m) and 33% of the gradient (1/3 FP: 1500 ± 400 m) are examined, respectively.

Table 3.5: Comparative perfomance of generalised additive models (GAMs) and generalised linear models (GLMs) for hawkmoth and bird communities across differing spatial extents. The tables summarise results for two diversity metrics (rarefied richness and Chao-corrected Simpson's D) at the species level across the full elevational extent (FP) and for truncated profiles (2/3 FP and 1/3 FP). Specifics are the explained deviance for GAM and GLM fits along with model complexity (C: degree of improvement of GAM over GLM), elevation of diversity peak (m) and shift in diversity peak (ΔP) in truncated profiles relative to the full profile. All data is from Eaglenest Wildlife Sanctuary.

Hawkmoth species:

Metric	Profile	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	FP	0.51	0.41	0.18	200	0
	2/3 FP	0.42	0.32	0.24	700	-500
	1/3 FP	0.12	0.12	0.00	1100	-900
Simpson's D (Chao-corrected	FP	0.39	0.29	0.24	200	0
	2/3 FP	0.21	0.21	0.00	700	-500
	1/3 FP	0.72	0.03	0.96	1100	-900

Bird species:

Metric	Profile	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	FP	0.78	0.01	0.98	1456	0
	2/3 FP	0.64	0.27	0.58	1344	112
	1/3 FP	0.99	0.03	0.97	1543	-87
Simpson's D (Chao-corrected	FP	0.83	0.06	0.93	1418	0
	2/3 FP	0.46	0.00	1.00	1521	-103
	1/3 FP	0.98	0.18	0.81	1571	-153

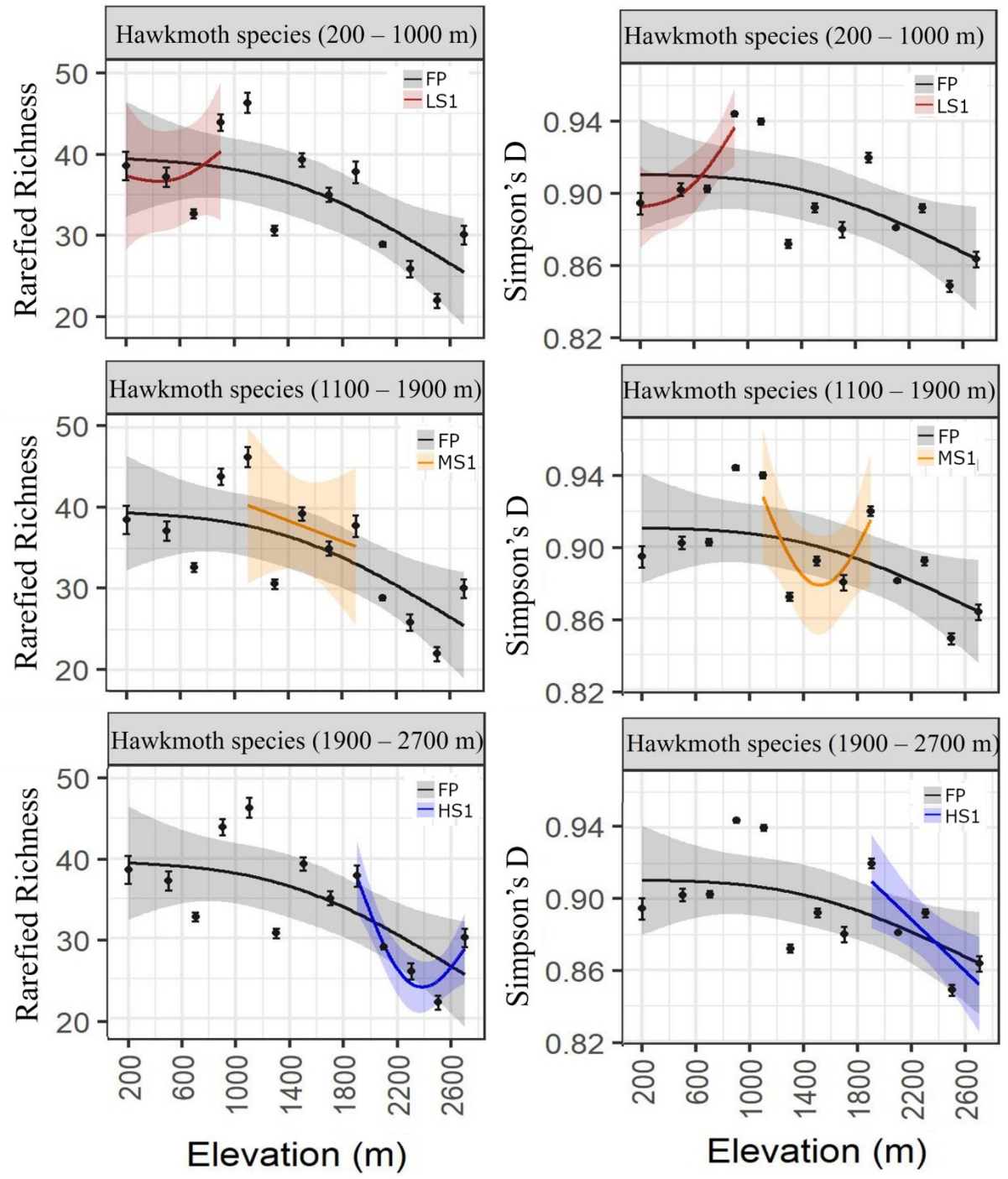


Figure 3.6: Hawkmoth species rarefied richness (left) and Chao-corrected Simpson's Diversity (right) across shifting 800 m elevational spans fitted using generalised linear models (GAMs). Solid black circles are raw diversity values with black fitted curves representing the GAM fit for the complete/untruncated (FP: 200–2700 m) gradient. Red, orange and red curves represent GAMs spanning 33% of the gradient at the lower (LS1: 200–900 m), middle (MS1: 1100–1900 m) and higher elevations (HS1: 1900–2700 m) respectively.

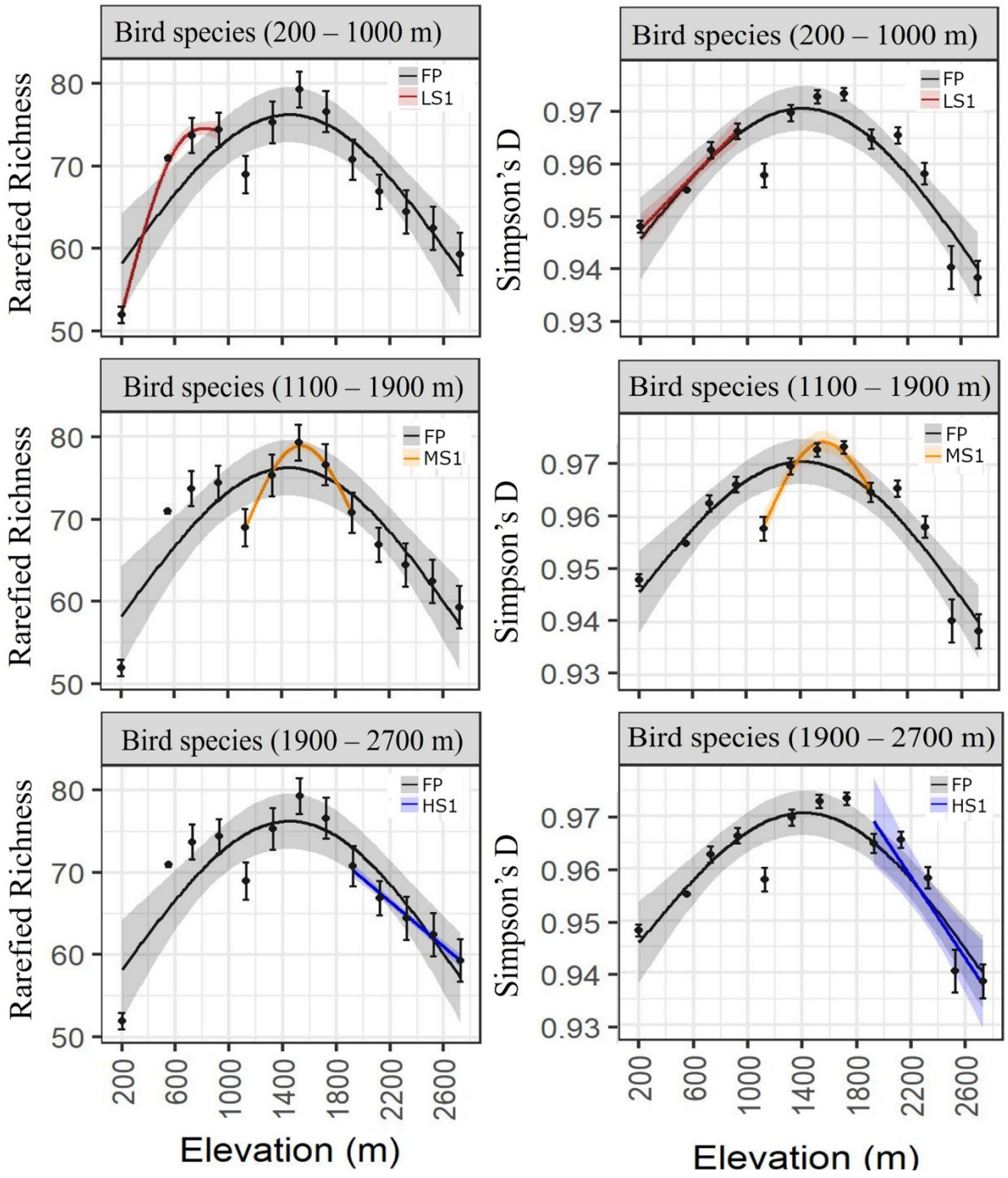


Figure 3.7: Bird species rarefied richness (left) and Chao-corrected Simpson's Diversity (right) across shifting 800 m elevational spans fitted using generalised linear models (GAMs). Solid black circles are raw diversity values with black fitted curves representing the GAM fit for the complete/untruncated (FP: 200–2700 m) gradient. Red, orange and red curves represent GAMs covering 33% of the gradient at the lower (LS1: 200–900 m), middle (MS1: 1100–1900 m) and higher elevations (HS1: 1900–2700 m) respectively.

Table 3.6: Performance of generalised additive models (GAMs) and generalised linear models (GLMs) in hawkmoth and bird communities with shifting (800 m) elevational extents. The tables provide results for two diversity metrics (rarefied richness and Chao-corrected Simpson's D) at the species level across the full elevational extent (FP) and 800 m elevational extents biased towards lower (LT1), middle (MT1) and higher elevation (HT1). For each profile, the tables contain the explained deviance for GAM and GLM fits along with model complexity (C: degree of improvement of GAM over GLM), elevation of diversity peak (m) and shift in diversity peak (ΔP) in shifting profiles relative to the full profile. All data is from Eaglenest Wildlife Sanctuary.

Hawkmoth species:

Metric	Profile	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	FP	0.51	0.41	0.18	200	0
	LT1	0.35	0.07	0.79	900	-700
	MT1	0.12	0.12	0.00	1100	-900
	HT1	0.92	0.36	0.60	1900	-1700
Simpson's D (Chao-corrected)	FP	0.39	0.29	0.24	200	0
	LT1	0.86	0.68	0.22	900	-700
	MT1	0.72	0.03	0.96	1100	-900
	HT1	0.70	0.70	0.00	1900	-1700

Bird species:

Metric	Profile	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	FP	0.78	0.01	0.98	1456	0
	LT1	1.00	0.85	0.15	816	640
	MT1	0.99	0.03	0.97	1543	-87
	HT1	0.99	0.99	0.00	1925	-469
Simpson's D (Chao-corrected)	FP	0.83	0.06	0.93	1418	0
	LT1	0.97	0.97	0.00	925	493
	MT1	0.98	0.18	0.81	1571	-153
	HT1	0.87	0.87	0.00	1925	-507

Table 3.7: Summary statistics of generalised linear models for fitted alpha diversity profiles in hawkmoth and bird species from Eaglenest. The table contains fitted estimates (± SE) and adjusted R^2 values for two diversity metrics (rarefied richness and Simpson's D). Fitted profiles include the full elevational profile (FP) and truncated profiles (2/3 FP and 1/3 FP). Asterisks denote levels of statistical significance ($p < 0.1^{*}$, $p < 0.05^{**}$, $p < 0.001^{***}$).

Across differing extents:

Dataset	Metric	Profile	Parametric Estimate	Std. Error	Adj.R^2
Hawkmoth	Rarefied Richness	FP	34.50^{***}	1.46	0.43
		2/3 FP	35.63^{***}	1.91	0.30
		1/3 FP	37.84^{***}	2.80	-0.17
	Simpson's D (Chao-corrected)	FP	0.89^{***}	0.01	0.30
		2/3 FP	0.90^{***}	0.01	0.10
		1/3 FP	0.90^{***}	0.01	0.48
Bird	Rarefied Richness	FP	68.86^{***}	1.10	0.73
		2/3 FP	72.28^{***}	1.10	0.53
		1/3 FP	74.20^{***}	0.20	0.99
	Simpson's D (Chao-corrected)	FP	0.96^{***}	0.00	0.80
		2/3 FP	0.97^{***}	0.00	0.30
		1/3 FP	0.97^{***}	0.00	0.95

Across (800 m) shifting extents:

Dataset	Metric	Profile	Parametric Estimate	Std. Error	Adj.R^2
Hawkmoth	Rarefied Richness	FP	34.50^{***}	1.46	0.43
		LT1	38.09^{**}	2.48	-0.15
		MT1	37.84^{***}	2.80	-0.17
		HT1	28.96^{**}	1.06	0.84
	Simpson's D (Chao-corrected)	FP	0.89^{***}	0.01	0.30
		LT1	0.91^{***}	0.01	0.71
		MT1	0.90^{***}	0.01	0.48
		HT1	0.88^{***}	0.01	0.61
Bird	Rarefied Richness	FP	68.86^{***}	1.10	0.73
		LT1	67.76^{**}	0.31	1.00
		MT1	74.20^{***}	0.20	0.99
		HT1	64.78^{***}	0.24	0.98
	Simpson's D (Chao-corrected)	FP	0.96^{***}	0.00	0.80
		LT1	0.96^{***}	0.00	0.96
		MT1	0.97^{***}	0.00	0.95
		HT1	0.95^{***}	0.00	0.83

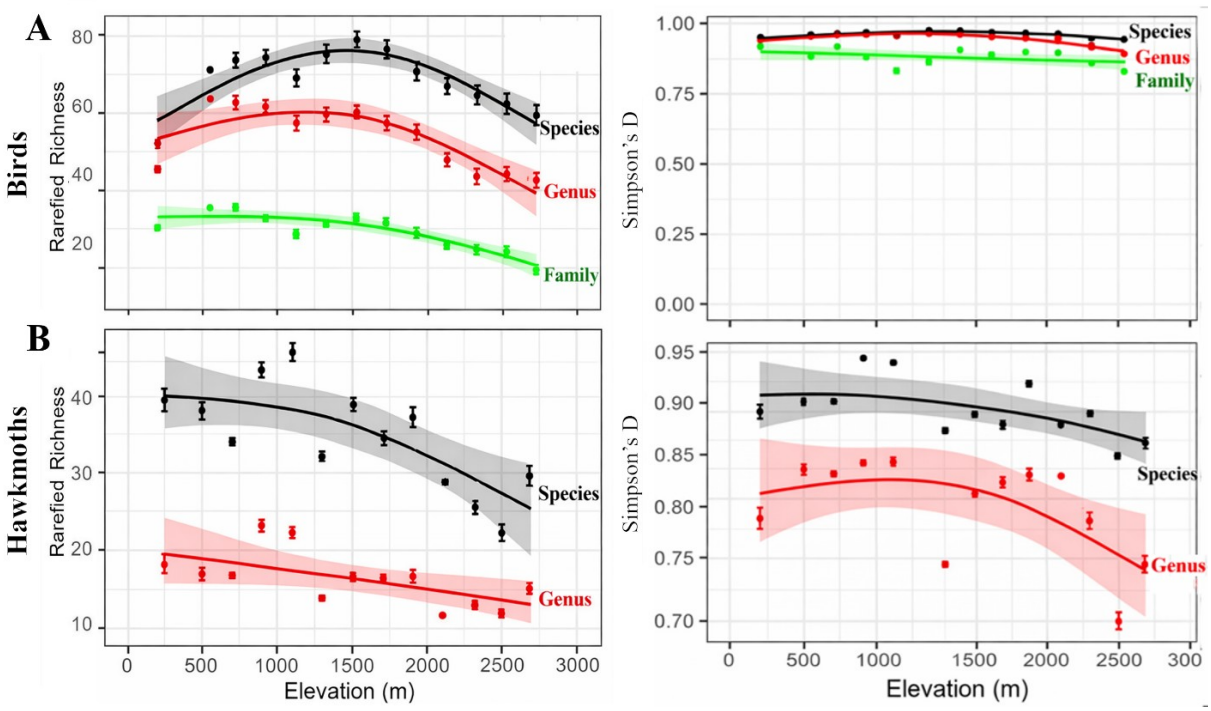


Figure 3.8: Taxonomic-scale dependent relationships between elevation and rarefied richness (left) and Chao-corrected Simpson's D (right) for bird communities (top) and hawkmoth communities (bottom). Raw richness and diversity values for elevational communities are represented by solid black circles. Generalised additive model (GAM) fits for birds and hawkmoths are represented by coloured curves, with familial (green) levels for birds only along with generic (red) and species (black) level for both hawkmoths and birds.

3.3.3 Impact of taxonomic scale on observed diversity profiles: Birds and Hawkmoths

At higher taxonomic scales, bird profiles across both metrics progressively increase in linearity **(Figure 3.8)**. Birds show a marked decline in non-linearity from species to familial level with a systematic shift in the richness peak towards lower elevations **(Table 3.8)**.

Hawkmoth profiles, on the other hand, show contrasting trends across both metrics. GAM-fitted rarefied richness shows a slight improvement over GLM-fitted rarefied richness in species, but not so at the genus level. However, based on Chao-corrected Simpson's D, hawkmoth genus profile appears to possess more curvature than species profile. Summary statistics for the GAM fitted models across differing taxonomic scales in birds and hawkmoths is listed in **Table 3.9.**

Table 3.8: Taxonomic scale-dependent changes in elevational diversity profiles in bird and hawkmoth dataset using two alpha metrics (rarefied richness and Chao-corrected Simpson's D). For each dataset-metric pair, all statistics are reported relative to the species-level values. The table contains explained deviance for generalised additive models (GAMs) and generalised linear models (GLMs), along with model complexity (C; higher values signify greater non-linearity), elevation at which diversity peaks (m) and shift in elevation at which diversity peaks (ΔP) at higher taxonomic levels compared to species-level peak.

Birds:

Metric	Taxonomic Rank	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	Species	0.78	0.01	0.98	1456	0
	Genus	0.75	0.37	0.51	1190	266
	Family	0.83	0.68	0.19	720	736
	Order	0.93	0.93	0.00	200	1256
Simpson's D (Chao-corrected	Species	0.83	0.06	0.93	1418	0
	Genus	0.91	0.38	0.58	1240	178
	Family	0.15	0.15	0.00	200	1218
	Order	0.90	0.87	0.03	200	1218

Hawkmoths:

Metric	Taxonomic Rank	Explained Deviance for GAM fits	Explained Deviance for GLM fits	Complexity (C)	Elevation of Peak Diversity (m)	ΔP (m)
Rarefied Richness	Species	0.51	0.41	0.18	200	0
	Genus	0.29	0.29	0.00	200	0
Simpson's D (Chao-corrected)	Species	0.39	0.29	0.24	200	0
	Genus	0.46	0.25	0.45	1067	-867

Table 3.9: Generalised additive model (GAM) summary statistics for alpha diversity profiles obtained across differing taxonomic scales in birds and hawkmoths. The table contains fitted parametric estimates (± SE) along with adjusted R^2 values from fitted GAMs for two diversity metrics (rarefied richness and Chao-corrected Simpson's D) employed at a given taxonomic scale. For birds, GAMs were fitted across familial-, genus- and species-level. For hawkmoths, GAMs were fitted across genus- and species-level. Asterisks denote levels of statistical significance ($p < 0.1^{*}$, $p < 0.05^{**}$, $p < 0.001^{***}$). All data is restricted to Eaglenest Wildlife Sanctuary.

Dataset	Metric	Taxonomic Rank	Parametric Estimate	Std. Error	Adj.R^2
Bird	Rarefied Richness	Species	68.86^{***}	1.10	0.73
		Genus	53.92^{***}	1.22	0.70
		Family	29.57^{***}	0.59	0.80
		Order	7.52^{***}	0.15	0.93
	Simpson's D (Chao-corrected)	Species	0.96^{***}	0.00	0.80
		Genus	0.94^{***}	0.00	0.89
		Family	0.88^{***}	0.01	0.07
		Order	0.19^{***}	0.01	0.88
Hawkmoth	Rarefied Richness	Species	34.50^{***}	1.46	0.43
		Genus	16.74^{***}	0.83	0.22
	Simpson's D (Chao-corrected)	Species	0.89^{***}	0.01	0.30
		Genus	0.80^{***}	0.01	0.36

3.3.4 Comparison of diversity profiles of two insect families at the same location: Ants (Family: Formicidae) v/s Hawkmoths (Family: Sphingidae)

Ant genera showed clearer elevational trends in three of five alpha metrics (**Figure 3.9).** On the other hand, hawkmoth genera show weak elevational trends across all five metrics. Rarefied richness declined significantly with elevation in ants (slope −4.69 genera/km, $p = 0.039$), whereas a steeper decline in hawkmoths was not significant (slope = −6.57 ± 3.78, $p = 0.16$). Likewise, Fisher's α decreased marginally in ants (slope = −1.98 ± 0.88, $p = 0.05$), but not in hawkmoths. Chao-corrected Simpson's D exhibited a substantial decline with elevation in ants (slope = −0.05 ± 0.01, adjusted $R^2 = 0.66$, $p < 0.01$), with no elevational trend detected for hawkmoths. Chao and ACE richness estimators showed no significant elevational patterns in both hawkmoth and ant

genera (all p > 0.25). Fisher's r-to-Z tests comparing differences in slope profiles between ants and hawkmoths were no significant for all five alpha metrics (p > 0.1).

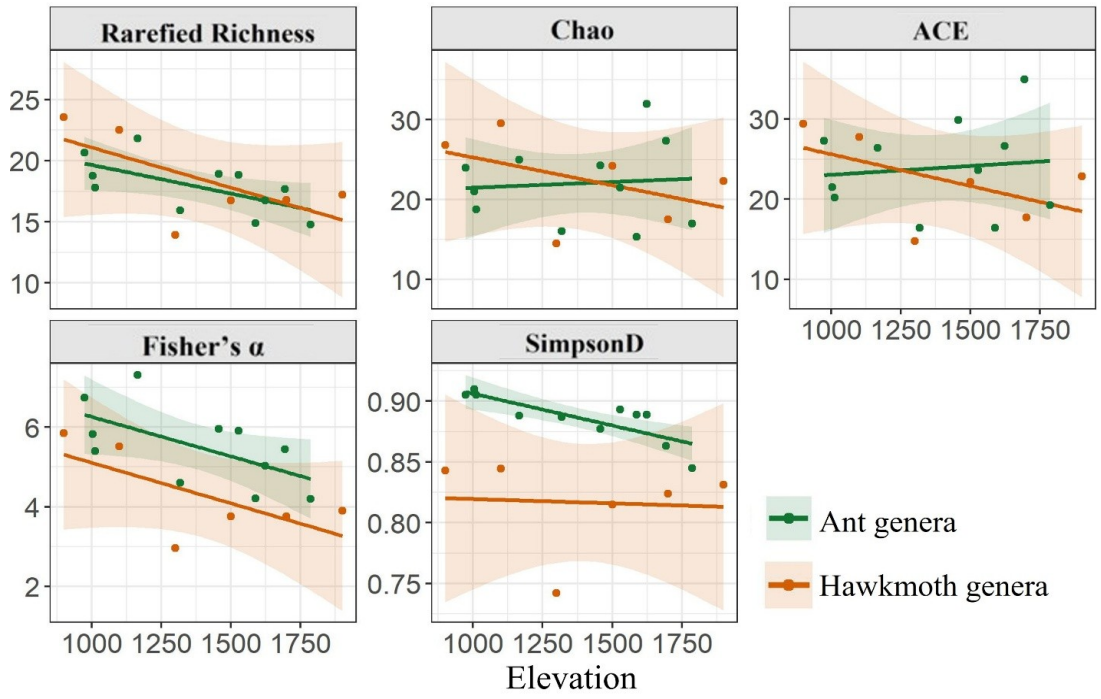


Figure 3.9: Relationships between elevation and five alpha-diversity metrics for ant and hawkmoth genera in Eaglenest across 1000–1800 m. Solid points represent the elevational communities (green = ant genera; vermillion = hawkmoth genera), and solid lines represent the fitted linear models for each taxon (green = ant genera; vermillion = hawkmoths). Note that ant genera have 11 elevational communities spaced 80-100 m apart while hawkmoths have 6 elevational communities spread 200 m apart.

Metric	Taxon	Slope ± SE per km	p	Adj.R^2	Z-statistic	p (for Z)
Rarefied Richness	Ants	-4.69 ± 1.95**	0.04	0.39	0.44	> 0.1
	Hawkmoths	-6.57 ± 3.78	0.16	0.43		
Chao	Ants	1.44 ± 5.74	0.81	0.01	0.95	> 0.1
	Hawkmoths	-6.97 ± 6.71	0.36	0.21		
ACE	Ants	2.20 ± 6.45	0.74	0.01	1.12	> 0.1
	Hawkmoths	-7.92 ± 6.38	0.28	0.28		
Fisher's α	Ants	-1.98 ± 0.88*	0.05	0.36	0.04	> 0.1
	Hawkmoths	-2.04 ± 1.12	0.14	0.45		
Simpson's D (Chao-corrected)	Ants	-0.05 ± 0.01**	0.00	0.66	-0.87	> 0.1
	Hawkmoths	-0.01 ± 0.05	0.90	0.00		

3.4 Discussion

Elevation is often used as a single predictor variable for diversity. However, it only serves as a surrogate for multiple climatic variables such as temperature, precipitation or net primary productivity, which are largely intercorrelated with each other in complex ways (Perrigo et al., 2019; Rahbek et al., 2019). Although elevation approximates these climatic variables reasonably well, the relationships can differ substantially across montane systems and taxa, limiting direct comparisons of communities found at similar elevations on different mountain slopes. For instance, tropical and temperate montane systems differ substantially in their climatic baselines, lapse rates and magnitude of seasonal fluctuations (Pepin et al., 2022). We see similar, albeit subtler, contrasts within the same montane system, for example between slopes differing in their aspect (Maheshwori et al. 2025) or ruggedness of the terrain (Dilts et al., 2023).

Majority of elevational gradient studies examine the role of environmental drivers and geometric constraints in shaping diversity–elevation relationships. Yet, little is understood of how and why their strength and direction varies on account of the spatial and taxonomic scales considered (Chase et al., 2018; Jarzyna & Jetz, 2018; Rahbek et al., 2019). We investigated this dependency of both spatial (elevational) and taxonomic scale in the observed diversity–elevation relationships across three elevational datasets spanning birds, hawkmoths and ants. For ant communities, we specifically examined the effect of differing slopes on diversity–elevation relationship.

1. Based on three of five alpha metrics, ant communities appeared to decline in richness and diversity along both Eaglenest and Khupi transects **(Figure 3.3)**. The strength of the relationship with elevation did not significantly differ between the two transects **(Table 3.4)**.
2. As expected, hawkmoth and bird profiles became more linear at 66% spatial extents. This trend was more apparent in bird profiles. Profiles across even shorter extents (33% extent) were highly variable **(Figure 3.4 & Figure 3.5)**, likely due to the dominance of noise in the data. It is important to note that many studies sample across short elevational extents (< 1000 m)(Guo et al. 2013); equivalent to 1/3 FP (33% extent), LS1, MS1 and HS1 spans examined in this study **(Figure 3.6 & Figure 3.7)**.
3. Across taxonomic scales, diversity–elevation profiles became increasingly linear at higher scales for both hawkmoth and bird communities **(Figure 3.8; also see Table 3.8)**. In birds, this spanned the full range of commonly observed patterns: a unimodal distribution at the

species level, a low-elevation plateau at the generic level, and a monotonic decline at the familial level.

Overall, we examined three key dimensions along which diversity–elevation can potentially vary: topographic factors (aspect of slope, terrain ruggedness), spatial (elevational) extent and taxonomic scale. While there are few other dimensions that are also important, some of which include lateral extents (Rahbek et al. 2019; Perrigo et al. 2020), spatial grain (Rahbek & Graves, 2001; Sanders et al., 2007) and phylogenetic depth (Tucker et al., 2018; Wang et al., 2025), they are beyond the scope of this discussion.

3.4.1 Slope-specific elevational diversity profiles of Ants

Ant species are reported to commonly exhibit a hump-shaped elevational richness pattern across all latitudes based on a global meta-analysis (Szewczyk & McCain, 2016). On the other hand, several recent studies from the tropical and subtropical regions report a monotonic decline in richness (Fontanilla et al., 2019; Kunene et al., 2022; Moses et al., 2023). This declining pattern in richness has been attributed to the thermophilic nature of ant species, whose distributions are strongly linked to temperature (Diamond et al., 2012; Nowrouzi et al., 2016). A study from the neighbouring Yunnan Province of China reported rapid decline in ant richness along a 3000 m elevational span. However, the study also spanned a broader latitudinal gradient between 21°N to 27°N, pooling elevational communities from three different slopes (Ashton et al., 2016; Fontanilla et al., 2019). In comparison, our study spanned a much narrower latitudinal gradient of 0.2 degrees of latitude at 27°N (27.03–27.21°N) and more crucially, assessed communities within a slope.

Recent studies from the region also report unimodal patterns. Ant species in the Darliang mountains of China (27°N to 33°N) exhibited a unimodal richness pattern which the authors attribute to a harsher hot and dry river valley at the base of the mountain compared to the more favorable semi-humid mid-elevations (You et al., 2025). Comparing studies reporting varying patterns emphasise the need to better understand how various climatic gradients, such as temperature gradients and moisture gradients, interact with each other to influence elevational diversity patterns in thermophilic insects.

In our study we sampled ants across a limited climatic gradient (1,000–2,000 m) along the two slopes, which we expected to differ in their climatic gradient due to differences in topography (**Table 2.1**). Within individual transects, Simpson's D was the only index that strongly declined in magnitude across elevation, although both rarefied richness and Fisher's α exhibited marginal decline **(Figure 3.3; also see Table 3.4)**. This indicated that higher elevations are largely dominated by fewer taxa, despite relatively stable generic richness. i.e. community composition seemed to change as a function of elevation but without significant changes in overall richness. We also expected differences in topography to impact ant richness and diversity patterns along the two slopes. However, there was no significant difference between the two slopes in the diversity-elevation relationship, regardless of the alpha metric employed (**Table 3.4)**.

Studies from the Indomalayan and Neotropical regions have shown that while species richness reduced, abundance remained constant till about 1000–1500 m due to density compensation, beyond which abundance along with richness declined sharply (Longino et al., 2019; Malsch et al., 2008). Despite this, we did not find a sharper decline in rarefied generic richness at higher elevations till 2000 m. As discussed earlier, flatter diversity profiles may arise when diversity is measured at higher taxonomic scales. Corroborating this, Marathe et al. (2020) documented a much steeper monotonic decline in species richness, with only six species recorded at higher elevations (2400 m) compared to 84 at lower elevations (600 m). However, their study spanned nearly twice the elevational extent of ours (~1800 m), suggesting that a decline in rarefied generic richness might also have emerged had our sampling extended to higher elevations. Thus, the absence of a decline in our case may reflect either, or both, the use of generic-level data and/or the limited elevational range sampled.

3.4.2 Impact of spatial extent on observed diversity profiles: Birds and Hawkmoths

Majority of studies on elevational diversity studies sample only part of the available elevational gradient. This is often due to limited funding, poor accessibility across large sections of the gradient, and human-induced disturbances at lower elevations, particularly in tropical and subtropical zones (Guo et al., 2013). Among the 68 studies we compiled on arthropod elevational diversity, with a focus on insect studies, across both regional datasets and meta-analyses, nearly half

began sampling above 500 m (Dolson & Kharouba, 2024). Of the 34 studies for which we had reliable elevational extents, about one-third spanned less than 1000 m.

When we investigated patterns along truncated extents in hawkmoth and bird datasets, the overall shape of the diversity profile remained largely unchanged across 66% of the sampled gradient (**Figure 3.4; Figure 3.5)**. However, truncating the dataset to one-third of the full extent revealed an increase in curvature in birds for both indices **(Figure 3.5)** and in moths for Chao-corrected Simpson's D but not rarefied richness **(Figure 3.4)**. The unexpected reversion to a unimodal profile in birds, when focused on a short extent covering only the mid-elevation section, is likely to be due to a single deviant elevational community at 1100 m **(Figure 3.5)**.

We also examined hawkmoth diversity across comparable spatial extents (800 elevational spans) but differing in their climatic baseline and range **(Figure 3.6)**. We found relatively shallower profiles at lower and middle elevational spans compared to a marked decline at higher elevational spans. This pattern is consistent with findings from Dolson and Kharouba (2024) which suggest that most insect orders follow a "low-plateau" richness pattern.

On the other hand, birds displayed an increasing pattern of richness when lower elevations were examined **(Figure 3.7)**. This could be due to the decline of insectivorous birds at lower elevations due to competitive interactions with *Oecophylla* species; a well-documented phenomenon across Indomalayan and Afrotopical montane systems (Srinivasan et al. 2024). However, both taxa exhibit a similar declining trend beyond 2,000 m (grey plots in **Figures 3.6 and 3.7,** representing species profiles across the full elevational range for both birds and hawkmoths). Decline in richness beyond 1500–2500 m has been previously reported in multiple plant and animal taxa from the Himalayas (Grytnes et al., 2002; Irungbam et al., 2025).

Overall, our findings highlight that the observed patterns and underlying processes may rely on the spatial extents over which biodiversity is measured. Nonetheless, similar elevational extents may not always be directly comparable due to differences in climatic extents (Perrigo et al. 2020; Rahbek et al. 2019). Even across broadly similar climatic spans, microclimatic differences and topographic features may give rise to differential responses within the same taxonomic group

(Lenoir et al., 2017; Serra-Diaz et al., 2014). Therefore, we emphasise the need to account for both spatial and climatic extents when analysing elevational gradients.

3.4.3 Impact of taxonomic scale on observed diversity profiles: Birds and Hawkmoths

Given the variation we see in distributional patterns across broad spatial scales, we can ask whether these patterns retain their overall shape or change completely across differing taxonomic units of observation (Peters et al., 2016; Storch & Šizling, 2008). Most investigators use morphospecies or barcode-informed species (MOTUs) as fundamental units of observation (Thormann et al., 2016). While this remains a reasonable approach, the taxonomic scales at which various ecological and evolutionary processes operate may differ in magnitude (Storch & Šizling, 2008). For example, trait evolution has been shown to differ across taxonomic scales, with a disproportionately larger fraction of the total morphological variation existing between birds orders than within the orders, even after accounting for the diversification rates (Crouch & Ricklefs, 2019). On the contrary, factors such as range-size distribution have been shown to be similar across taxonomic scales in mammalian lineages (Hadly et al., 2009). While competitive interactions among congeneric species limit their individual range sizes, niche conservatism at higher taxonomic levels allows for range expansion of congenerics following extinctions, thereby maintaining stable range-sizes at higher taxonomic levels.

However, niche conservatism may not necessarily scale up to higher taxonomic levels in some cases. Some amphibian species of salamanders and treefrogs exhibit narrow thermal ranges and reduced desiccation tolerances, with their distributions largely dictated by abiotic factors (Kozak & Wiens, 2010, 2006). At higher taxonomic levels, however, congenerics or confamilials may diverge in their environmental tolerances due to a combination of differential adaptations and competitive interactions, resulting in clades that collectively occupy a wider niche space. Hence larger hierarchical groupings representing greater taxonomic depth are often associated with a wider range of adaptive strategies (Weiser et al., 2018; Wiens et al., 2007).

Peters et al. (2016) demonstrated that at the generic and family level, and across multiple groups of plants and animals, abiotic constraints that would otherwise limit the distribution of individual

species with narrower niches are smoothed out, with elevational richness profiles becoming increasingly flatter with only a decline at higher elevations indicating temperature as the primary driver of richness. Consistent with these findings, we observed that in our bird and hawkmoth datasets, diversity–elevation relationships increasingly converged to simpler linear forms at higher taxonomic scales. For birds, the species profile showed a clear unimodal pattern with the generic showing a low-plateau followed by a decline beyond 1500 m while bird families showed a monotonic decline. Hawkmoths, on the contrary, already show a low plateau at the species level but similarly decline beyond 1500 m. This indicates that while taxon-specific processes may operate at lower elevations, both groups responded similarly to temperature constraints at higher elevations, with richness consistently declining at higher elevations. Examples of taxon-specific processes at lower elevations may be precipitation-driven resource availability or trophic interactions for birds, or host-plant availability for hawkmoths.

One probable reason for the difference between the two taxa lies in taxonomic coverage: our bird elevational dataset spans 245 species across multiple orders, whereas hawkmoths are a single family with 80 species. Reduced taxonomic coverage, which somewhat approximates reduced phylogenetic breadth, can yield simpler richness–elevation patterns. This may explain the low plateau profiles even at the species level in hawkmoths (Storch & Šizling, 2008; Peters et al. 2016). Therefore, if we examined bird species within families instead of the entire class of Aves, we may likely observe simpler species profiles for at least some families. On the other hand, a global meta-analysis across four insect orders showed a prevalence of species richness plateaus at low-mid elevations in Lepidopterans and even in in Coleopterans, despite possessing a large taxonomic coverage (Dolson & Kharouba, 2024). While this may suggest taxon-specific responses, there may be other reasons for this pattern such as under-sampling of lower elevations or reduced spatial extents prevalent in many studies (Guo et al. 2013).

Taken together, our results highlight the importance of the taxonomic scale at which biodiversity is measured while interpreting the observed patterns. When richness is measured at coarser taxonomic levels or when taxonomic coverage is limited, the influence of small-scale abiotic factors is attenuated, with diversity–elevation profiles converging on simpler linear patterns driven by large-scale abiotic factors such as temperature (Peters et al., 2016).

3.4.4 Comparison of diversity profiles of two insect families at the same location: Ants (Family: Formicidae) v/s Hawkmoths (Family: Sphingidae)

Within insects, Dipteran and Hymenopteran communities differ markedly in their thermal niches in the European Alps (Sommaggio et al., 2022). Syrphid flies possess greater cold tolerance and are the major pollinators at higher elevations, whereas bees dominate at lower elevations characterised by higher temperatures and longer warm seasons. We expected taxon-specific patterns across elevation in hawkmoth and ant communities due to divergence in thermal physiology and resource requirements, as discussed in the hypothesis section.

Furthermore, studies from the neighbouring province of Yunnan Province of China report a more rapid logarithmic decline in ant richness (Fontanilla et al., 2019) as opposed to a linear decline in moths sampled at the same locations (Ashton et al., 2016).

However, in our study, hawkmoth generic profiles were not very different from that of ants when compared across the elevational span common to both, though the error-bars of the fit are large. Short elevational extents may not represent enough variability of different climatic factors. In our case, the highest elevation we could compare was 1800 m, which may still present favourable conditions for most insect groups.

Future investigation needs to compare similar climatic extents across larger spatial scales to relate patterns to mechanistic underpinnings. Nevertheless, we emphasise on the dependence of diversity–elevation relationships on both the climatic scales at which it is examined and its interaction with taxon-specific physiological and ecological traits.

3.5 Conclusion

Comparing studies that measure diversity across different montane landscapes presents multiple challenges. Firstly, comparable elevational spans may not necessarily imply similar environmental gradients, even within the same mountain range. Slope orientation and inclination along with local peak height influences the balance of temperature and precipitation along with levels of solar incidence across elevation. Secondly, anthropogenic disturbances common at lower elevations as well as logistical issues can hinder complete sampling of the elevational gradient. Consequently, truncated sampling can lead to capturing narrower ranges of environmental gradients, potentially omitting the effects of crucial limiting factors present at gradient edges.

Along with spatial considerations, the taxonomic scale of study presents an additional axis of challenge. Taxonomic units of study tend to adhere to traditional divisions based on centuries of natural history and are contingent on the ease of identification. For instance, the taxonomic knowledge and ease of identification of bird species surpasses identification of insects. Furthermore, taxonomic assemblages examined often widely differ in their coverage. Birds belong to a class while butterflies or moths are an order of insects. In this chapter, we show that both the spatial and taxonomic scales we employ to measure biodiversity impacts the observed patterns.

Chapter 4

Beta Diversity across spatial and taxonomic scales

4.1 Introduction

Spatial heterogeneity in the structure and composition of communities — beta diversity — provides insights into the processes governing community assembly (Cadotte et al., 2019; Petchey & Gaston, 2006; Swenson, 2011). Spatial patterns of diversity arise due to deterministic niche-related processes and stochastic neutral processes, which differ in their reliance on environmental correlates (Hubbell, 2005). Variation in species' coexistence patterns can be linked to their niche, defined in terms of abiotic conditions, resources and biotic interactions. On the other hand, neutral factors such as dispersal and drift could also influence spatial compositional heterogeneity (Svenning et al., 2010). Hence, studying beta diversity provides insights into the relative contributions of niche- and neutral processes in structuring communities across space.

Despite theoretical advancements, estimating the relative contributions of niche and neutral dynamics remains challenging (Adler et al., 2007; Tucker et al., 2016). Studies generally partition beta diversity patterns into measurable environmental and geographic factors (Godsoe et al., 2022; Qian et al., 2005). Along elevational gradients, abiotic conditions and resource availability largely determine species co-occurrence and community turnover (Rivera-Reyes et al., 2025), though patterns are also driven by pool size, dispersal abilities, and colonization-extinction dynamics (Myers et al., 2013; Tatsumi et al., 2020). Consequently, environmental and geographic distances serve as reliable proxy predictors, as they independently and interactively influence spatial composition (Cerroti et al., 2025). But these proxies may not fully capture all underlying factors (Chase & Myers, 2011; Soininen et al., 2018). For clarity, community composition in this chapter refers to taxonomic identities, with or without abundances, depending on the context.

Baselga (2010) proposed partitioning the total observed beta diversity into two additive components — turnover and nestedness — that arise from different ecological processes. Pure turnover is the complete replacement of taxa between sites, while nestedness results in communities that are

subsets of others. The relative contributions of the two components along environmental gradients usually depend on (i) the strength of the environmental gradient and (ii) the geographic connectivity across the landscape (Hu et al., 2022; Peláez & Pavanelli, 2019; Stein et al., 2014).

Steeper environmental gradients host greater densities of habitats and microhabitats, consequently encouraging niche sorting as taxa with distinct physiological tolerances and resource requirements replace one another to optimize fitness (Cavarzere et al., 2021; Choi & Jang, 2022; Stein et al., 2014). But along shallower gradients with broadly uniform climates, compositional shifts are likely driven by dispersal abilities, available area, and site-to-site connectivity rather than niche-based replacement (Freestone & Inouye, 2006). While high connectivity attenuates dispersal-related differences by, instead highlighting microclimatic heterogeneity (Leibold et al., 2017), reduced connectivity amplifies these differences via varying colonization-extinction rates, where strong dispersers become more widespread than limited ones (Padial et al., 2014; X. Zhang et al., 2022). This often results in nested richness patterns that are further intensified along sharp productivity gradients, where reduced carrying capacity restricts certain sites to species-poor communities (Jiang et al., 2022).

Mountains, with their steep climatic gradients and topographic variations, are excellent systems to study environmental and geographic correlates of spatial heterogeneity (Rahbek et al., 2019). Steep environmental gradients result in the replacement of closely related taxa with divergent physiological tolerances (McCain & Grytnes, 2010; Steinbauer et al., 2016). Topographic variation interacts with steep environmental gradients to create a matrix of varying connectivity, forming both physical and climatic barriers within and across mountain slopes (Thormann et al., 2016, 2018). Examining multiple taxonomic groups differing in their physiological limits, ecological requirements and dispersal abilities across the same landscape provides insights on general drivers of beta diversity patterns (Fontana et al., 2020; Santoandré et al., 2024).

4.1.1 State of the Field

Fewer studies have examined beta diversity compared to alpha diversity. We found 2377 studies on elevational alpha diversity, but only 706 studies on elevational beta diversity on the Web of Science. Tibeto-Himalayan region accounted for only 5% (35 of 706) of beta diversity studies we compiled, with most studies from the Neotropics and temperate regions (53%). Arthropods were

surveyed in 25% of all beta diversity studies, and associated with similar bias in geographic representation. Arthropod research in the Himalayas is limited by taxonomic knowledge, with many species undescribed (Basnet et al., 2019; Rana et al., 2021). Scarcity of baseline data and complete inventories prevents basic analyses of ecological patterns, let alone deeper process-based ecological inferences.

Despite the increasing recognition that insights from beta diversity complement alpha diversity (Socolar et al., 2016), only 20% of studies investigated both, of which 79% (385 of 490) were published in the last ten years **(Figure 4.1)**. In spite of this recent surge, meaningful insights are hindered by conceptual and methodological inconsistencies, such as (i) the various theoretical and operational definitions of beta diversity employed across studies (Tuomisto, 2010), (ii) the variability in interpretations from incidence-based and abundance-based metrics (Legendre & De Cáceres, 2013).

Our literature survey revealed 21 montane systems, including 10 from the Old Tropics, in which beta diversity of ant communities was measured. However, only 8 of those studies explicitly partitioned into turnover and nestedness. Across these studies, ant communities tend to become

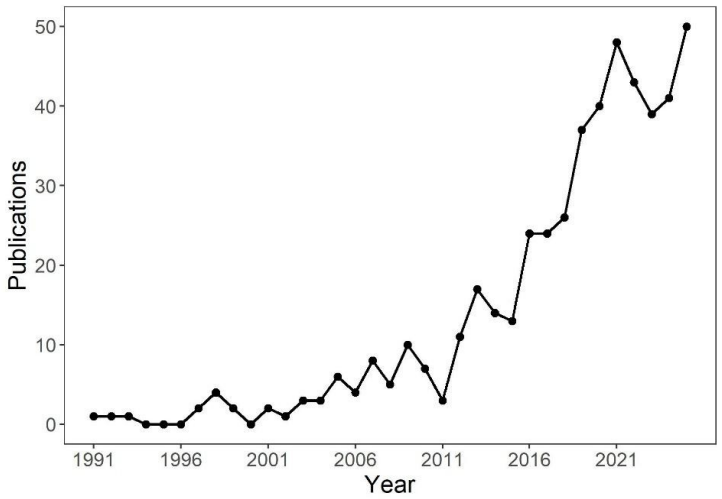


Figure 4.1: Surge in the number of peer-reviewed publications reporting both alpha and beta diversity between 2011–2025. Each point represents publications from one year. Notice a surge in the number of studies from 2011–2016. The key words used in Web of Science to find studies that jointly examine alpha and beta diversity were ("alpha diversity" OR "species richness") AND ("beta diversity" OR "community turnover" OR "species turnover") AND ("elevational gradient" OR "altitudinal gradient" OR "elevation gradient").

more dissimilar with increasing elevational separation, with turnover dominating over nestedness (Bishop et al., 2015; Flores et al., 2018; Fontanilla et al., 2019; Muluvhahothe et al., 2021). However, note that Marathe et al., 2021 reported the dominance of nestedness beyond 600 m separation in ant communities of Eaglenest. In any case, taxonomic turnover did not necessarily translate to functional turnover, with studies reporting functional redundancy and nestedness rather than replacement (Bishop et al., 2015; Fontanilla et al., 2019; de Castro et al., 2020). Seasonality (Nunes et al., 2020; Kongnoo et al., 2025), habitat type (Lasmar et al., 2020) and vertical stratum sampled (Leahy et al., 2024) seemed to have substantial effects on the elevational composition of ant communities.

Early formulations of beta diversity focused on richness differences without considering shared species (Lande, 1996; Veech et al., 2002). Current measures that include pairwise dissimilarity indices look at compositional differences between sites (Anderson et al., 2011; Baselga, 2010; Legendre & De Cáceres, 2013). While abundance-based dissimilarity captures shifts in dominance and rarity, occurrence-based data highlights differences in species identities, though it is more sensitive to rare species turnover (Barwell et al., 2015). Despite the merit of using abundance data, 70% of studies utilize occurrence-based metrics like Sørenson or Jaccard due to the logistical and resource-intensive nature of collecting abundance data (Buonaiuto et al., 2025; Yin & He, 2014). Nevertheless, both abundance and incidence offer process-based insights, particularly as they can be partitioned into turnover and nestedness components linked to specific ecological processes (Baselga, 2010; Chase et al., 2011).

Nestedness is primarily reported in communities facing extreme environmental stressors, such as high-elevation summits (Ibalim et al., 2024; Ohwaki et al., 2021) or anthropogenic disturbances like habitat loss, invasives, and infrastructure (Guzmán-Jacob et al., 2020; Lal et al., 2025; Z. Li et al., 2023), as well as in taxa with varying dispersal abilities (Timoner et al., 2022). Beyond ecology, sampling factors like taxonomic resolution and vertical extent influence observed patterns (Wu et al., 2024); nestedness often prevails at generic or familial levels, likely obscuring species-level turnover driven by narrower niches and habitat specialization (Bishop et al., 2015). Consequently, the balance between turnover and nestedness may depend on the specific climatic range and taxonomic resolution of the data (Soininen et al., 2018).

Beyond using elevation as a sole predictor, incorporating interacting topographic variables like slope inclination and aspect reveals microclimatic heterogeneity that can reinforce or nullify broad-scale climatic effects on community assembly (Körner, 2007; Scherrer & Körner, 2011; Thakur et al., 2022). Examining these interactions helps discern the influence of microclimatic variability on beta diversity patterns (X. Wang et al., 2025). Furthermore, taxonomic groups show idiosyncratic responses based on their unique life histories. Cross-taxon assessments aid in determining the strength of environmental filters (Toranza & Arim, 2010), constituting 12% of all surveyed studies. They ranged from studies comparing diversity of directly interacting species, such as plant-pollinators, to broad-scale comparisons across phyla or kingdoms (Devoto et al., 2009; Fontana et al., 2020; X. Wang et al., 2025).

In this chapter, we explored the structure of community composition along an elevational gradient and the extent to which these patterns are shaped by the geographic context and taxon-specific ecologies. First, we examined within-transect compositional dissimilarity in ant communities as a function of elevational distance and whether elevational position influences the magnitude of dissimilarity. Then, we assessed whether there are transect-specific patterns owing to the various topographic and microclimatic factors, and the extent to which they modulate elevational patterns in ant communities. Next, we looked at within-elevation beta diversity to quantify baseline compositional heterogeneity driven by small-scale microclimatic differences in ant communities. We also compared differences within elevation between nearby transects on the same mountain slope as well as distant transects on different mountain slopes. Finally, we supplemented the ant data with two other taxa (hawkmoths and birds) sampled along the same mountain slope and compared beta diversity profiles at the generic level. Together, these analyses allow us to examine how environmental and topographic heterogeneity, along with taxon-specific ecologies, shape the composition and abundance structure of communities in montane landscapes.

4.1.2 Objectives and Hypotheses

1. **Elevation profiles of taxonomic beta diversity (TβD) in ant communities**

   We examined the role of elevation in shaping compositional differences within transects in Eaglenest and Khupi. See Figure 4.2 for schematic representations of the hypotheses.

   i. **Hypothesis 1a (H1a):** Based on the distance-decay model (but using dissimilarity as a response variable instead of similarity), we expected that compositional dissimilarity increases as a function of elevational distance between sites, at all elevations.

   ii. **Hypothesis 1b (H1b):** Following the widely reported pattern seen in arthropods we expected the dissimilarity to be dominated by turnover

   Based on Steven's mechanism (Stevens, 1989), an extension of Rapoport's rule (Rapoport, 1975), the elevational position influences the effect of elevational distance on beta diversity via differences in range sizes. Larger range sizes at higher elevations would result in greater overlap and co-occurrence of taxa, which would reduce step-wise beta diversity. Here, step-wise beta diversity refers to the dissimilarity between adjacent sites along the elevational transect. Consequently, we expected:

   i. **Hypothesis 1c (H1c): a** negative relationship between step-wise beta diversity and elevation.

   ii. **Hypothesis 1d (H1d):** step-wise turnover dominates at lower elevations but nestedness takes over at higher elevations. This is because harsher abiotic conditions, reduced resources and smaller available area at higher elevations would shrink community composition and size to subsets of lowland communities (Fontana et al., 2020).

2. **Transect-specific influence on elevational taxonomic beta diversity in ants**

   We expected that topographic and microclimatic differences between the two sites, Eaglenest (south-facing, large elevational span, high ridge) and Khupi (north-facing, small span, lower ridge), would modify elevational beta diversity patterns in ant communities, which are known to respond sensitively to environmental conditions at localised scales (Gilgado et al., 2022).

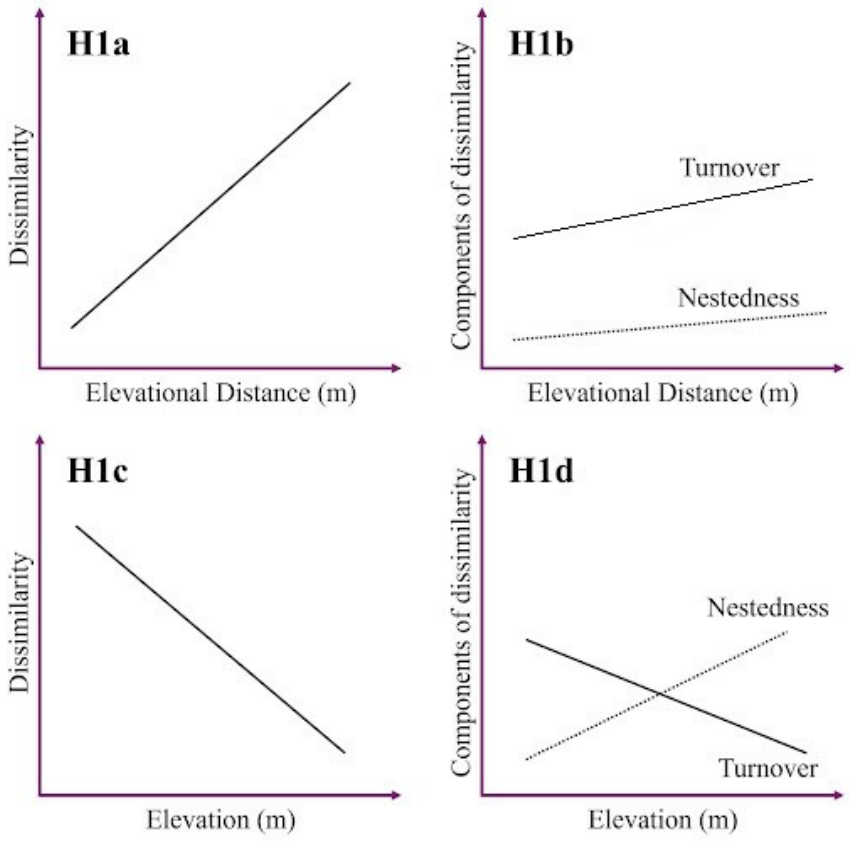


Figure 4.2: Schematic of predictions of elevational profiles of community dissimilarity (taxonomic beta diversity) in ants.

Topographic factors expected to determine community composition include slope aspect (Maheshwori et al., 2025), terrain inclination and ruggedness (Bergamaschi, 2024; Cavarzere et al., 2021) and mountain height and orientation (Diamond & Bishop, 2022).

These features can create microclimatic gradients in soil nutrient profiles (Jiang et al., 2022), water availability (Waldo et al., 2024) and plant productivity (Maheshwori et al. 2019). Furthermore, mountain heights impact range limits of taxa by influencing the available area for optimal fitness (Elsen et al., 2020). The combined effect of these factors can result in the same taxa occupying different elevational ranges on different slopes (Linck, 2025), even those spanning identical elevational extents. However, in this study, we are limited in our ability to separate the contributions of these various topographic and microclimatic factors in influencing beta diversity patterns between the two mountain slopes.

Table 4.1: Number of sampling nodes (sets of three quadrats) for transects examined along with the lowest and highest elevation of sampled quadrats within each transect. Note that KH is a transect obtained by pooling KH1 and KH2 placed 0.2–1.8 km apart.

Transect	Sampling Nodes	Lowest Elevation (m)	Highest Elevation (m)
KH1	97	1035	2079
KH2	120	1043	2042
EN	188	909	1847
KH	217	1035	2079

3. **Horizontal (within-elevation) taxonomic beta diversity (TβD):**

The two transects in Khupi (KH1 and KH2) are separated by 200–1800 m, while Khupi (KH=KH1+KH2) and Eaglenest transects are about 100 km apart (both distances are measured along the elevational contour lines). We investigated if the beta diversity between KH1 and KH2, on the one hand, and between Khupi (KH) and Eaglenest (EN), reflected the contour distance between them. If composition is largely determined by microhabitat heterogeneity, we expect comparable beta diversity between both pairs of elevational transects. Next, we examined if this compositional difference between the pairs of transects changed with elevation. We expected sites at higher elevations to have greater dissimilarity compared to sites at lower elevations (following predictions from Malumbres-Olarte et al. 2025). The sampled elevational span of transects in Eaglenest and Khupi along with the number of sampling nodes are mentioned in **Table 4.1.** Note that each sampling node consists of three quadrats **(refer to Figure 2.4)**.

4. **Cross-taxa comparison of patterns of elevational beta (taxonomic) diversity**

We investigated beta diversity patterns of three taxa (birds, hawkmoths and ants) with widely varying life histories along the same mountain slope in Eaglenest. They differ in thermoregulatory strategies, dispersal abilities, foraging strata and associated microhabitat conditions and biotic interactions. Taxa with higher dispersal abilities, such as birds and hawkmoths, are expected to exhibit a shallower decline in beta diversity across elevational distance. Endotherms such as birds are expected to respond less sensitively to thermal gradients along elevation compared to ectotherms such as ants and hawkmoths. The vertical strata along which taxa forage, and their trophic interactions, can dictate their distribution

along elevation. Ground-dwelling arthropods such as ants are likely to respond more directly to soil conditions (Gilgado et al., 2022) compared to foliar arthropods or understory and canopy-dwelling birds.

4.2 Materials and Methods

4.2.1 Estimation of beta diversity

We employed genus-level abundance data for all analyses involving ants. The comparison between birds and hawkmoths used both genus- and species-level data.

We square-root transformed the community abundance data to minimise the influence of disproportionately abundant taxa while still retaining information on differences in relative abundances between elevational sites (Anderson & Santana-Garcon, 2015). They were used to calculate beta diversity along elevational gradients using the abundance-based Bray-Curtis dissimilarity in R package '*BAT' v.2.11.0* (Cardoso et al., 2015). The total dissimilarity obtained for each pairwise comparison was partitioned into turnover (also called balanced variation) and nestedness (alternatively, abundance gradient) components. The Bray–Curtis (d_{BC}) dissimilarity between any pair of communities, *j* and *k,* is given by:

$$d_{BC} = 1 - \frac{2\sum_{i=1}^{s} min(T_{ij}, T_{ik})}{\sum_{i=1}^{s} (T_{ij} + T_{ik})}$$

Where T_{ij} and T_{ik} are the square-roots of the abundances, N_{ij} and N_{ik}, of ith taxon in the communities j and k, respectively. For ants, we summed over all genera for each pairwise combination of sites analysed. In the case of hawkmoths and birds, we calculated separate values by treating species and genus as the taxonomic unit. $d_{BC\text{-}turn}$ and $d_{BC\text{-}nest}$ are the additive components i.e. turnover and nestedness components of total Bray-Curtis dissimilarity (d_{BC}).

We estimated total Bray-Curtis dissimilarity and its components as a function of elevation by pairing communities in two different ways.

i. Step-wise dissimilarity: We examined the variation of dissimilarity between adjacent elevational communities as a function of elevation. The adjacent communities were 200 m apart in elevation in hawkmoths and birds, and ~100 m in ants.

ii. As a function of elevational distance: We calculated beta diversity between all possible pairs of elevational communities to determine its dependence on elevational separation.

We determined the elevational profile of turnover and nestedness in both cases. We estimated the slope of elevational profiles (change of beta per kilometre) using linear regression. Transect was used as an interaction term to separate the effects of elevation and transect on taxonomic beta diversity profiles of ants in Eaglenest and Khupi (KH=KH1+KH2).

4.2.2 Horizontal (within-elevation) beta diversity

We also quantified beta diversity between communities at the same elevation in (i) Khupi (KH1 v/s KH2) and (ii) between Eaglenest and Khupi (KH=KH1+KH2).

To do this, we first defined a series of elevational communities along each transect (KH1, KH2, EN, KH) by successively treating each sampling node as a reference elevation and including all higher sampled nodes within 100 m of that elevation. **Figure 4.3** shows the comparative plots of abundance and mean elevations of these overlapping communities (KH1 v/s KH2 and EN v/s KH). We then calculated beta diversity between pairs of communities (on the different transects) that satisfied two conditions which were (i) |mean elevation| < 5 m and (ii) 0.67 < abundance ratios < 1.5. We note that these communities, formed by a forward-sliding elevational window, are not independent of each other. However, communities which differ from each other by ~100 m are expected to be non-overlapping and hence independent.

4.2.3 Effect of Incomplete Sampling on Beta Diversity

We compensated for an observed correlation between beta diversity and abundance disparity between paired communities by analysing 100 rarefied subsamples of the two communities using the vegan::rrarefy function in R.

The correlation between beta diversity and abundance may suggest incomplete sampling of the community, which then yields incorrect estimates of beta diversity. We quantified this effect by comparing taxonomic beta diversity between communities within the same elevational band along the (single) Eaglenest transect. We did this by separating alternate sampling nodes within 100 m elevation bands into two separate communities as shown in **Figure 4.4** (also see **Table 4.2**).

This should yield two identical communities considering that they occupy the same 100 m elevational band, i.e. Bray-Curtis dissimilarity = 0. Alternatively, the variability in dissimilarity values for this configuration provides a baseline level of heterogeneity, below which dissimilarity values from the remaining analyses are not statistically significant. Note that we excluded one elevational band (~1100–1200 m) in our analyses due to low abundance (< 40 per community). Also, we could not replicate this exercise within the two Khupi transects due to the low abundance observed in each transect individually.

Table 4.2: Mean and standard deviation of total Bray-Curtis dissimilarity (d_{BC}) within nine 100 m elevational bands in Eaglenest. Within each band, alternate sampling nodes were assigned to Community 1 (all odd nodes) and Community 2 (all even nodes). The abundance of communities in each 100 m band formed from odd (Community 1) and even (Community 2) sampling nodes is mentioned in the table along with the total abundance.

Elevational Band (m)	d_{BC}	Total Abundance	Abundance of Community 1	Abundance of Community 2
909–1010	0.33 ± 0.01	310	148	162
1013–1103	0.34 ± 0.03	161	87	74
1116–1216	0.61 ± 0.04	63	30	33
1224–1322	0.23 ± 0.03	138	64	74
1342–1441	0.28 ± 0.04	91	49	42
1457–1559	0.39 ± 0.02	239	103	136
1562–1663	0.25 ± 0.02	303	157	146
1668–1763	0.31 ± 0.02	179	95	84
1773–1847	0.35 ± 0.03	93	45	48

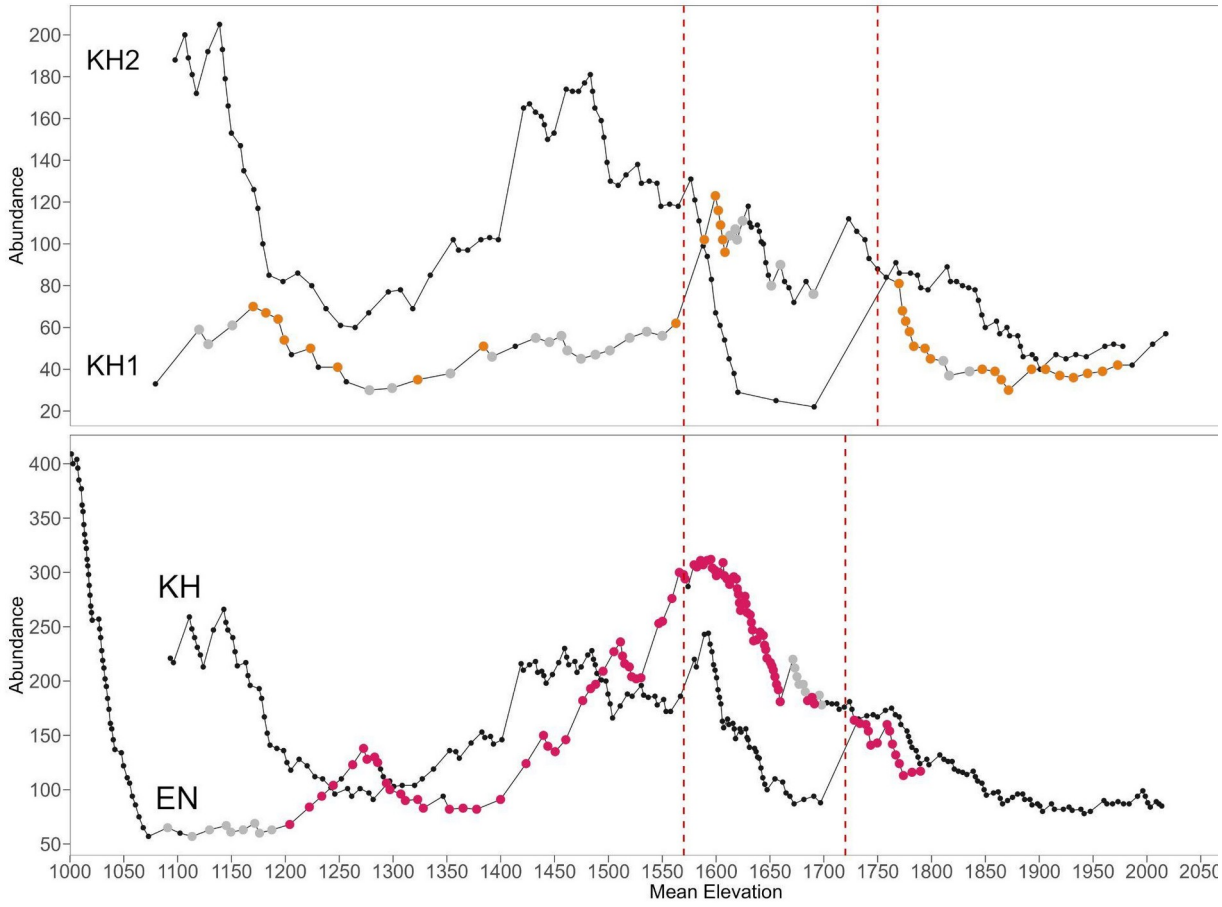


Figure 4.3: Abundance profiles of 100 m sliding elevational communities along each transect. Each point represents a sliding elevational window for a given transect. The top panel compares abundance profiles between KH1 and KH2, while the bottom panel compares profiles between EN and KH (KH1+KH2). Paired communities that fell within ± 5 m of mean elevation are highlighted in grey solid circles for one of the two paired transects i.e. KH1 is highlighted for KH1 v/s KH2 in the top row and EN for EN v/s KH in the bottom row. Orange (KH1 v/s KH2) and reddish-pink (EN v/s KH) solid points depict between-transect pairs of communities that are (i) within ± 5 m of mean elevation and (ii) exhibit ≤ 50% difference in abundance. The red dashed lines indicate where the road in Khupi passes and the elevational range ± 50 m on either side of it. Note that it is broader in KH1-KH2 comparison due to a wider sampling gap in KH1 compared to KH2.

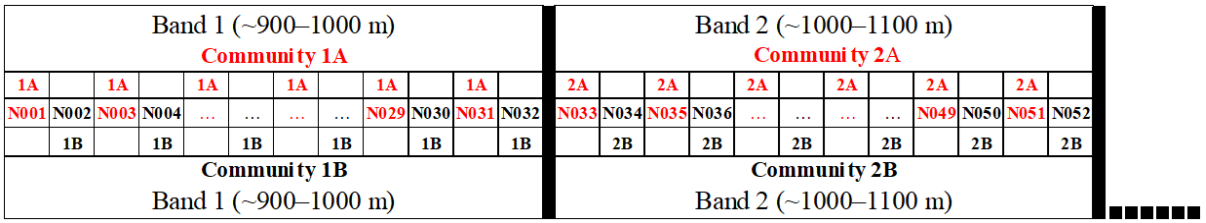


Figure 4.4: Schematic depicting the community configuration for determining threshold for significant detection of beta diversity. Alternate sampling nodes within ~100 m elevation bands along the same transect were split into two separate communities for estimating dissimilarity. We repeated this exercise for 8 elevational bands in Eaglenest, of which two are shown in this figure. The threshold of beta diversity was estimated for all 8 bands.

4.2.4 Environmental and Geographic distances

Studies have generally employed multiple abiotic variables as measures of environmental distances (Fattorini, 2024; Marathe et al., 2021; Peters et al., 2016; Silvestre et al., 2021; Svenning et al., 2010) to examine the predictive strength of each abiotic variable in observed elevational patterns. We employed elevational distance as a single integrated proxy for environmental distance, especially given the short geographic extents of our transects (3–6 km) coupled with the coarse spatial resolution (~ 0.9 km) of abiotic layers available from WorldClim. Moreover, there is a strong correlation between climatic variables (temperature, precipitation) with elevation in our study site (Mungee & Athreya, 2021). All geographic distances (straight-line or contour distances) were measured using R packages for geodata analyses and raster processing which include '*sf*' *v.1.0.24*, '*terra*' *v.1.8.93* (Hijmans et al., 2023) and '*elevatr*' *v.0.99.1* (Hollister, 2017). Using these tools, we constructed a contour map (20 m resolution) showing KH1 and KH2 at Khupi **(Figure 4.5)**.

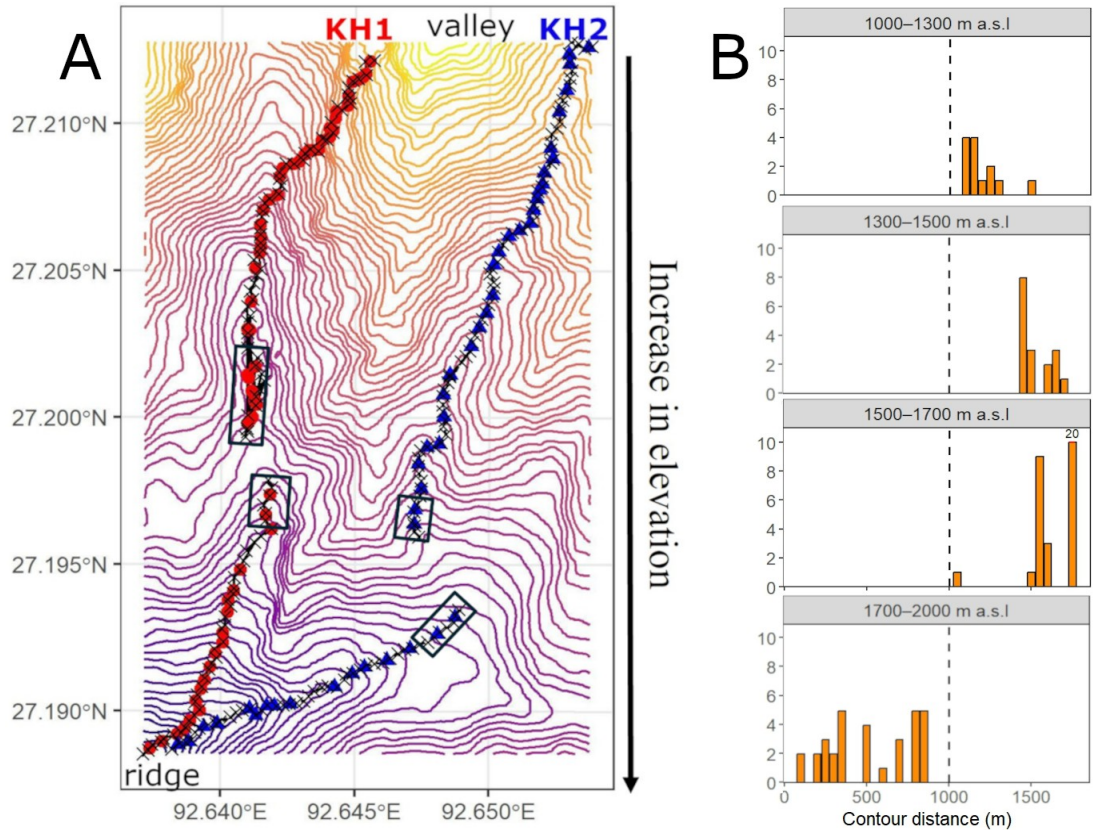


Figure 4.5: Contour map (A) and frequency distribution of contour distances (B) between the two proximal transects (KH1-KH2) in Khupi. In Panel A, note that the ridge is at the bottom left corner of the map while the valley is at the top of the map since Khupi is a north-facing slope. The two transects (KH1: red; KH2: blue) cut across contour lines (20 m resolution), with darker lines representing higher elevations closer to the ridge (bottom left corner) and paler lines representing lower elevations closer to the valley. Crosses along each transect indicate sampling nodes while red and blue solid dots indicate the nearest contour line for each sampling node (or each cross) along KH1 and KH2, respectively. The purpose of the four bounded boxes with black borders is to highlight the intervening elevations (100 m) on either side of the National Highway cutting across the length of both transects at Khupi. **Panel B** plots the histogram of contour distances separating sampling locations in KH1 and KH2 falling within 1000–1300 m, 1300–1500 m, 1500–1700 m and 1700–2000 m elevational bands. Note that the 1700–2000 m range falls above the highway.

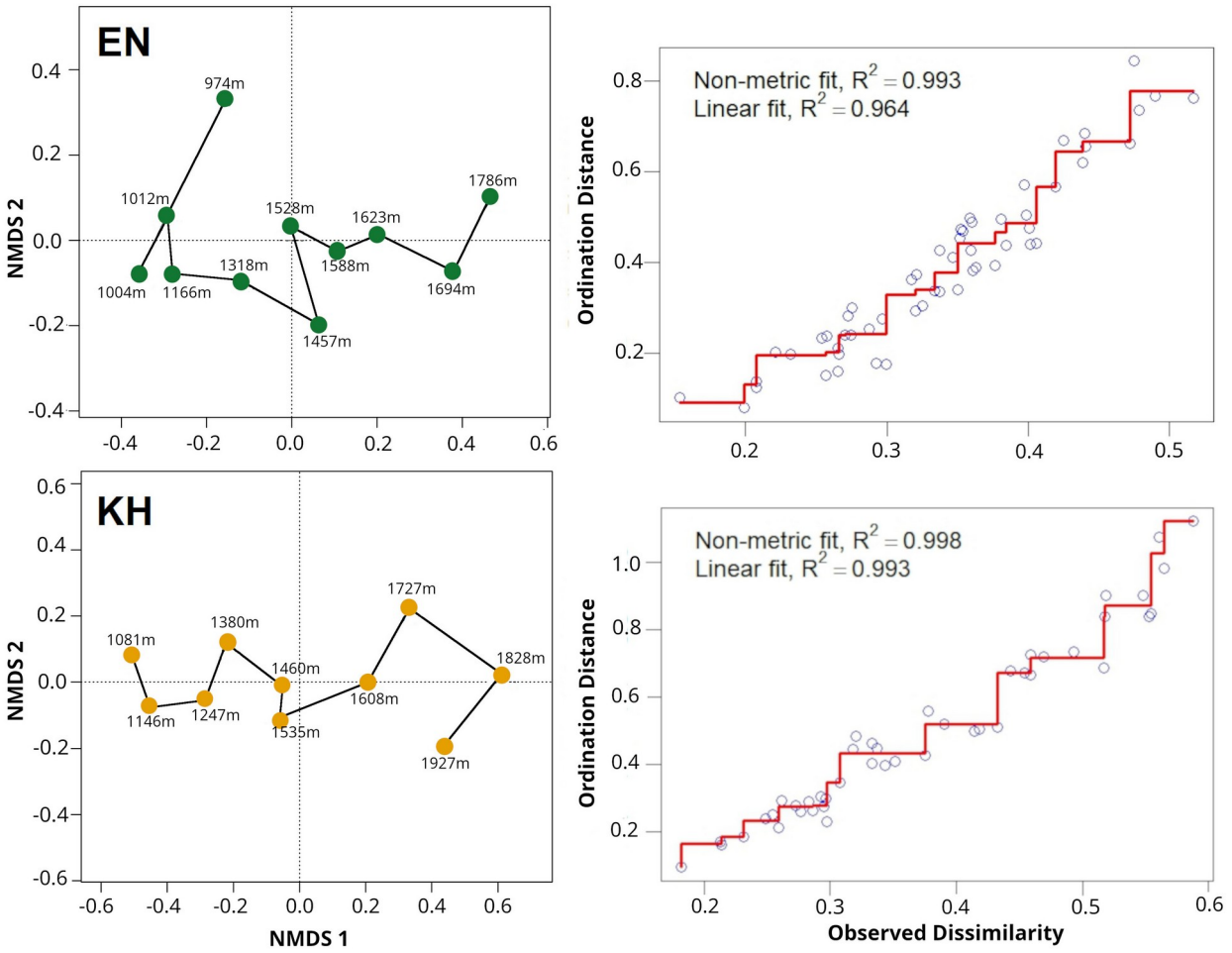


Figure 4.6: NMDS plots of ant elevational communities in Eaglenest and Khupi based on Bray-Curtis index of dissimilarity, and their associated stress plots. The line in the NMDS plot connects the communities in elevational sequence

4.3 Results

We examined compositional relatedness of elevational communities of ants within Eaglenest and Khupi transects using Non-metric Multidimensional Scaling i.e., NMDS **(Figure 4.6).** We observed a progression of dissimilarity with increasing elevational separation. However, there did not seem to be any clustering of communities in either Eaglenest or Khupi.

4.3.1 Elevational profiles of taxonomic beta diversity in ant communities

i. *Step-wise dissimilarity: Between successive neighbouring communities*

Total Bray-Curtis dissimilarity along with its components showed variable trends within Eaglenest and Khupi **(Figure 4.7 & Table 4.3)**. In Eaglenest (EN), total dissimilarity moderately declined

with elevation (slope = −0.11 ± 0.11 per km, p = 0.38, R^2 = 0.12), but increased substantially with elevation in Khupi (slope = 0.21 ± 0.10 per km, p = 0.06, R^2 = 0.40). Despite a weak elevational trend in total dissimilarity (d_{BC}) at Eaglenest, the turnover component declined substantially with elevation (slope = −0.17 ± 0.06 per km, p = 0.02, R^2 = 0.50). As expected, since nestedness and turnover add up to the total, nestedness showed a weak positive slope to (slope = 0.06 ± 0.07 per km, R^2 = 0.08). In Khupi, elevational patterns of turnover and nestedness increased with elevation even though neither were strong enough to be significant at the 95% level.

ii. *Dissimilarity as a function of elevational distance*

We observed a substantial increase in total dissimilarity with increasing elevational separation between communities in both Eaglenest and Khupi **(Figure 4.8 & Table 4.4).** Khupi experienced a much steeper rate of increase in total dissimilarity (slope = 0.51 ± 0.07 per km; R^2 = 0.44) compared to Eaglenest (slope = 0.27 ± 0.04 per km, R^2 = 0.57). In both Eaglenest and Khupi, turnover

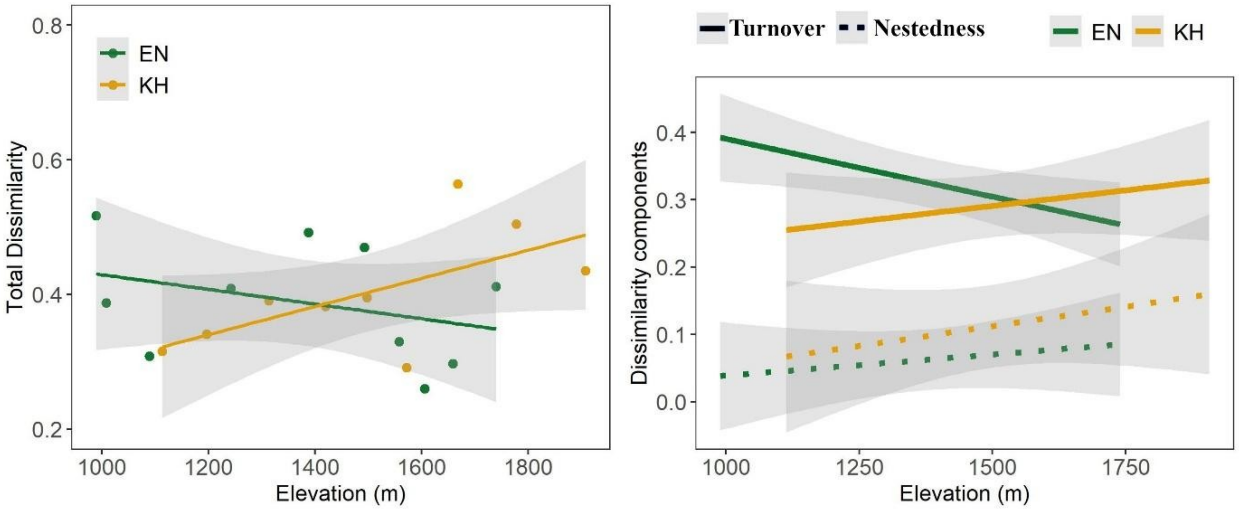


Figure 4.7: Total Bray-Curtis dissimilarity (d_{BC}) between adjacent elevational ant communities (left plot) along with turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) components (right plot) in Eaglenest (EN) and Khupi (KH). Green and orange solid points represent pairwise measures between adjacent elevations for Eaglenest and Khupi respectively. Solid lines on the left represent linear fits with 95% confidence intervals for total Bray-Curtis dissimilarity. On the right, solid lines represent turnover, while dashed lines represent the nestedness. Note that Turnover + Nestedness = Total Dissimilarity (EN = 11 communities, Kh = 10 communities).

Table 4.3: Statistics summarising the relationship of stepwise total Bray-Curtis (d_{BC}) dissimilarity along with its components (turnover:$d_{BC\text{-}turn}$; nestedness: $d_{BC\text{-}nest}$) with elevation i.e. between adjacent/neighbouring communities spaced 100 m apart in ants of Eaglenest (EN) and Khupi (KH). Slope ± SE represents change in Bray-Curtis dissimilarity per km of elevation. Along with estimated slope, the table lists associated p-value and R^2 values. Asterisks indicate levels of statistical significance ($p < 0.1^{*}$, $p < 0.05^{**}$).

Site	Metric	Slope ± SE per km	p-value	R^2
EN	d_{BC}	-0.11± 0.11	0.38	0.12
	$d_{BC\text{-}turn}$	-0.17 ± 0.06**	0.02	0.50
	$d_{BC\text{-}nest}$	0.06 ± 0.07	0.42	0.08
KH	d_{BC}	0.21 ± 0.10*	0.06	0.40
	$d_{BC\text{-}turn}$	0.09 ± 0.08	0.27	0.16
	$d_{BC\text{-}nest}$	0.12 ± 0.10	0.30	0.15

Table 4.4: Summary of relationship between total beta diversity (d_{BC}) and its components (turnover:$d_{BC\text{-}turn}$; nestedness: $d_{BC\text{-}nest}$) in ant communities as a function of elevational distance in Eaglenest (EN) and Khupi (KH). Slope ± SE represents change in Bray-Curtis dissimilarity per km of elevational distance. Along with estimated slope, the table lists associated p-value and R^2 values. Asterisks indicate levels of statistical significance ($p < 0.1^{*}$, $p < 0.05^{**}$, $p < 0.01^{***}$, $p < 0.001^{****}$).

Site	Metric	Slope ± SE per km	p-value	R^2
EN	d_{BC}	0.27 ± 0.04****	< 0.001	0.44
	$d_{BC\text{-}turn}$	0.29 ± 0.03****	< 0.001	0.62
	$d_{BC\text{-}nest}$	-0.02 ± 0.03	0.48	0.01
KH	d_{BC}	0.51 ± 0.07****	< 0.001	0.57
	$d_{BC\text{-}turn}$	0.28 ± 0.04****	< 0.001	0.52
	$d_{BC\text{-}nest}$	0.23 ± 0.07***	< 0.01	0.20

Table 4.5: **Interaction models assessing whether elevational profiles of stepwise beta diversity (TβD) and change in beta diversity with elevation distance differ significantly between transects.** The table lists the p-values for the Elevation × Transect interaction term and the model fit (R^2) for total beta diversity (d_{BC}) and its components (turnover:$d_{BC\text{-}turn}$; nestedness: $d_{BC\text{-}nest}$).

Type	Metric	Interaction β	Interaction p
Stepwise TβD	d_{BC}	-0.32 ± 0.15**	< 0.05
	$d_{BC\text{-}turn}$	0.26 ± 0.10	< 0.05
	$d_{BC\text{-}nest}$	0.05 ± 0.13	0.68
TβD with elevational distance	d_{BC}	0.24 ± 0.08***	< 0.01
	$d_{BC\text{-}turn}$	-0.02 ± 0.05	0.75
	$d_{BC\text{-}nest}$	0.26 ± 0.07****	< 0.001

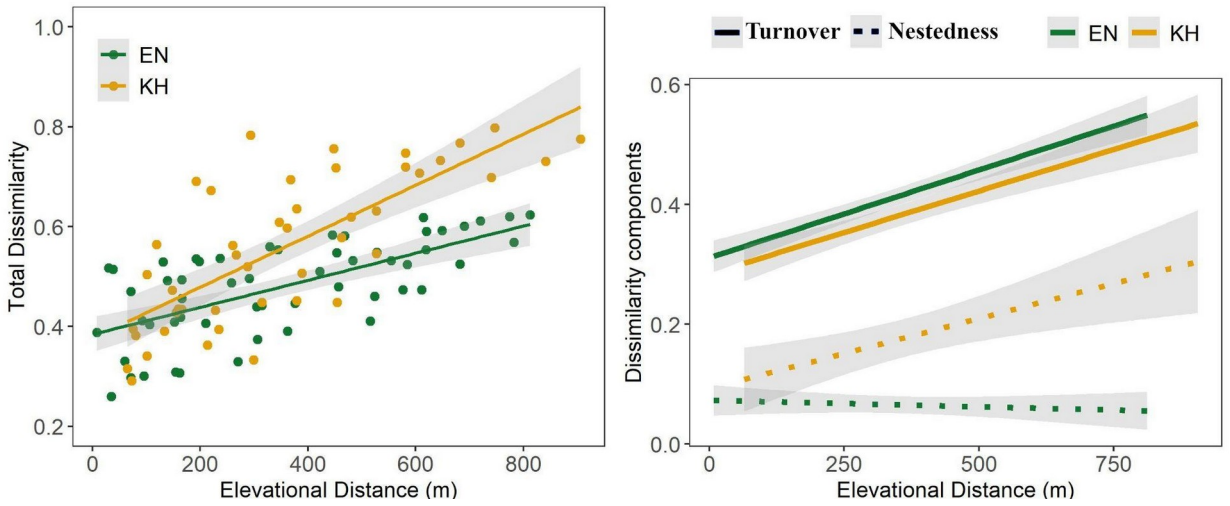


Figure 4.8: Total Bray-Curtis dissimilarity (d_{BC}) as a function of elevational distance in ant communities (left plot) along with turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) components (right plot) in Eaglenest (EN) and Khupi (KH). Green and orange solid points represent dissimilarity measures between all pairs of communities in Eaglenest and Khupi respectively. Solid lines on the left represent linear fits with 95% confidence intervals for total Bray-Curtis dissimilarity. On the right, solid lines represent turnover, while dashed lines represent the nestedness. Note that Turnover + Nestedness = Total Dissimilarity (EN = 11 communities, KH = 10 communities).

increased significantly with elevational distance (EN: slope = 0.29 ± 0.03 per km, R^2 = 0.62; KH: slope = 0.28 ± 0.04 per km, R^2 = 0.52). Slope of change in nestedness was not significant with elevational distance in Eaglenest (slope = −0.02 ± 0.03 per km; R^2 = 0.01; p = 0.48). However, nestedness increased significantly with elevational distance in Khupi (slope = 0.23 ± 0.07 per km; R^2 = 0.20; $p < 0.01$).

4.3.2 Transect-specific influence on elevational ant beta diversity

We detected a significant interaction component between elevation and transect (Eaglenest and Khupi) which suggests that the slope made a difference to the beta diversity of the ant community. Step-wise turnover accounted for differences in the step-wise dissimilarity profiles between Eaglenest and Khupi **(Table 4.5).** On the contrary, nestedness accounted for transect-specific differences in elevational distance patterns ($p < 0.001$, R^2 = 0.40), while turnover did not play a significant role (p = 0.75, R^2 = 0.59) **(Table 4.6)**.

4.3.3 Horizontal (within-elevation) beta diversity

The beta diversity for communities sharing the same elevation (by choosing alternate sampling nodes) was in the range 0.31 ± 0.11 (mean ± 2 SD). Therefore, beta = 0.42 sets the statistically significant detection threshold for the rest of the analysis (**Figure 4.9).**

At elevations below 1700 m, within-elevation dissimilarity values between distant transects (EN vs KH; ~100 km apart) was similar to the above threshold, but was much higher at elevations above 1700 m. On the other hand, KH1 v/s KH2, which are separated by only 1-2 km showed substantially higher dissimilarity at elevation below 1700 m. However, at higher elevations (>1700 m), where the communities were separated by 100–900 m along the contour **(Figure 4.5B),** dissimilarity values were within the error threshold.

Dissimilarity in composition increased as a function of contour distance between KH1 and KH2 communities at comparable elevations **(Figure 4.10)**. However, note that elevation is also

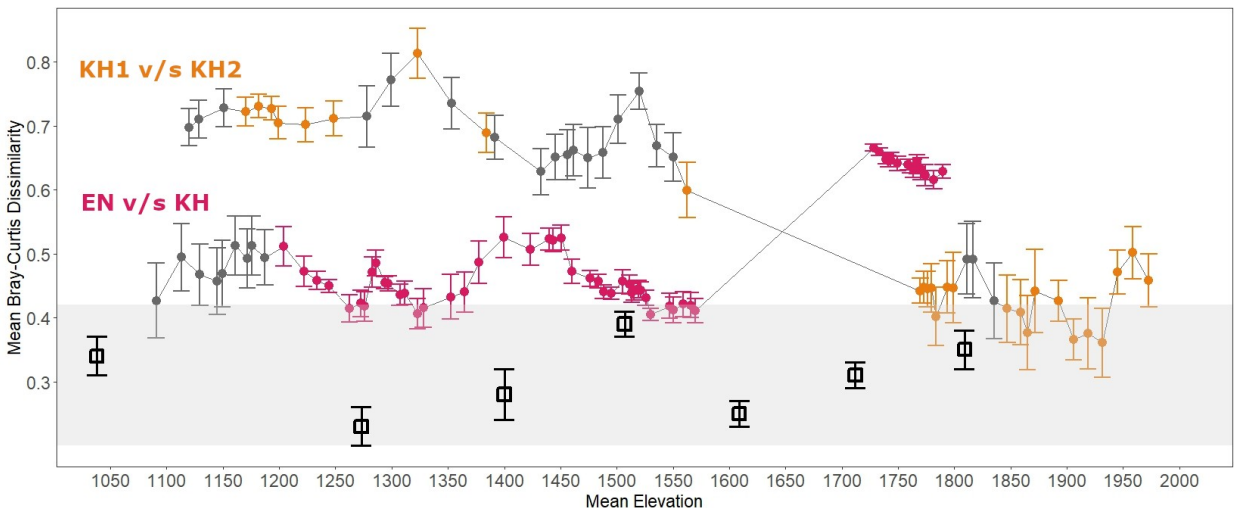


Figure 4.9: Bray–Curtis dissimilarity (mean ± 1 SD) between transects at comparable elevations, calculated after filtering pairs of sliding-window communities whose mean elevations differed by no more than ±5 m. Among these, solid green and orange points indicate community pairs with ≤50% difference in abundance for KH1 v/s KH2 and EN v/s KH comparisons, respectively. Hollow square points represent baseline dissimilarity values (mean ± 1 SD) within 100 m elevational bands in Eaglenest. The grey band denotes the range within ±2 SD of the mean dissimilarity across all seven 100 m elevational bands. The ~1100–1200 m elevational band in Eaglenest was excluded as an outlier.

correlated with contour distances. Communities > 1700 m are separated by less than 1 km, while communities < 1700 m are separated by 1-2 km **(Figure 4.5B).**

4.3.4 Cross-taxa comparison of elevational beta diversity profiles in Eaglenest (elevational span: 1000–2000 m)

i. *Step-wise dissimilarity*

All three taxa (ants, hawkmoths and birds) showed a weak declining elevational trend in elevational dissimilarity at the genus level (**Table 4.6** & **Figure 4.11**). However, hawkmoth genera showed a moderate decline in the turnover component (slope = −0.05 ± 0.02, p = 0.08, R^2 = 0.70), mirroring the patterns observed in ants. However, bird genera exhibit a substantial decline in the nestedness component of dissimilarity (slope = −0.08 ± 0.02, p = 0.04, R^2 = 0.81) rather than turnover.

ii. *Dissimilarity as a function of elevational distance*

All three taxa exhibit a substantial increase in total dissimilarity with elevational distance **(Figure 4.12 & Table 4.8)**, birds: slope = 0.38 ± 0.09 per km, R^2 = 0.60; ants: slope = 0.27 ± 0.04 per km,

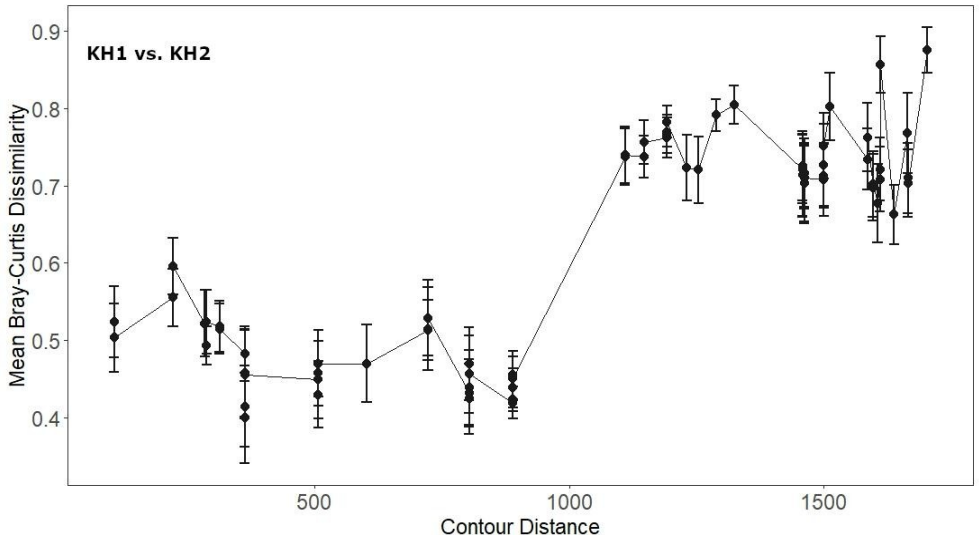


Figure 4.10: Bray–Curtis dissimilarity (mean ± 1 SD) of sliding-window communities (Δmean elevation within ±5 m) comparing nearby transects, KH1 and KH2, as a function of contour distance. Communities are separated by 100–1800 m along contour distances. Sliding communities with mean elevations ±50 m a.s.l from the elevation at which the highway occurs were excluded.

R^2 = 0.44; and, hawkmoths: slope = 0.32 ± 0.10, R^2 = 0.43. The dissimilarity was primarily driven by turnover for all 3 taxa, while nestedness did not change significantly with elevational distance.

Table 4.6: Stepwise dissimilarity profiles (~100 m step size in ants; 200 m step size in hawkmoth and bird communities) across elevation in Eaglenest. Ants, hawkmoths and birds genera surveyed between 900-1900 m. The table lists slope ± SE per kilometre of elevation, p-value and R^2 values for total dissimilarity (d_{BC}), turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$).

Taxon	Metric	Slope ± SE per km	p-value	R^2
Ants	d_{BC}	-0.11 ± 0.11	0.33	0.12
	$d_{BC\text{-}turn}$	-0.17 ± 0.06**	0.02	0.50
	$d_{BC\text{-}nest}$	0.06 ± 0.07	0.42	0.08
Hawkmoths	d_{BC}	-0.22 ± 0.10	0.12	0.61
	$d_{BC\text{-}turn}$	-0.05 ± 0.02*	0.08	0.70
	$d_{BC\text{-}nest}$	-0.17 ± 0.11	0.21	0.46
Birds	d_{BC}	-0.19 ± 0.10	0.16	0.53
	$d_{BC\text{-}turn}$	-0.11 ± 0.12	0.43	0.21
	$d_{BC\text{-}nest}$	-0.08 ± 0.02**	0.04	0.81

Table 4.7: Association of beta diversity with elevational distance in Eaglenest. Ants, hawkmoths and birds genera surveyed between 900-1900 m. The table includes the slope ± SE per kilometre of elevational distance, p-values and R^2 values for total beta diversity (d_{BC}) turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$).

Taxon	Metric	Slope ± SE per km	p-value	R^2
Ants	d_{BC}	0.27 ± 0.04****	< 0.001	0.44
	$d_{BC\text{-}turn}$	0.29 ± 0.03****	< 0.001	0.62
	$d_{BC\text{-}nest}$	-0.02 ± 0.03	0.48	0.01
Hawkmoths	d_{BC}	0.32 ± 0.1***	< 0.01	0.43
	$d_{BC\text{-}turn}$	0.30 ± 0.07***	< 0.01	0.56
	$d_{BC\text{-}nest}$	0.02 ± 0.08	0.77	0.01
Birds	d_{BC}	0.38 ± 0.09****	< 0.001	0.6
	$d_{BC\text{-}turn}$	0.40 ± 0.09****	< 0.001	0.61
	$d_{BC\text{-}nest}$	-0.02 ± 0.02	0.35	0.07

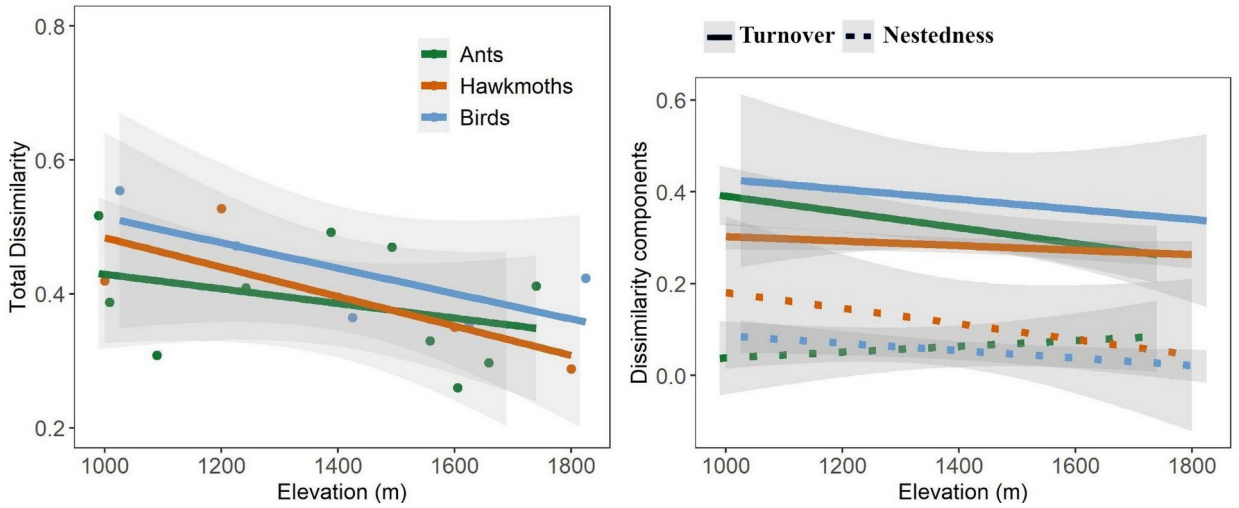


Figure 4.11: Total step-wise dissimilarity (d_{BC}) in ants, hawkmoths and birds (left plot), along with turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) profiles in Eaglenest. Green, brown and blue solid points represent pairwise measures between adjacent ant, hawkmoth and bird genera respectively. Solid lines on the left represent linear fits with 95% confidence intervals for total dissimilarity. On the right, solid lines represent turnover, while dashed lines represent the nestedness. Note that Turnover + Nestedness = Total Dissimilarity.

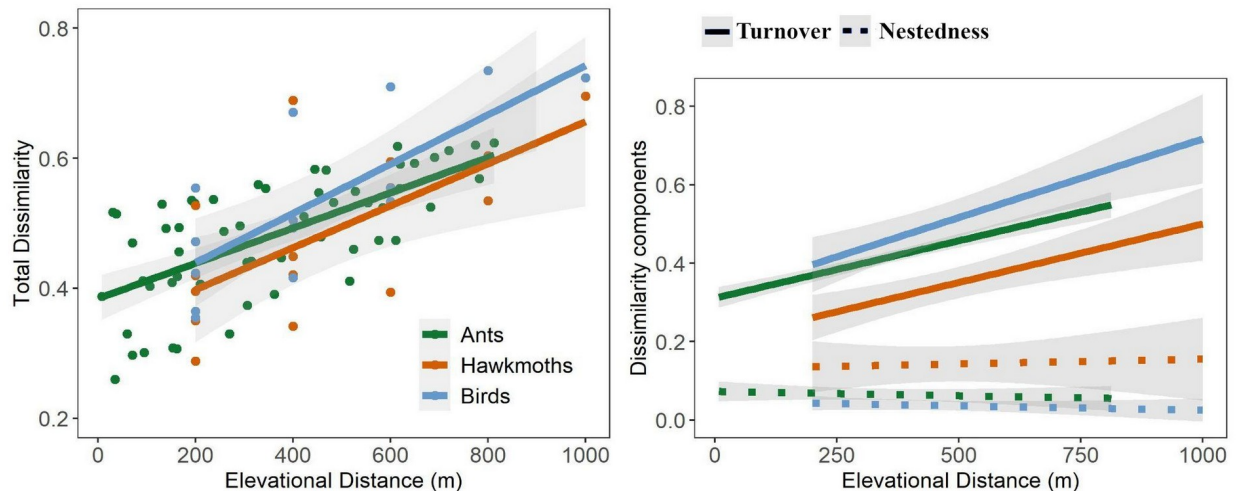


Figure 4.12: Total dissimilarity (d_{BC}) as a function of elevational distance in communities of ants, hawkmoths and birds (left plot), with turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) profiles (right plot) in Eaglenest. Green, brown and blue solid points represent profiles for ant, hawkmoth and bird genera respectively. Solid lines on the left represent linear fits with 95% confidence intervals for total Bray-Curtis dissimilarity. On the right, solid lines represent turnover, while dashed lines represent nestedness. Note that Turnover + Nestedness = Total Dissimilarity.

Table 4.8: Cross-taxa comparisons of stepwise beta diversity (TβD) and beta diversity as a function of elevational distance along with turnover and nestedness profiles in Eaglenest. For each pair of taxa compared, the table provides Z-statistics and significance values of the difference in the slope of total beta diversity (d_{BC}),turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) with elevation and elevational distance. Ants, hawkmoths and birds are compared at the generic level between 900−1900 m elevational extent. For stepwise beta diversity we paired neighbouring communities spaced ~100 m apart in elevation for ant communities and 200 m apart in elevation in hawkmoth and bird communities.

Type	Comparison	Metric	Z-statistic	p-value
Stepwise TβD	Ants v/s Hawkmoths	d_{BC}	0.11	0.76
		$d_{BC\text{-}turn}$	-0.12	0.48
		$d_{BC\text{-}nest}$	0.23	0.13
	Ants v/s Birds	d_{BC}	0.08	0.86
		$d_{BC\text{-}turn}$	-0.06	0.82
		$d_{BC\text{-}nest}$	0.14	0.43
	Hawkmoths v/s Bird	d_{BC}	-0.03	0.98
		$d_{BC\text{-}turn}$	0.06	0.87
		$d_{BC\text{-}nest}$	-0.09	0.76
TβD with elevational distance	Ants v/s Hawkmoths	d_{BC}	-0.05	0.84
		$d_{BC\text{-}turn}$	-0.01	1.00
		$d_{BC\text{-}nest}$	-0.05	0.76
	Ants v/s Birds	d_{BC}	-0.11	0.48
		$d_{BC\text{-}turn}$	-0.11	0.33
		$d_{BC\text{-}nest}$	0.00	1.00
	Hawkmoths v/s Bird	d_{BC}	-0.06	0.88
		$d_{BC\text{-}turn}$	-0.10	0.51
		$d_{BC\text{-}nest}$	0.05	0.83

Table 4.8 show that the slopes of the elevational profiles, both of step-wise dissimilarity and with elevational distance, did not differ significantly among the taxa.

Across taxonomic scale in hawkmoths and birds

i. *Step-wise dissimilarity:*

Hawkmoths do not significantly change in terms of total dissimilarity or nestedness/turnover with elevation at the species and generic levels **(Figure 4.13 & Table 4.9)**. For bird species, we observed a marginal decline in total dissimilarity (slope = −0.20 ± 0.08, p = 0.10, R^2 = 0.64) and turnover (slope = −0.23 ± 0.10, p = 0.10, R^2 = 0.65), but not in nestedness (slope = 0.04 ± 0.09, p = 0.72, R^2

= 0.05). However, nestedness declined significantly for bird genera (slope = −0.08 ± 0.02, p = 0.04, R^2 = 0.81).

Table 4.9: Stepwise beta diversity in hawkmoths and birds, and its dependence on the taxonomic scale at which changes are examined. For this analysis, hawkmoths and birds were surveyed at the species and generic level between 900−1900 m in Eaglenest. The table lists the slope ± SE per kilometre of elevation, p-values and R^2 values for total stepwise dissimilarity (d_{BC}), turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$). Note that adjacent communities are 200 m apart in elevation in both hawkmoth and bird communities.

Taxon	Level	Metric	Slope ± SE per km	p-value	R^2
Hawkmoths	Species	d_{BC}	-0.14 ± 0.15	0.41	0.23
		$d_{BC\text{-}turn}$	-0.07 ± 0.12	0.59	0.11
		$d_{BC\text{-}nest}$	-0.07 ± 0.18	0.74	0.04
	Genus	d_{BC}	-0.22 ± 0.10	0.12	0.61
		$d_{BC\text{-}turn}$	-0.05 ± 0.02*	0.08	0.70
		$d_{BC\text{-}nest}$	-0.17 ± 0.11	0.21	0.46
Birds	Species	d_{BC}	-0.20 ± 0.08*	0.10	0.64
		$d_{BC\text{-}turn}$	-0.23 ± 0.10*	0.10	0.65
		$d_{BC\text{-}nest}$	0.04 ± 0.09	0.72	0.05
	Genus	d_{BC}	-0.19 ± 0.10	0.16	0.53
		$d_{BC\text{-}turn}$	-0.11 ± 0.12	0.43	0.21
		$d_{BC\text{-}nest}$	-0.08 ± 0.02**	0.04	0.81

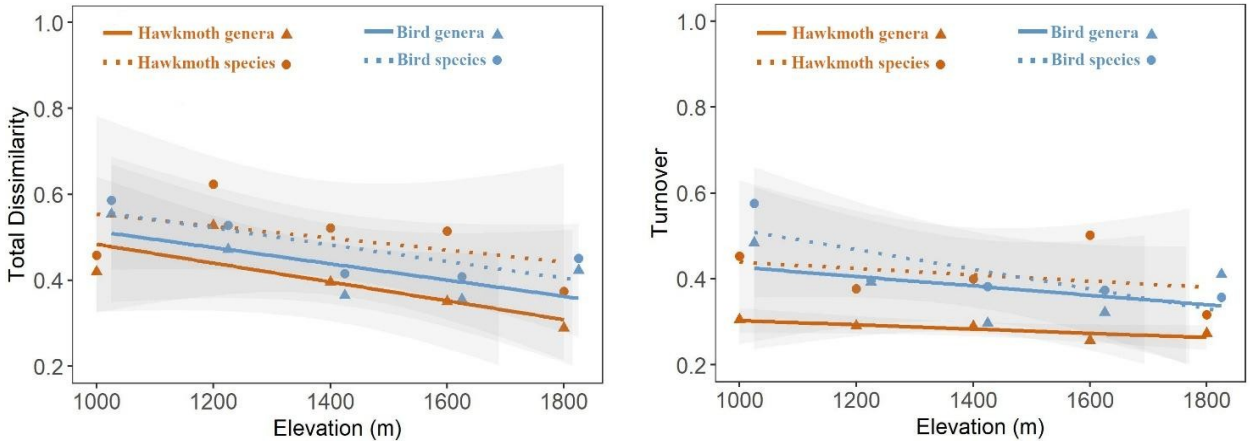


Figure 4.13: Stepwise dissimilarity (left plot: d_{BC}) and turnover profiles (right plot: $d_{BC\text{-}turn}$) with elevation in hawkmoth and bird communities surveyed between 900−1900 m, at species and generic level. Brown and blue solid circles (fitted profiles: dotted lines) represent hawkmoth and bird species, respectively while brown and blue solid triangles (fitted profiles: solid lines) represent hawkmoth and bird generic profiles respectively. Communities were sampled every 200 m of elevation. Note that Turnover + Nestedness = Total Dissimilarity.

ii. *Dissimilarity as a function of elevational distance*

Hawkmoth and bird communities exhibited a strong decline in total dissimilarity with increasing elevational separation at both generic and species level **(Figure 4.14 & Table 4.10).**

Table 4.10: Relationship between total Bray-Curtis dissimilarity (and its components) with elevational distance in hawkmoths and birds species and genera. Taxa were surveyed between 900−1900 m in Eaglenest. The table lists the slope ± SE per kilometre of elevation, p-values and R^2 values for ttotal beta diversity (d_{BC}), turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$).

Taxon	Level	Metric	Slope ± SE per km	p-value	R^2
Hawkmoths	Species	d_{BC}	$0.40 \pm 0.08^{****}$	< 0.001	0.67
		$d_{BC\text{-}turn}$	$0.38 \pm 0.06^{****}$	< 0.001	0.78
		$d_{BC\text{-}nest}$	0.02 ± 0.07	0.78	0.01
	Genus	d_{BC}	$0.32 \pm 0.10^{***}$	< 0.01	0.43
		$d_{BC\text{-}turn}$	$0.30 \pm 0.07^{***}$	< 0.01	0.56
		$d_{BC\text{-}nest}$	0.02 ± 0.08	0.77	0.01
Birds	Species	d_{BC}	$0.51 \pm 0.07^{****}$	< 0.001	0.81
		$d_{BC\text{-}turn}$	$0.50 \pm 0.07^{****}$	< 0.001	0.82
		$d_{BC\text{-}nest}$	0.01 ± 0.05	0.79	0.01
	Genus	d_{BC}	$0.38 \pm 0.09^{****}$	< 0.001	0.60
		$d_{BC\text{-}turn}$	$0.40 \pm 0.09^{****}$	< 0.001	0.61
		$d_{BC\text{-}nest}$	-0.20 ± 0.02	0.35	0.07

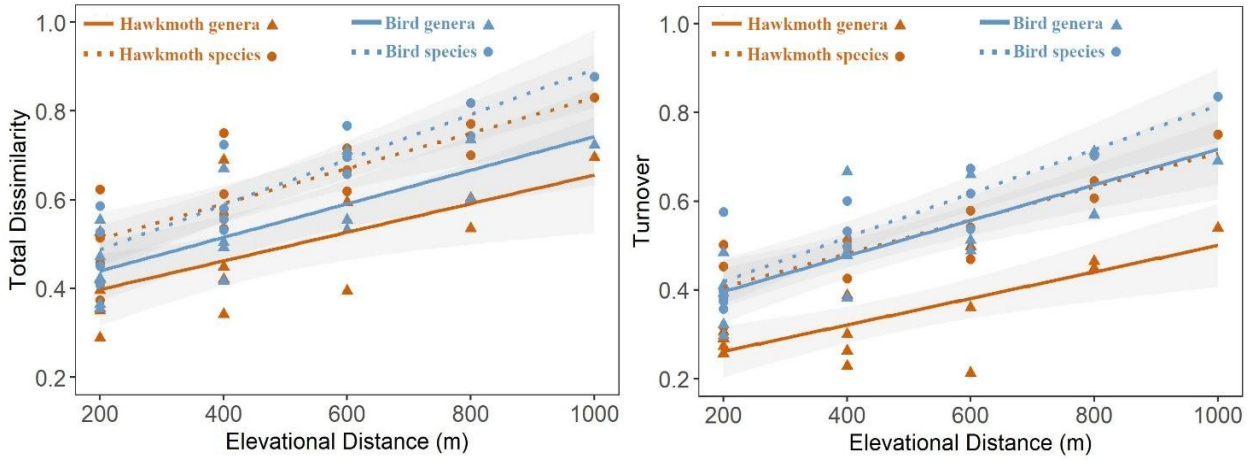


Figure 4.14: Total Bray-Curtis dissimilarity (left plot: d_{BC}) and turnover (right plot: $d_{BC\text{-}turn}$) as a function of elevational distance in hawkmoth and bird communities, at species and generic level. Brown and blue solid circles (fitted profiles: dotted lines) represent hawkmoth and bird species, respectively while brown and blue solid triangles (fitted profiles: solid lines) represent communities of hawkmoth and bird genera, respectively. Note that Turnover + Nestedness = Total Dissimilarity.

Hawkmoth and bird species showed a steeper profile of increase ($slope_{HAWKMOTH}$ = 0.40; $slope_{BIRD}$ = 0.51) compared to their generic counterparts ($slope_{HAWKMOTH}$ = 0.32; $slope_{BIRD}$ = 0.38). Elevational dissimilarity in both species and generic composition was driven by turnover (> 95%) with no significant contribution from nestedness.

Overall, we found no substantial difference in elevational profiles (between neighbouring communities and with elevational distance) for both hawkmoths and birds across taxonomic scales (**Table 4.11)**. However, in birds we observed a shift in the component that contributes to differences between neighbouring communities, from turnover dominating at the species level to nestedness at the generic level (**Table 4.9)**.

Table 4.11: Test of difference in profiles at varying taxonmic scales. Z-statistics and significance values test the difference, across taxonomic scale, in the slope of total beta diversity (d_{BC}), turnover ($d_{BC\text{-}turn}$) and nestedness ($d_{BC\text{-}nest}$) components. All paired comparisons yield non-significant results indicating no differences in elevational patterns of total beta diversity or its components. Communities were surveyed between 900−1900 m in Eaglenest.

Type	Comparison	Metric	Z-statistic	p-value
Stepwise TβD	Hawkmoth species v/s genus	d_{BC}	0.08	0.96
		$d_{BC\text{-}turn}$	-0.02	1.00
		$d_{BC\text{-}nest}$	0.10	0.91
	Bird species v/s genus	d_{BC}	-0.01	1.00
		$d_{BC\text{-}turn}$	-0.12	0.82
		$d_{BC\text{-}nest}$	0.12	0.89
TβD with elevational distance	Hawkmoth species v/s genus	d_{BC}	0.08	0.92
		$d_{BC\text{-}turn}$	0.08	0.87
		$d_{BC\text{-}nest}$	0.00	1.00
	Bird species v/s genus	d_{BC}	0.13	0.70
		$d_{BC\text{-}turn}$	0.10	0.79
		$d_{BC\text{-}nest}$	0.04	0.98

4.4 Discussion

We explored variation in the generic composition of ant communities with elevation on each slope and between the two mountain slopes. Macro-climatic factors linked to elevation may shape elevational beta diversity patterns at regional scales (Liang et al., 2025). On the other hand, local topography and microclimatic heterogeneity may govern fine-scale differences between slopes and even within a single slope (Choi & Jang, 2022). We found striking differences in elevational beta diversity patterns of the two mountain slopes despite sampling similar elevational extents, which suggests the role of topographical and microclimatic factors in determining the structure of ant communities. While we cannot mechanistically link each of these factors to the observed patterns, we argue that several transect-specific variables may modulate the influence of elevation on the assembly of communities along mountain slopes (Wani et al., 2023).

4.4.1 Elevational beta diversity in ant communities

As expected, we observed increasing total dissimilarity with elevational distance in ant communities in both Eaglenest and Khupi. Studies across the Neotropical (Fichaux et al., 2021; Pérez-Toledo et al., 2022; Perillo et al., 2021), Palearctic (Fontana et al., 2020), Nearctic (Smith, 2015), Afrotropical (Bishop et al., 2015) and Indomalayan (Marathe et al., 2021) regions have reported similar trends. The slope of dissimilarity with elevational distance across these studies ranged from 0.2 to 0.5 per km. For instance, in the Maloti-Drakensberg Mountains of South Africa, total dissimilarity increased from approximately 0.4 at 250 m separation to 0.95 at 2100 m separation, yielding an estimated slope of 0.3/km (Bishop et al., 2015). A slightly higher rate of 0.4/km was observed in the European Alps across 1500 m sampled gradient (Fontana et al., 2020). We observed comparable change (0.27 ± 0.04 per km) in total dissimilarity within ~1000 m elevational range in Eaglenest. In the rupestrian grasslands of Brazil experiencing more extreme climate conditions (Perillo et al., 2021), total dissimilarity increased at a higher rate of ~0.5/km; matching the estimated slope in Khupi (0.51 ± 0.07). On the other hand, Fichaux et al. (2019) reported a slope of only 0.08/km, which may be due to the limited elevational range sampled (400–800 m). However, it is important to note that the same elevational spans at different latitudes do not correspond to the same temperature differences.

The dominance of turnover in place of nestedness is widely reported across studies in arthropods (Bishop et al., 2015; Flores et al., 2018; Muluvhahothe et al., 2021; Perillo et al., 2021; Santoandré et al., 2024), though, curiously, Santoandre et al. (2024) reported that nestedness was the dominant driver in the case of ants. In the Alps, for instance, turnover accounts for 90.3% of total dissimilarity in ants (Fontana et al., 2020). Similarly, highland ant communities in Mexico represent entirely different lineage compositions rather than mere subsets of lowland fauna (Perez-Toledo et al. 2022). Entire genera of ants, and not just species, are known to favour particular elevations. For instance, members of *Adelomyrmex* and *Stenamma* are habitat specialists in central American montane forests, never occurring at elevations below the cloud forest (Smith, 2015). Prevalence of habitat or climate specialists in ant genera may favour turnover over nestedness.

Despite the prevalence of turnover, a previous study conducted in Eaglenest found that the nestedness component started to dominate over turnover at elevational distances exceeding 600 m (Marathe et al., 2021). We did not find this to be the case in either mountain slope. However, we note that nestedness increased considerably with elevational distance in Khupi, even though turnover remained the dominant component.

We found a negative relationship, albeit statistically insignificant, between elevation and step-wise beta diversity in Eaglenest. Beta diversity within a community (Section 4.3.3) showed that our data is not sensitive to beta values below ~0.3. The values of step-wise dissimilarity that we measured, between communities separated by only 100 m of elevation, are similar to this threshold, which may explain the lack of an elevational pattern in step-wise beta. On the other hand, Fontana et al., (2020) also reported a flat elevational profile for step-wise beta for multiple arthropod taxa in the Alps, though in their case they argued that the large step size (500 m) may have been responsible. It would seem that step-wise beta has a flat profile for a large range of step sizes. A study examining subtropical, temperate and arid montane systems in China reported no elevational trends in stepwise beta diversity in 31 of 40 gradients (Tang et al., 2012). This suggests that the extension of Rapoport's rule to elevation (i.e. Stevens' mechanism) invoking higher climatic variability (and therefore, lower dissimilarity) at high latitudes may not always hold at higher elevations (Tang et al., 2012). Furthermore, the limited elevational range of our study does not allow us to reach a more general conclusion at the lowest and highest elevations.

Previous work in Eaglenest observed Rapoport's pattern in ant communities, i.e. lower dissimilarity at higher elevations, within 600-2400 m of elevational span (Marathe et al., 2021). The author suggested that alternate models may explain this pattern rather than mechanisms invoked by Climatic Variability Hypothesis. Ant communities (at the species level) were increasingly nested towards higher elevations. We did not detect a similar increase in nestedness with elevation at Eaglenest, although this may be because we analysed these patterns across a shorter elevational span (900−1850 m). While we observed a significant decrease in step-wise turnover with elevation (implying an increase in nestedness), the slopes of both total dissimilarity and nestedness were not statistically significant. However, since total = turnover+nestedness, it is either (i) flat-total + increasing-nestedness or (ii) negative-total + flat-nestedness.

We observed a significant increase in step-wise dissimilarity with elevation in Khupi (which would arise from an anti-Rapoport pattern according to the previous argument), within a similar elevational extent **(Figure 4.5)**. While assumed to be relatively uncommon, anti-Rapoport's pattern has been observed in some studies (Michel et al., 2023; Steinwandter & Seeber, 2023; Toko et al., 2023). The available area at 2000 m is much smaller at Khupi (close to the ridge) than at Eaglenest. Any two highland communities may be more dissimilar than counterpart lowland pairs merely due to chance sampling, especially as the area shrinks, rather than due to some ecological process.

4.4.2 Transect-specific beta diversity patterns in ant communities

Taxonomic beta diversity patterns in ant communities have been linked to a host of factors including temperature distance (Perez-Toledo et al., 2021; Bishop et al., 2015), changes in soil properties (Fichaux et al., 2019) and light conditions (Wallis et al., 2017). These factors may widely vary at local scales resulting in the beta diversity patterns differing between one mountain slope and the next. In our data, the slope of dissimilarity versus elevational distance was steeper in Khupi compared to Eaglenest **(Figure 4.8 & Table 4.4).**

The contributions of turnover and nestedness to transect-specific differences differed between step-wise dissimilarity **(Figure 4.7)** and dissimilarity across elevational distance **(Figure 4.8).** The difference between the profiles of step-wise dissimilarity was predominantly determined by the change in turnover. Turnover had a negative slope with elevation in Eaglenest but a positive slope

in Khupi, while nestedness had a similar trend in both places. On the other hand, the difference between the profiles of dissimilarity with elevational distance was driven by nestedness, flat in Eaglenest and positive in Khupi. The change in turnover with elevational distance was similar in both places.

Muluvhahothe et al. (2021) have reported that the difference in dissimilarity profiles across elevational distance along two aspects of a mountain was driven by turnover; nestedness was essentially the same in both cases. In our study, nestedness significantly contributed to compositional dissimilarity in Khupi, but not Eaglenest. The transects at Khupi terminate very close to the ridge at 2100 m. The reduction in available area near the ridge may lead to (random) attrition of communities resulting in dominance of nestedness; the ridge assemblies are likely to be species-poor subsets of the richer lowland communities (Almeida-Neto et al., 2008; Ulrich et al., 2025). Similar patterns have been reported in island systems varying in size and degree of isolation i.e. distance from the mainland (Chen et al., 2020; S. Li et al., 2025) Alternatively, Khupi shows a small but consistently higher temperature seasonality relative to Eaglenest **(Figure 4.15).** If this small difference is ecologically significant it may explain its increased nestedness, as greater seasonality is associated with higher extinction rates and dominance of nestedness (Liang et al., 2025; Qian et al., 2020).

Studies spanning a wide range of taxa show that beta diversity patterns are influenced by the combined effects of elevation and other topographic variables. Most of these studies are on plants (Bennie et al., 2006; Qian et al., 2021; Wani et al., 2022; X. Zhang et al., 2022), which are perhaps more sensitive to soil nutrient gradients (Jiang et al., 2023) and moisture (Waldo et al., 2020), which are greatly influenced by aspect and topography. Studies of insect assemblages have also revealed that elevational patterns are influenced by other factors, resulting in variation of the profile within the region (Choi & Jang, 2022; Cómbita et al., 2022; Muluvhahothe et al., 2021; Theron et al., 2022). Ground-dwelling beetle assemblages in a subtropical montane system seemed to respond more sensitively to prey abundance gradients via soil organic matter and pH levels, rather than elevation per se (Choi & Jang, 2021). Compositional patterns in grasshopper assemblages were primarily driven by “topoclimates” i.e. a combination of elevation, cold air drainage and aspect (Theron et al., 2022).

Slope inclination was revealed as the primary driver of beta diversity in bird communities of Brazil (Cavarzere et al. 2021). Reduced tree density along steeper slopes coupled with more frequent tree falls, lower old tree density and higher regeneration rates seemed to drive both abundance and composition of bird communities (Rodrigues Coelho et al., 2018; Salomão et al., 2021).

A more direct impact of aspect may be related to the angle of incidence of solar radiation, which may be of higher relevance to ectotherms, especially in colder and more humid regions. Abundance and turnover of ectotherm communities may be mediated by changes in moisture conditions and phenology which may vary among sites at similar elevations (König et al. 2024; Feldmeier et al. 2020; Lawson et al. 2014).

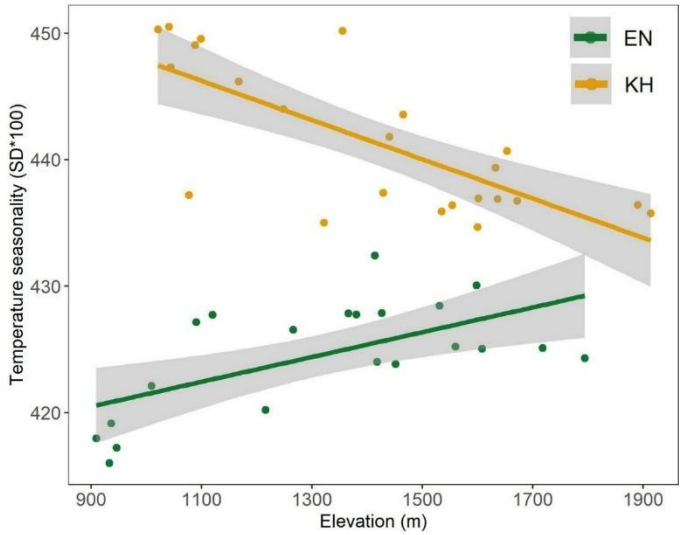


Figure 4.15: Changes in temperature seasonality across the sampled extent (900–2000 m) along Eaglenest (EN) and Khupi (KH). Seasonality values were extracted from 30 arc second square grids within a 5 km square grid centred on the midpoint of each transect (EN: green solid circles, KH: orange solid circles). We fitted linear models with 95% confidence intervals. Temperature seasonality is measured as the standard deviation of mean monthly temperatures multiplied by 100. The data was obtained from BIOCLIM (30-arc second resolution).

4.4.3 Within-elevation beta diversity in ant communities

Studies across regions and taxonomic groups suggest that compositional changes in montane landscapes occur along both vertical (across elevations) and horizontal (within elevations) dimensions, although their relative contributions may differ (Doležal & Šrůtek, 2002; Jankowski et

al., 2013; Rutten et al., 2015). Some studies revealed greater dissimilarity between communities compared across elevations than within an elevation. This is attributed to steeper climatic gradients (e.g. temperature) along elevation than along a contour at the same elevation (Castro et al., 2020; Y. Shen et al., 2022; Sreekar et al., 2017). On the other hand, horizontal beta diversity may dominate due to microclimatic variations caused by topographic factors leading to precipitation (Jankowski et al., 2009; Zhang et al., 2020) and light regime (Zellwegger et al., 2019) gradients, and also by edaphic factors (Colla et al., 2026; Kotas et al., 2018; Sukri et al., 2012)

We evaluated horizontal beta diversity in 3 different ways: (i) within-community dissimilarity in Eaglenest by segregating alternate sampling nodes within a 100 m elevation band into “separate communities”, or essentially zero separation (ii) comparison between the two transects in Khupi, separated by 100-1800 m along a contour, and (iii) comparison between Eaglenest and (combined transects in) Khupi, separated by ~100 km of contour distance.

The within-community comparison in Eaglenest provides an estimate of baseline beta diversity in ants found at the same elevation. The eight communities (each within 100 m) yielded a mean beta-diversity of 0.31 ± 0.11 (2 SD). The communities at a single elevation (~1100-1200 m) had very low abundance and exhibited much higher dissimilarity (0.61) than the mean value. This may be a general feature of communities which are greatly influenced by micro-habitat heterogeneity — we observed an anti-correlation between beta diversity and sample size, and a positive correlation between beta diversity and abundance disparity between communities. This has been reported in other studies as well (Meier & Hofer, 2016; Tello et al., 2015). We did not conduct within-community comparisons in the individual Khupi transects because the abundance within a community was considerably lower.

In Eaglenest, the within-community beta diversity is comparable to step-wise dissimilarity between communities spaced 100 m apart (0.38 ± 0.18, 2SD spread). This may suggest that community differences at this elevational scale are driven by microhabitat heterogeneity rather than the macroclimatic gradient across elevation. Jankowski et al. 2009 observed substantial differences in bird species composition at the same elevation in a tropical montane system, attributing this to fine-scale changes in moisture and epiphyte cover.

We expect horizontal dissimilarity to increase with geographic (contour) distance. This has been seen in tropical bird communities separated by 5 km v/s 80 km (Sorensen dissimilarity changing from 0.18 to 0.48) along the 1600-1700 m elevational band (Blake & Loiselle, 2000; Jankowski et al., 2009). However, the magnitude of this change can also depend on the elevation sampled (Malumbres-Olarte et al., 2025). Greater variability in forest composition has been documented at lower elevations in the tropics compared to mid- and high-elevation cloud forests (Jankowski et al., 2009). In Khupi, we observed high horizontal beta diversity of 0.70 ± 0.09 (2SD) between sites separated by 1000-1800 m contour distances. On the other hand, the horizontal beta between Khupi (KH1+KH2) and Eaglenest is considerably lower (0.46 ± 0.07) even though they are separated by ~100 km. A partial explanation for this may lie in the increased abundance per community observed when Eaglenest and Khupi were compared (contra- KH1 and KH2), but we think this suggests that distance plays less of a role than habitat heterogeneity at small scales.

The two transects in Khupi are relatively steeper (1000 m of elevational difference across ~3 km of ground distance) than the one in Eaglenest (~1000 m across 5.6 km). Since we sampled at fixed intervals of 30 m in ground distance, each Khupi transect contains fewer sampling quadrats than the Eaglenest one within each elevational (climatic) band. Individually, the two Khupi transects are likely to have captured fewer microhabitats within a given elevational (climatic) band. When the two Khupi transects were combined for comparison with Eaglenest, the abundance as well as the number of micro-habitats increased within each Khupi community. Both these factors are likely to have contributed to the lower dissimilarity between Khupi and Eaglenest (vis-a-vis KH1 v/s KH2). A study of alpine grasslands found that the sampling design (random vs maximum-variance sampling) can strongly affect beta diversity estimates (Meier & Hofer, 2016). Greater coverage of microhabitats within fixed grids (maximum-variance sampling) tends to yield lower beta-diversity estimates than randomly placed plots within the same grid.

Taxa with limited dispersal abilities like ants respond more sensitively to fine-scale microclimatic chnages in their surroundings (Polato et al., 2018). Such taxa arre more likely to shift to local microrefugia with warming climate as opposed to species with greater dispersal that shift upslope (Soifer et al. 2026)

We found much higher beta diversity between high-elevation sites in Eaglenest and Khupi (KH1+KH2) than between sites in Khupi (KH1 v/s KH2). The greater difference between Eaglenest and Khupi may be related to landscape connectivity: the Khupi transects terminated close to the local ridge line, with the highest elevation at 2100 m and elevations above 1900 m isolated from the surrounding hills. On the other hand, the Eaglenest transect terminates at 1850 m (well below the ridge line at 3250 m) resulting in greater connectivity to adjacent elevational sites. Similar patterns of increased dissimilarity among high-elevation sites have also been reported in spider communities (Malumbres-Olarte et al. 2025).

The low level of dissimilarity (0.43 ± 0.08) between the two Khupi transects at high elevations is very likely a distance effect. The transects are separated by only 100-900 m of horizontal distance. We note that these values are comparable to the within-community beta diversity in Eaglenest. A

4.4.4 Taxon-specific beta diversity patterns in ants, birds and hawkmoths

Comparative analyses of elevational beta diversity patterns across multiple taxa consistently reveal turnover as the major component driving compositional differences along elevational gradients (Du et al., 2021). A study from Argentina reported dominance of nestedness over turnover in ant communities only, while turnover dominated in plants, spiders and birds along the elevational transect (Santoandre et al., 2024). The authors argue that cold stress at higher elevations may prevent the establishment of many ant species present in the more favourable lowlands, resulting in complete turnover of species. Overall dissimilarity rates are largely influenced by dispersal abilities, thermal niches, body size, trophic position and latitudinal position of focal taxa (Dobrovolski et al., 2012; C. Shen et al., 2025; Soininen et al., 2018).

We found no difference in the elevational patterns of total dissimilarity and its components between ant, hawkmoth and bird communities **(Figure 4.11 & Figure 4.12)**, despite their widely different thermal niches, dispersal abilities and microhabitat preference.

Shared environmental drivers may nullify any effects of idiosyncratic taxon-specific responses in shaping community structure. Plants and associated orthopteran assemblages exhibit similar beta

diversity patterns due to a shared response to abiotic factors and strong biotic interactions despite widely differing life histories (Ramos et al., 2024). Rather than shared environmental drivers, we suggest that the lack of difference may have arisen due to one or both of the following factors: the comparatively coarse taxonomic (genus) level and the limited elevational extent (1000–2000 m) across which we measured community diversity. In fact, the species-level pattern across a larger extent (200–2800 m) differs significantly for hawkmots and birds (Mungee, 2018).

Ants, hawkmoths and birds are approximately similar in the order of magnitude of their species diversity but occupy very different taxonomic levels: ants and hawkmoths are families, while birds are a class. Our study demonstrates differences in the contribution of beta components within the same dataset, depending on the taxonomic scale at which diversity is measured. Recent studies have focused on implications of cross-taxa comparisons of elevational beta diversity patterns across differing phylogenetic scales: by “uprooting” and comparing different clades often originating at different evolutionary depths (Qian et al., 2021). Du et al. (2022) discuss the effects of species pool size and taxonomic scale on beta diversity patterns.

4.5 Conclusion

As far as we know, there have been only three other studies of compositional change of insect communities with elevation in the Himalayas: hawkmoths (Mungee, 2018), ants (Marathe, 2021), and butterflies (Dewan et al., 2022). This study may lack the elevational span of the other three but analyses data collected at both very fine (10s of metres) and very distant (~100 km) spatial scales. We also analysed the influence of topography on distribution of ant communites. This offers insight into the role of microclimatic factors as key determinants of community composition. Supplementing this data with other taxa at the same location aids in separating features in the patterns which are taxon-specific from those related to macro-climatic gradients.

This chapter closely follows a BioRxiv preprint (https://doi.org/10.64898/2026.06.11.731772) titled "*Differences in functional guild responses to elevation and topography in Himalayan ant communities*" (authors: N. Kadambi, M. Mungee, R. Athreya).

Chapter 5

Elevational responses of ant functional guilds

5.1 Introduction

Community structure is often quantified in terms of spatial changes in species' identities and abundances (McGlinn et al., 2021). However, traits of individuals may interact with the biotic and abiotic components of the environment, consequently determining phenotype survival and proliferation, and ultimately shaping community composition (Kraft et al., 2015). Based on the trait dispersion model (Weiher et al., 1998), it is not the systematic relationships between taxa per se that drive community structuring, but rather the distribution of intra- and interspecific traits or phenotypes related to ecosystem functioning (Garnier & Navas, 2012; Wong et al., 2019; Westerband et al., 2021). Strong environmental filtering results in the systematic clustering of trait values, whereas biotic interactions such as competition leads to limiting similarity and overdispersion of trait values (Herben & Goldberg, 2014; Cadotte et al., 2019). On the other hand, taxa can coexist in communities independently of their traits via stochastic assembly, which is neither driven by environmental filtering nor competition (Matthews & Whittaker, 2015). Therefore, tracking changes in the distribution of trait values, rather than just changes in taxonomic composition, provides better insights into the relative contribution of these three processes (environmental filtering, biotic filtering, stochastic assembly) along environmental gradients (H. Zhang et al., 2015; Loranger et al., 2018).

Since the distribution of trait values indicates which assembly rules dominate, there is growing interest in examining spatial changes in their distribution, especially along environmental gradients (Spasojevic & Suding, 2012; Montaño-Centellas, 2020; Rosbakh et al., 2022). Consequently, several conceptual and operational frameworks have emerged to quantify various aspects of trait distributions (Petchey & Gaston, 2006; Villéger et al., 2010; Denelle et al., 2019; Palacio et al., 2025). There is increasing recognition of the merits in supplementing knowledge of taxonomic diversity with approaches based on functionality, especially for understanding general patterns of community structure (Villéger et al., 2010; Weiss & Ray, 2019). Communities that do not overlap

in species composition can still be compared using functional frameworks (A. Andersen, 1997). Further, trait distributions allow for process-based evaluation of spatial structuring patterns. By examining both functional and taxonomic diversity we can identify factors that jointly and differentially influence each (Castro et al., 2020)

However, quantifying various aspects of trait distributions, otherwise known as functional diversity, would entail sampling traits that are "functional," i.e. those that relate to an ecosystem service (Violle et al., 2007; Funk et al., 2017; Streit & Bellwood, 2023) and deciding how many such traits need to be sampled. The choice of the number and type of traits is subjective and depends on the taxonomic group and, especially, the ease of trait measurement (Jansen et al., 2018; Dawson et al., 2021). For instance, many studies may focus on easily quantifiable morphological traits, potentially ignoring equally (ecologically) relevant physiological or behavioural traits (Dawson et al. 2021).

Any of the traits sampled, morphological or otherwise, may not necessarily be "functional". The unintentional selection of "non-functional" traits leads to erroneous interpretations of ecological processes underlying community structure and composition (Mlambo, 2014; Bellwood et al., 2019). On the other hand, determining the predictive strength of traits in ecosystem functioning is non-trivial (Mazziotta et al., 2019; Chacón-Labella et al., 2023; Hagan et al., 2023). One may need to establish function independently — using approaches such as stable isotope analyses, thermal performance curves/niche modelling or natural history observations — and test associations between these functions and selected traits to determine their relevance as proxies (Kearney et al., 2010; Murphy et al., 2020; Drager et al., 2023).

Drager et al. (2023) found no association between mandible size and trophic level, despite the expectation that predators have larger mandibles. In some cases, other traits may modulate links between the selected traits and ecological functions. Ant species with larger eyes are associated with carnivory, where vision aids in successful prey capture. However, microhabitat differences are a confounding factor, as subterranean predators have smaller eyes than epigaeic omnivores or herbivores. Therefore, an insufficient understanding of the system may lead to inaccurate assumptions of trait-function relations. It is important to determine how "functional" traits are before interpreting ecological processes from estimates of functional diversity.

Many studies also rely on species' mean values due to logistical constraints associated with sampling at finer intraspecific resolution (Albert et al., 2012), even though functional traits are defined at the individual level. Therefore, the resolution at which traits are measured, along with the number and type of traits, may be more influenced by convenience of sampling rather than ecological relevance, limiting our ability to form a general understanding of the underlying processes shaping community structure.

An alternative approach has been to examine responses of discrete functional types or groups, rather than functional traits (Blaum et al., 2011). Global syntheses have revealed trait syndromes — clusters of correlated traits — such as those used to define plant functional groups along the fast-slow spectrum of plant economics (Mathot & Frankenhuis, 2018). This approach may offer more biologically secure links to community processes than connecting individual traits to their hypothesised ecological functions (Raffard et al., 2017). Functional groupings also provide a simpler framework to understand community processes by reducing data dimensionality. Moreover, given the current state of data deficiencies across multiple taxa, the functional group framework offers a more pragmatic approach for examining functional diversity in communities (Swenson & Rubio, 2025). Despite its merits, this approach ignores intragroup (and intraspecific) variation, which we know can substantially influence community structure (Spasojevic & Suding, 2012; Palacio et al. 2025). Nevertheless, it provides biologically relevant insights, albeit at broader ecological scales.

Functional groups have been referred to synonymously as “guilds”, “ecological groups”, “functional types”, “functional strategies”, “structure-function groups”, and “adaptive syndromes” (Wilson, 1999), though some have attempted to distinguish between these terms. For example, guilds are defined as groups of taxa that share resource-acquisition strategies (Blondel, 2003), while functional groups are more explicitly linked to ecosystem services (Blaum et al. 2011; Blondel et al. 2003). Despite these subtle distinctions, all terms broadly group species based on a shared ecological attribute, whether it be a shared environmental niche, resources, or behaviour.

Ants are an excellent system to examine community assembly patterns and processes. Ants constitute one of the most abundant and speciose faunal groups engaged in a diverse set of

ecological functions, from seed harvesters and sap-feeders to specialised predators. They also respond sensitively to environmental changes such as temperature, resources or disturbance levels. Multiple studies argue that competitive hierarchies play a major role in influencing coexistence patterns in ants (Davidson, 1998, but also see Cerda et al., 2014). Thus, the strong influence of both environmental and biotic filters in ant distributional patterns has led to significant progress in ant functional ecology, especially since the inception of the Global Ants Database in 2006 (Gibb et al., 2017). Only two datasets from India feature in the database, and neither provide abundance. Thus, our study which records abundance adds significantly to the existing knowledge from the region.

In this chapter, I shall be using guilds to refer to groups of ant genera with shared (i) resource strategies, (ii) thermal physiology and (iii) competitive dominance. Although these functional dimensions in isolation differ in their sensitivity to environmental and biotic filters, together they reflect the contribution of both processes. All ants belong to a single family (*Formicidae* in the order Hymenoptera), yet they host a remarkable diversity of guilds, unlike the order Lepidoptera in which, for instance, the feeding guild is almost entirely herbivorous. Very few taxa exhibit this guild diversity at the family level. Other taxa comprising multiple guilds include order-level mammals like rodents (McShea et al., 2024), and class-level groups like avian communities (Raffard et al., 2017; Sedláček et al., 2023) and Arachnida (Cardoso et al., 2011). The tight correlation between narrowly defined taxonomic groups (family or lower) and (functional) guilds in most faunal groups makes it difficult to disentangle the contribution of common evolutionary descent from environmental filtering on the observed shared set of traits. However, the multi-guild framework seen in the single family constituting all the ants can aid in addressing this issue to some extent.

The earliest functional classification schemes for ants were based on interspecific competition , which drew parallels with existing plant functional group frameworks (Andersen, 1995, 1997). Ant colonies were considered functionally similar to plants: they are often fixed in place (“rooted” or “nested”) with well-segregated vegetative (workers) and reproductive (queen) units. Bharti et al., (2013) adapted this classification scheme for Himalayan ants, though at the level of genera due to the limited natural history information at the species level in the region. They defined seven functional groups or guilds spanning climate and competitive ability, viz. generalist, opportunist,

subordinate, predators, hot-climate specialists, cold-climate specialists and tropical-climate specialists. Most of the genera were assigned a single guild even though the seven guilds occupy different functional axes.

5.1.1 Elevational profiles of guilds

Strong abiotic and biotic filters that are often characteristic of steep environmental gradients, such as elevational gradients, largely influence the combination of traits that can persist at different altitudes. Studies have recorded systematic shifts in functionality with elevation to accommodate differing physiological and ecological requirements of organisms, such as body size (Mungee et al., 2021; Malumbres-Olarte et al., 2025), dispersal ability (Tiede et al., 2018; Malumbres-Olarte et al. 2025), fecundity (Alice Boyle et al., 2016) or escape responses (Garcia et al., 2009).

Ant communities experience notable shifts in ecological roles (guilds) with elevation. A previous study in Eaglenest carried out between 600 m and 2400 m noted progressive increase in the dominance of opportunistic ants and cold-climate specialists at higher elevations (Marathe et al., 2021). Despite such shifts, a primary finding of this study was that the taxonomic diversity within each guild reduced with elevation, albeit to varying degrees, suggesting that similar environmental filters may be limiting taxonomic and functional diversity. Due to this reduction in taxonomic richness within each guild, high elevation communities are not only less taxonomically diverse but also possess low functional redundancy. On the other hand, lowland communities are defined by high species turnover and high functional redundancy. It is interesting to note that high elevation ant communities exhibit shifts in profiles of guilds across seasons despite low turnover and low redundancy in a given season compared to low elevations (Nunes et al., 2020). Examining the effects of both elevation and seasonality can provide more useful insights to the processes influencing the assembly of ant communities.

5.1.2 Relationship between functional and taxonomic alpha diversities

Niche complementarity hypothesis postulates that each taxon contributes a unique set of traits in a community (Tilman et al., 1997). However, several previous studies have shown that an increase in the number of taxa does not always correspond to a proportional increase in the number of traits

(Mouillot et al., 2021). Consequently, taxonomic diversity is higher or lower than functional diversity based on the degree of niche overlap between taxa (Dalerum et al., 2012; Sadeghinia et al., 2023). Thus, studying only one dimension of diversity (i.e. the taxonomic dimension) can provide an incomplete picture of the true nature of diversity (de Bello et al., 2017). Incorporating guild diversity along with taxonomic diversity can reveal the extent to which higher taxonomic diversity translates to a larger range of functional roles in the community. In ant communities, for instance, guild diversity allows us to assess the relative dominance of predatory ants relative or herbivorous or omnivorous ants. This aids in understanding trophic structure and dominant drivers of energy flow i.e. top-down processes (predator-driven) or bottom-up forces (primary productivity). Hence, studying the relationship between taxonomic and functional components of diversity is crucial to fully understand the community-environment relationship.

5.1.3 Functional beta diversity along elevation

Functional beta diversity (FβD) quantifies the extent of non-overlap in the functional composition of communities across sites. Many studies have examined overall changes in the functional composition of elevational assemblages, comparing it with rates at which taxonomic composition changes. A commonly observed pattern across studies is the decoupling of taxonomic and functional beta diversity across elevation, with high taxonomic but relatively lower (or random) functional turnover (de Bello et al., 2017; Mungee & Athreya, 2021). Relatively fewer studies have decomposed multi-trait responses of communities to guild- or trait-specific responses to examine the identity and proportion of guilds that primarily drive overall compositional heterogeneity with elevation. Therefore, studies that continue to represent elevational responses of multiple traits or guilds in the form of a single index without decomposing to guild-specific responses potentially risk obscuring significant elevational trends in a few guilds/traits (Boyce et al., 2019; Q. Zhang et al., 2020).

Examining guild-specific responses aids in assessing the relative influence of abiotic filtering and biotic filtering mechanisms with elevation. For instance, Neotropical ant communities display unevenness in the proportional occupation of guilds at both and high elevations, with some guilds dominating over others due to environmental filtering (Warne, 2013). However, at mid-elevations,

proportionality in guild membership is more even than expected by chance, suggesting the dominance of competitive interactions over environmental filtering. In avian communities, highland assemblages are functionally clustered and composed of understory insectivores and canopy dwellers (Boyce et al. 2019). Decomposition of multi-trait indices revealed links to tarsus length (locomotion) and bill shape (resource acquisition) drove functional composition in bird communities. Therefore, microhabitat structure and prey-size distribution associated with resource acquisition can act as primary determinants of functional composition at high elevations, rather than commonly assumed factors such as physiological tolerance.

5.1.4 Guild framework in this thesis

We used the genus-level guild framework to identify a total of 11 guilds in 3 functional dimensions, viz. thermal, trophic and competitive dominance**.** The functional dimensions and the guilds are described below. Each genus was assigned to one guild in each of the 3 functional dimensions. The guild score of each genus is shown in **Table 5.1**. Note that a genus is marked positive for only one guild in each dimension. Hence each genus is only placed in three of eleven guilds along the three dimensions. We could not obtain trait data for two of forty genera in the dataset. However, they constituted only 0.008% of total abundance (25 of 3090).

Functional axis 1: Thermal niche (implicated in abiotic adaptation)

- **a)** Tropical-climate specialists (TCS): Genera originating in the tropics that only occupy regions with warm climates.
- **b)** Cold-climate specialists (CCS): Genera originating in the temperate regions that only occupy regions with cold climates.
- **c)** Thermal generalists (TG): Genera that may originate in the tropics or the temperate regions with widespread distribution across regions experiencing both warm and cold climates.

Functional axis 2: Trophic level (implicated in interspecific interactions)

- **a)** Herbivores (HB): Genera that entirely feed on sugary sap, seed or plant material
- **b)** Omnivores (OM): Genera that feed on both plant material and other arthropods, via active predation or detritivory.

c) Small predators (SP): Cryptic predatory ants that hunt within small subterranean crevices and in the layers of leaf litter.

d) Large predators (LP): Predatory ants that primarily hunt on more planar surfaces and are unable to access small crevices.

Functional axis 3: Competitive dominance (implicated in interspecific interactions)

a) Dominant (DM): Behaviourally aggressive and numerically superior genera that directly outcompete other genera via interference competition.

b) Subordinate (SB): Genera co-existing with dominant genera by employing submissive strategies, such as foraging in smaller territories, maintaining smaller colonies or nesting in suboptimal sites.

c) Opportunistic (OP): Genera that exhibit flexible ecological strategies, thriving in disturbed and stressful habitats.

d) Specialists (SL): Genera that avoid competition by separating their nesting or foraging niche.

5.1.5 Objectives and Hypotheses

1. Relative abundance of the guilds

We quantified the relative abundance of each guild within each of the three functional axes (Thermal Niche, Trophic Level and Competitive Dominance). First, we compared the evenness of guild abundance within a given functional axis across Eaglenest and Khupi. Thereafter, we compared the two slopes (Eaglenest and Khupi) to assess how similar the relative abundances of guilds were along each axis.

Table 5.1: Genus-level assignment of binary scores along three functional dimensions/axes (thermal niche, trophic level and competitive dominance) examined. Each genus is assigned into mutually exclusive guilds within an axis (1 = presence, 0 = absence). Abbreviations: TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; Herb = herbivore, Omni = omnivore, SP = small predator, LP = large predator; SL = specialists/competition avoiders, OP. = opportunists, SB = subordinates, DM = dominants.

		Thermal Niche			Trophic Level				Competitive Dominance			
	Genus	TCS	CCS	TG	HB	OM	SP	LP	DM	SB	OP	SL
1	*Anochetus*	1	0	0	0	0	0	1	0	0	0	1
2	*Aphaenogaster*	0	0	1	0	1	0	0	0	0	1	0
3	*Brachyponera*	1	0	0	0	1	0	0	0	0	1	0
4	*Camponotus*	0	0	1	0	1	0	0	0	1	0	0
5	*Carebara*	1	0	0	0	0	1	0	1	0	0	0
6	*Cataulacus*	1	0	0	0	1	0	0	0	0	0	1
7	*Cerapachys*	1	0	0	0	0	0	1	0	0	0	1
8	*Crematogaster*	0	0	1	0	1	0	0	1	0	0	0
9	*Diacamma*	1	0	0	0	0	0	1	0	0	0	1
10	*Discothyrea*	1	0	0	0	0	1	0	0	0	0	1
11	*Dolichoderus*	0	0	1	0	1	0	0	0	0	1	0
12	*Ectomomyrmex*	1	0	0	0	0	0	1	0	0	0	1
13	*Emeryopone*	1	0	0	0	0	1	0	0	0	0	1
14	*Hypoponera*	1	0	0	0	0	1	0	0	0	0	1
15	*Lasius*	0	1	0	0	1	0	0	0	1	0	0
16	*Leptogenys*	1	0	0	0	0	0	1	0	0	0	1
17	*Lophomyrmex*	1	0	0	0	1	0	0	0	0	0	1
18	*Monomorium*	0	0	1	0	1	0	0	0	0	1	0
19	*Myopopone*	1	0	0	0	0	0	1	0	0	0	1
20	*Myrmecina*	0	0	1	0	0	1	0	0	0	0	1
21	*Myrmoteras*	1	0	0	0	0	0	1	0	0	0	1
22	*Nylanderia*	1	0	0	0	1	0	0	0	0	1	0
23	*Odontomachus*	1	0	0	0	0	0	1	0	0	0	1
24	*Ooceraea*	1	0	0	0	0	1	0	0	0	0	1
25	*Pheidole*	0	0	1	0	1	0	0	1	0	0	0
26	*Polyrhachis*	1	0	0	0	1	0	0	0	1	0	0
27	*Ponera*	0	0	1	0	0	1	0	0	0	0	1
28	*Pristomyrmex*	1	0	0	0	0	1	0	0	0	1	0
29	*Proceratium*	1	0	0	0	0	1	0	0	0	0	1
30	*Pseudolasius*	1	0	0	1	0	0	0	0	0	0	1
31	*Stictoponera*	1	0	0	0	0	0	1	0	0	0	1
32	*Strumigenys*	1	0	0	0	0	1	0	0	0	0	1
33	*Stigmatomma*	1	0	0	0	0	1	0	0	0	0	1
34	*Technomyrmex*	1	0	0	0	1	0	0	0	0	1	0
35	*Temnothorax*	0	1	0	0	1	0	0	0	0	0	1
36	*Tetramorium*	0	0	1	0	0	1	0	0	0	1	0
37	*Vollenhovia*	1	0	0	0	0	1	0	0	0	0	1
38	*Vombisidris*	1	0	0	1	0	0	0	0	0	0	1

2. Change in relative abundance of guilds with elevation

a) *Thermal Niche axis:* the relative abundance of tropical-climate specialists should reduce towards higher elevations, while that of cold-climate specialists increases at higher elevations. Compared to specialists, I expect the proportion of thermal generalists to change more gradually with elevation.

b) *Trophic Level axis:* the relative abundance of omnivores and herbivores should reduce at higher elevations due to reduced primary productivity. Small predators may remain stable throughout the gradient, since they occupy a separate nesting and foragin niche (subterranean or lower levels of leaf-litter). Additionally, they often predate on small-sized soil invertebrates such as collembolans or eggs and larvae of arthropods that may continue to persist at higher elevations. In contrast, larger predators (surface foragers) should reduce in proportion at higher elevations due to reduction in total arthropod abundance at higher (cooler) elevations.

c) *Competitive Dominance axis:* the relative abundance of dominants, which typically have larger colonies and require more resources, should reduce at higher elevations.

Between the two slopes: Microclimatic factors are known to largely influence distributional patterns in ant communities (Nascimento et al., 2022; Pérez-Sánchez et al., 2023). However, it is unclear whether they contribute towards heterogeneity in functional composition of communities.

3. To assess the relationship between guild and taxonomic alpha diversities

I expect functional guild diversity to increase linearly with generic diversity along both slopes (Eaglenest and Khupi).

4. To investigate patterns of composite and guild-specific functional beta diversity

a) I expect the slope of the multi-variate FβD (composite of all guilds) to be higher in Khupi than EWS because the steeper environmental gradient along Khupi would necessitate a higher turnover of traits to facilitate local adaptations across elevations.

b) I expect a steeper slope of single guild FβD for specialists compared to generalists

- **i.** Cold-climate and Tropical-climate specialists v/s Thermal generalists.
- **ii.** Herbivores and Predators v/s Omnivores.

5.2 Methods and Analysis

Using the genus-abundance data described in Chapter 2 and the genus-guild association in **Table 5.1**, we constructed a guild-abundance data for Eaglenest (N = 1568) and Khupi (N = 1497). This is listed in **Table 5.2**.

We estimated the mean relative abundances of each guild (within each axis) in both Eaglenest and Khupi assuming a binomial distribution, and calculated Wilson confidence intervals around the estimated mean values. We also examined the change in the relative abundance of each guild with elevation in both Eaglenest and Khupi.

We employed Gower's distance (Gower, 1971) to measure functional distance between genera across the three functional axes. We assigned a Gower distance of 0 between any two genera if they belonged to the same guild along a particular functional axis and 1 if they belonged to different guilds. Averaged over all 3 axes the average distance between a genus pair could be any of 0, 0.33, 0.66 and 1.

We used Rao's quadratic entropy (Rao's Q) as a measure of functional alpha diversity (using trait distances weighted by abundance) at an elevation using the *dbFD* function in the R package '*FD*' v1.0.12.3 (Laliberté et al., 2009). In our case, guilds are mutually exclusive nominal variables and therefore all distances are the same. Any differences in guild assignment between genera within a functional dimension are equally weighted. We estimated Rao's Q as follows:

$$Q_i = \sum \sum p_a p_b d_{ab} \qquad \ldots \text{Eq. 5.1}$$

where Q_i is the value for the i-th elevation, p_a and p_b refer to the relative abundances of genus a and genus b, and d_{ab} is the functional Gower distance (across all 3 functional axes) between the two genera.

We calculated functional beta diversity ($F\beta D$) using R package '*BAT*' v.2.11.0 (Cardoso et al., 2015), which uses the following equation:

$$F\beta D = \frac{Q_{ij} - \frac{Q_i + Q_j}{2}}{max\left(Q_{ij} - \frac{Q_i + Q_j}{2}\right)} \quad \ldots \text{Eq. 5.2}$$

Q_i and Q_j are the functional alpha diversity for the ith and j^{th} elevational community, obtained from Equation 5.1. Q_{ij} represents the functional alpha diversity of the ith and j^{th} elevational communities pooled as a single community. The total functional dissimilarity (FβD) was partitioned into its components, turnover and nestedness.

Using Equation 5.2, we calculated the total (composite) FβD values for the elevational communities as a whole (i.e. using all the genera) and also within each guild (considering only those genera for which the particular guild score = 1; see **Table 5.1)**. We then examined profiles of composite and guild-specific FβD as a function of elevational distance between communities.

Where necessary, we used the transect identity (Eaglenest v/s Khupi) as an interaction term in the linear models. This enabled us to test whether elevational responses of guilds differed substantially between Eaglenest and Khupi.

Finally we assessed whether, and to what extent, closely related genera tend to occupy the same set of guilds across the three functional axes than expected by chance. For this, we conducted a Mantel (Spearman rank) test (using the R package *vegan* v2.7.2 (Oksanen et al. 2025) to test the strength of association between functional Gower distance and phylogenetic distance among ant genera. We assessed the significance of Mantel's r statistic by permutating the functional distance matrix 999 times to estimate the null (randomised) correlation. Phylogenetic distances between genera was extracted from a topology-only tree of Formicidae available at the generic level (Moreau, C. S. 2009; Ward et al., 2015; Boudinot et al., 2022). The number of edges separating each generic pair was used as a measure of distance in place of evolutionary time or degree of genetic change.

Table 5.2: Total abundance of ant guilds along three functional axes (thermal niche, trophic level and competitive dominance) at each elevation in Eaglenest (EN) and Khupi (KH). N is the community size/total abundance. Total abundance and proportional abundance of each guild is highlighted in bold for each of the two sites. Abbreviations are : TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders. Note that relative abundances of all guilds within a functional axis adds up to 1.

Site	Alt (m)	N	Thermal Niche			Trophic Level				Competitive Dominance			
			TCS	CCS	TG	HB	OM	SP	LP	DM	SB	OP	SL
EN	974	144	99	0	45	0	62	72	10	21	2	36	85
	1012	144	91	2	51	0	60	66	18	43	2	38	61
	1004	143	92	0	51	1	49	73	20	30	0	54	59
	1166	138	78	1	59	0	67	55	16	47	0	49	42
	1318	144	86	0	58	0	54	68	22	44	2	56	42
	1457	139	63	0	76	1	70	36	32	37	0	61	41
	1528	141	62	2	77	0	44	82	15	31	1	58	51
	1588	144	79	0	65	0	24	80	40	41	0	30	73
	1623	143	78	1	64	0	38	60	45	47	1	24	71
	1694	143	97	1	45	1	34	41	67	40	2	19	82
	1786	145	103	2	40	0	26	44	75	26	2	20	97
	Total	**1568**	**928**	**9**	**631**	**3**	**528**	**677**	**360**	**407**	**12**	**445**	**704**
	%	**—**	**59.2**	**0.6**	**40.2**	**0.2**	**33.7**	**43.2**	**23.0**	**26.0**	**0.8**	**28.4**	**44.9**
KH	1081	153	94	0	59	4	64	69	16	60	1	44	48
	1146	145	87	0	58	5	62	59	19	52	2	43	48
	1247	140	82	0	58	2	65	51	22	41	2	55	42
	1380	147	74	9	64	0	86	50	11	62	10	50	25
	1460	152	91	2	59	0	75	65	12	46	2	63	41
	1535	151	82	0	69	0	54	79	18	72	1	34	44
	1608	153	69	13	71	0	42	102	9	52	13	32	56
	1727	149	54	13	82	0	52	82	15	18	13	59	59
	1828	153	25	4	124	0	33	120	0	13	4	68	68
	1987	154	38	27	89	0	56	95	3	26	27	58	43
	Total	**1497**	**755**	**68**	**773**	**11**	**623**	**815**	**148**	**468**	**75**	**534**	**519**
	%	**—**	**48.2**	**4.4**	**49.3**	**0.7**	**39.7**	**52.0**	**9.4**	**29.8**	**4.8**	**34.1**	**33.1**

5.3 Results

5.3.1 Relative abundance of guilds.

The fractional distribution of the guilds shows considerable variation between Khupi and Eaglenest (**Figure 5.1 & Table 5.3)**. Statistical significance in the difference of relative abundances of guilds within each functional axis and between transects is depicted in **Figure 5.2** and **Figure 5.3,** respectively.

Thermal Niche axis

- **a)** Cold-climate specialists (CCS) were the least abundant in both Khupi and Eaglenest. The fraction was higher in Khupi by a factor of 5.
- **b)** Tropical-climate specialists (TCS) dominated over thermal generalists (TG) in Eaglenest, but were of similar abundance in Khupi.

Trophic Level axis

- **a)** Herbivores (HB) were a negligibly small fraction in both Eaglenest and Khupi
- **b)** Predatory ants were more abundant (56–70 %) than omnivorous ants (30–41 %).
- **c)** Small (leaf-litter) predatory ants (SP) were more abundant than the larger (surface-foraging) predatory ants (LP) in both Eaglenest and Khupi. However, the latter were more numerous in Eaglenest (LP = 20–25 %) than in Khupi (LP = 7–10 %).

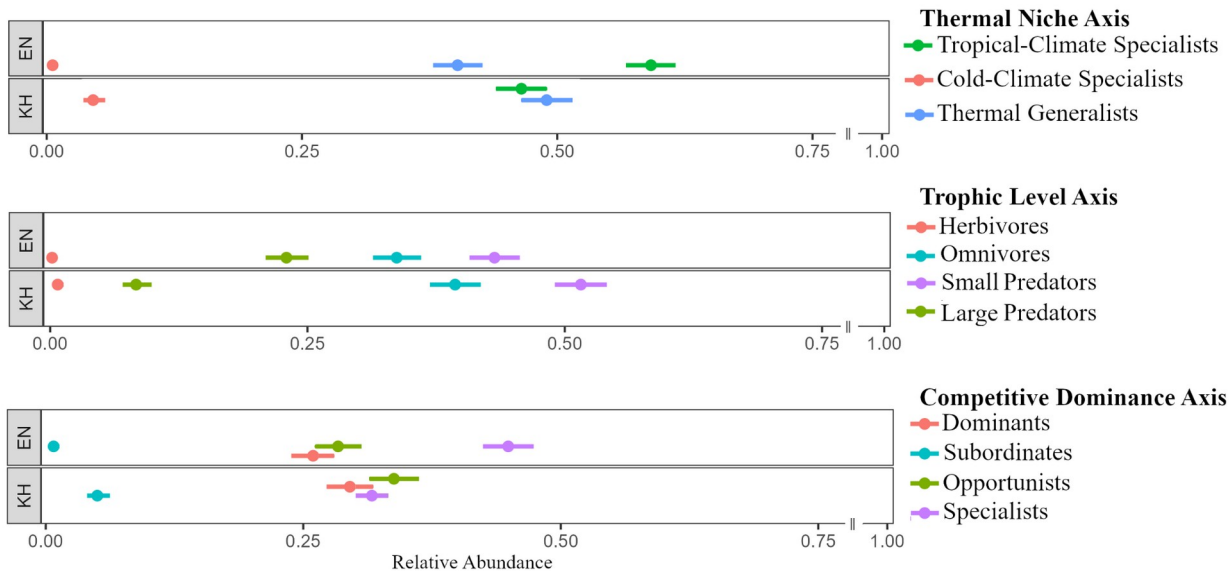


Figure 5.1: Proportional representation of all eleven ant guilds along each of the three functional axes in Eaglenest and Khupi. The three panels represent proportions of each guild in each of the three functional axes (Thermal Niche, Trophic Level and Competitive Dominance), with each panel consisting of values in Eaglenest (EN) at the top and Khupi (KH) at the bottom. Mean proportions for each guild is obtained from a binomial distribution and plotted alongside Wilson's binomial confidence intervals (95%). The key to the eleven guilds is provided on the right under each of the three functional axes.

Competitive Dominance axis

a) Subordinate ants (SB) were the least abundant in Eaglenest and Khupi.

b) The other three guilds were more evenly abundant in Khupi, while in Eaglenest niche specialists were 1.5-2 times more abundant than the other two.

Table 5.3: Mean proportion of 11 ant guilds along three functional axes (thermal niche, trophic level and competitive dominance) at Eaglenest (EN) and Khupi (KH) along with lower and upper bounds of 95% Wilson's confidence intervals. Total abundance in each transect is indicated by n in brackets for each of the two sites/transects. Abundance of each guild for each site along with mean ± 95% CI is reported after rounding off to 3 d.p. Abbreviations are as follows: TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders.

Functional Axis	Transect	Guild	Abundance	Mean Proportion	Lower (95% CI)	Upper (95% CI)
Thermal Niche	EN (n = 1568)	TCS	928	0.592	0.567	0.616
		CCS	9	0.006	0.003	0.011
		TG	631	0.402	0.378	0.427
	KH (n= 1497)	TCS	696	0.465	0.440	0.490
		CCS	68	0.045	0.036	0.057
		TG	733	0.490	0.464	0.515
Trophic Level	EN (n = 1568)	HB	3	0.002	0.001	0.006
		OM	528	0.337	0.314	0.361
		SP	677	0.432	0.407	0.456
		LP	360	0.230	0.209	0.251
	KH (n= 1497)	HB	11	0.007	0.004	0.013
		OM	589	0.393	0.369	0.418
		SP	772	0.516	0.490	0.541
		LP	125	0.084	0.071	0.099
Competitive Dominance	EN (n = 1568)	DM	407	0.260	0.238	0.282
		SB	12	0.008	0.004	0.013
		OP	445	0.284	0.262	0.307
		SL	704	0.449	0.425	0.474
	KH (n= 1497)	DM	442	0.295	0.273	0.319
		SB	75	0.050	0.040	0.062
		OP	506	0.338	0.314	0.362
		SL	474	0.317	0.294	0.341

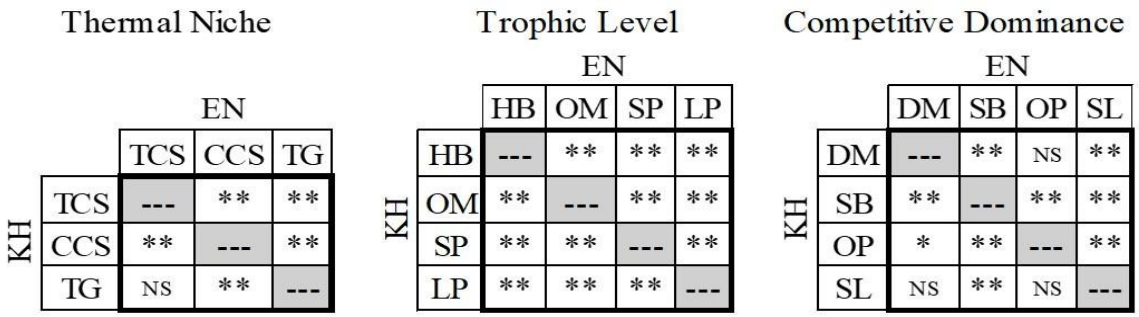


Figure 5.2: Comparison of within-transect differences in relative abundances of guilds in each of the three functional axes examined. Matrices from left to right: Thermal Niche, Trophic Level and Competitive Dominance. Asterisks indicate the extent of difference in the (binomial) distribution of relative abundances between any two guilds within Eaglenest (EN) and Khupi (KH). Two asterisks represent paired guild comparisons with relative abundance distributions well beyond ± 95% Wilson's CI. A single asterisk: abutting relative abundance distributions. NS: overlapping relative abundance distributions. CS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; Herb = herbivore, Omni = omnivore, SP = small predator, LP = large predator; SL = specialists/competition avoiders, OP. = opportunists, SB = subordinates, DM = dominants.

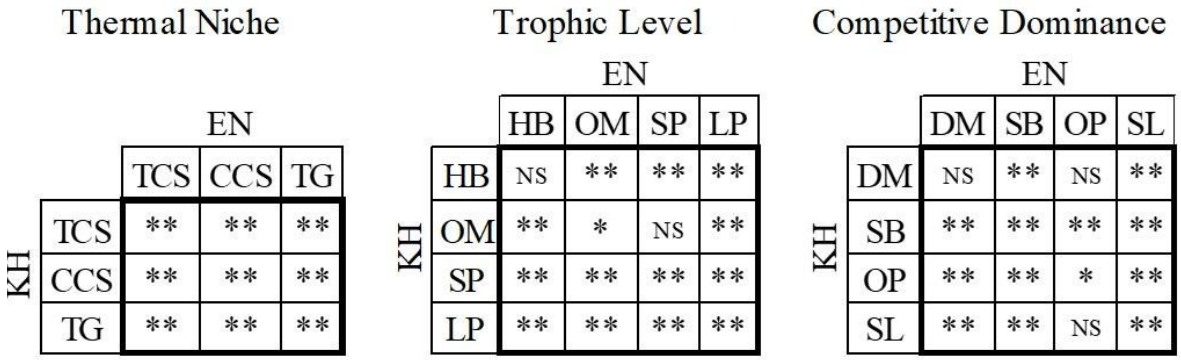


Figure 5.3: Between-transect comparison of relative abundances of guilds across the three functional axes examined. Matrices from left to right: Thermal Niche, Trophic Level and Competitive Dominance. Asterisks indicate the extent of difference in the (binomial) distribution of relative abundances between any two guilds from the two transects, Eaglenest (EN) and Khupi (KH). Two asterisks represent paired guild comparisons with relative abundance distributions well beyond ± 95% Wilson's CI. A single asterisk: abutting relative abundance distributions. NS : overlapping relative abundance distributions. TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; Herb = herbivore, Omni = omnivore, SP = small predator, LP = large predator; SL = specialists/competition avoiders, OP = opportunists, SB = subordinates, DM = dominants.

5.3.2 Elevational profiles of guild abundance

We examined elevational profiles of relative abundances for each guild within each functional axis, obtained from values of total abundances **(Table 5.2).**

The three guilds along the thermal niche axis did not show a significant change in relative abundance with elevation in Eaglenest **(Figure 5.4 & Table 5.4).** However, in Khupi, the relative abundance of cold-climate specialists ($R^2 = 0.56$) and thermal generalists ($R^2 = 0.57$) increased towards higher elevations, at the expense of tropical-climate specialists ($R^2 = 0.79$).

The abundance of herbivores was too small to interpret elevational profiles in both Eaglenest and Khupi. Predatory ants increased in relative abundance (vis-a-vis omnivores), but this increase was driven by large predators in Eaglenest ($R^2 = 0.68$) and by small predators in Khupi ($R^2 = 0.58$) **(Figure 5.5 & Table 5.4)**.

The elevational segregation of competitive dominance guilds is weak along Eaglenest **(Figure 5.6 & Table 5.4).** In Khupi, the subordinate guild (SB) increases in relative abundance (vis-a-vis the dominant guild) towards higher elevations.

The effect of slope on elevational effects is apparent across all three functional axes **(Table 5.5)**. Along the thermal niche axis, generalists largely respond similarly in both Eaglenest and Khupi ($\beta = 0.29 \pm 0.14$, $p = 0.06$), while thermal specialists exhibit slope-specific responses. Trophic restructuring differs along the two slopes with respect to predators but not omnivores. Along the competitive dominance axis, slope-specific differences are observed in dominant and subordinate guilds, but not in opportunistic and niche specialist guilds.

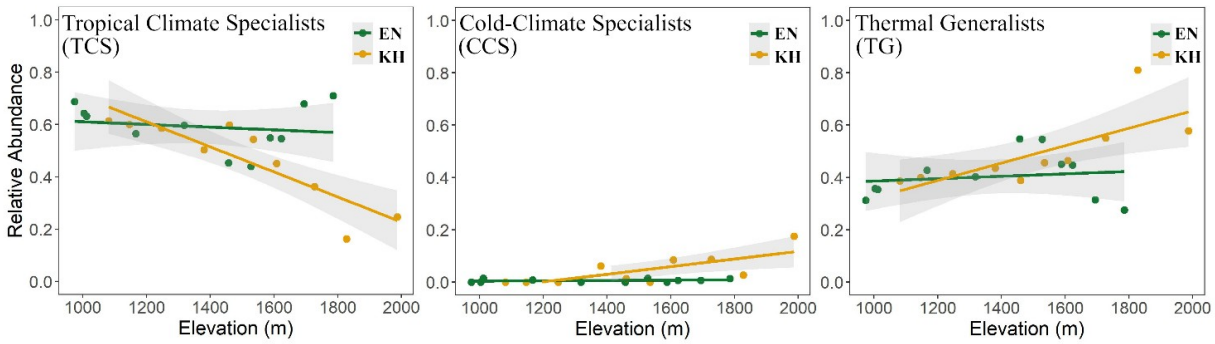


Figure 5.4: Change in the relative abundance of ant thermal guilds with elevation along Eaglenest (EN) and Khupi (KH). Each green and yellow solid circle represent an elevational community in Eaglenest and Khupi, respectively. Green and yellow trend lines are the linear fits showing the magnitude of change in the proportion of each thermal guild with elevation (1000–2000 m). Abbreviations: TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists.

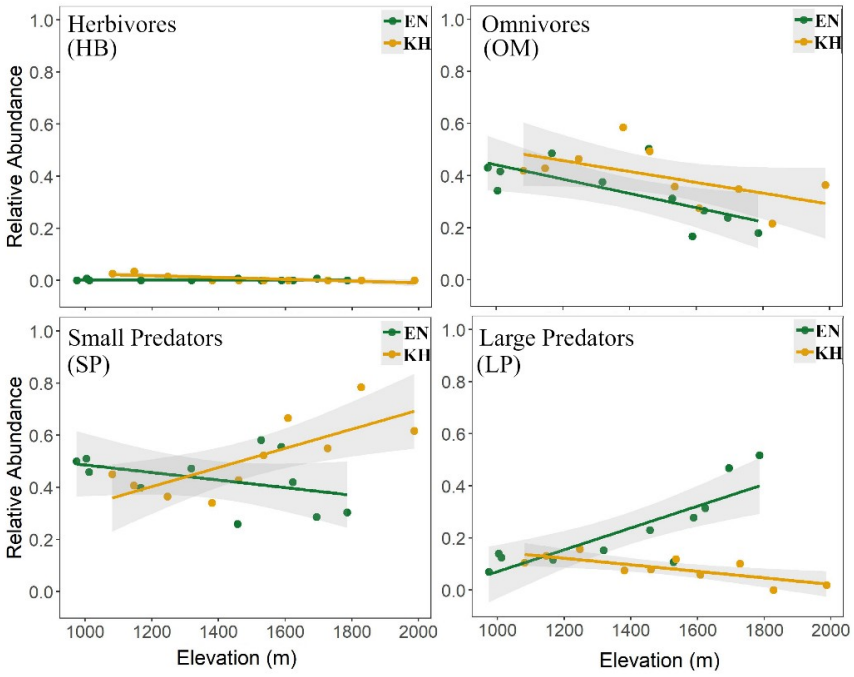


Figure 5.5: Change in the relative abundance of ant trophic guilds with elevation along Eaglenest (EN) and Khupi (KH). Each green and yellow solid circle represent an elevational community in Eaglenest and Khupi, respectively. Green and yellow trend lines are the linear fits showing the magnitude of change in the proportion of each trophic guild with elevation (1000–2000 m). Abbreviations: HB = herbivore, OM = omnivore, SP = small predator, LP = large predator.

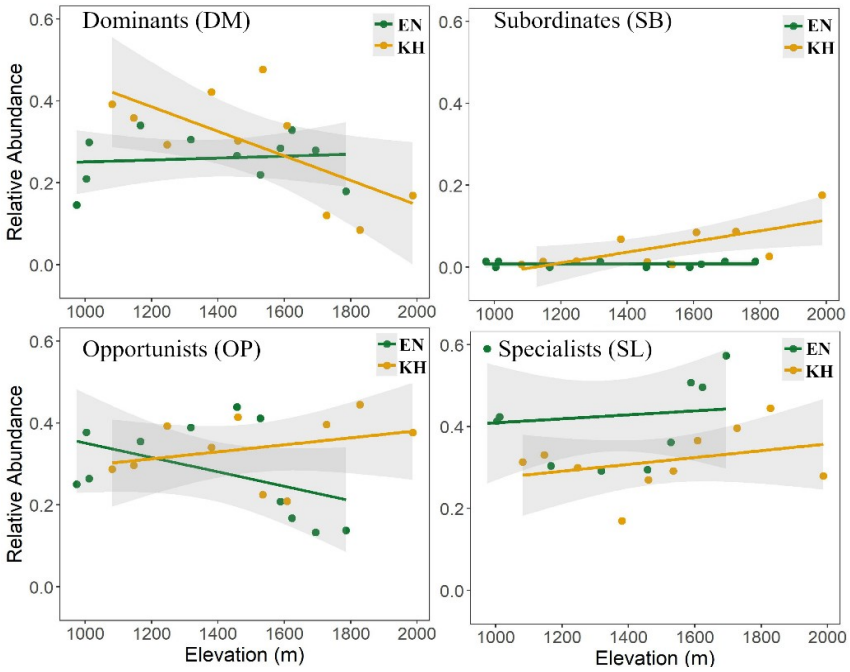


Figure 5.6: Relative abundance profiles of competition guilds with elevation in Eaglenest (EN) and Khupi (KH). Green and yellow solid circle represent an elevational community in Eaglenest and Khupi, respectively. Abbreviations: DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders.

Table 5.4: Summary of guild relative abundance profiles in Eaglenest (EN) and Khupi (KH). Slopes ± SE (per km) and R^2 values are listed for all guilds. TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders. ($p < 0.1^{*}$, $p < 0.05^{**}$, $p < 0.01^{***}$, $p < 0.001^{****}$). Note that proportions of guilds in an axis are negatively correlated e.g., opposite slopes of TCS and TG along the thermal axis are not entirely independent of each other.

Functional axis	Guild	EN Slope ± SE	EN R^2	KH Slope ± SE	KH R^2
Thermal Niche	TCS	-0.05 ± 0.09	0.03	-0.48 ± 0.01***	0.79
	CCS	0.01 ± 0.03	0.08	0.14 ± 0.03****	0.56
	TG	0.05 ± 0.10	0.02	0.33 ± 0.11***	0.57
Trophic Level	HB	< 0.001	< 0.01	-0.03 ± 0.01***	0.60
	OM	-0.27 ± 0.10**	0.49	-0.21 ± 0.10*	0.33
	SP	-0.15 ± 0.10	0.16	0.27 ± 0.13**	0.58
	LP	0.42 ± 0.08****	0.68	-0.13 ± 0.10	0.58
Competitive Dominance	DM	0.02 ± 0.09	0.01	-0.30 ± 0.10***	0.46
	SB	0.00 ± 0.03	< 0.01	0.13 ± 0.03****	0.50
	OP	-0.18 ± 0.10	0.21	0.09 ± 0.11	0.10
	SL	0.15 ± 0.11	0.12	0.08 ± 0.12	0.11

Table 5.5: Elevation × Transect interaction effects from linear models examining changes in the relative abundance of guilds across Eaglenest (EN) and Khupi (KH). The table includes interaction coefficients (β ± SE) and p values for guilds linked to thermal niche, trophic level and competitive dominance. Abbreviations are as follows: TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders. *Asterisks indicate levels of statistical significance ($p < 0.1^{*}, p < 0.05^{**}, p < 0.01^{***}, p < 0.001^{****}$).*

Functional axis	Guild	Interaction β	Interaction p
Thermal Niche	TCS	$-0.43 \pm 0.14^{***}$	< 0.01
	CCS	$0.14 \pm 0.04^{***}$	< 0.01
	TG	0.29 ± 0.14	0.06
Trophic Level	HB	$-0.03 \pm 0.01^{***}$	< 0.01
	OM	0.07 ± 0.14	0.64
	SP	$0.43 \pm 0.16^{**}$	< 0.05
	LP	$-0.55 \pm 0.12^{****}$	< 0.001
Competitive Dominance	DM	$-0.32 \pm 0.13^{**}$	< 0.05
	SB	$0.13 \pm 0.04^{***}$	< 0.01
	OP	$0.26 \pm 0.15^{*}$	0.09
	SL	-0.07 ± 0.17	0.69

5.3.3 Relationship between guild and taxonomic alpha diversities

Functional alpha diversity (Rao's Q) did not change substantially with increase in either Simpson's D or Fisher's alpha in both Eaglenest and Khupi **(Table 5.6 &Figure 5.7)**. Despite excluding an outlier value in Khupi, the relationship between functional and taxonomic alpha diversity remained weak.

Table 5.6: Summary of the relationship between ant functional alpha diversity (RaoQ) and taxonomic alpha diversity (Simpson's D and Fisher's α) in Eaglenest (EN) and Khupi (KH). The model fit is across the entire elevational extent including outliers values. The table reports the estimates of slope ± SE (per km) and p-values.

	RaoQ ~ SimpsonD			RaoQ ~ Fisher's alpha		
Site	Slope	R^2	p	Slope	R^2	p
EN	-0.17 ± 0.25	0.05	0.52	-0.00 ± 0.01	0.03	0.58
KH	0.38 ± 0.20	0.31	0.10	0.01 ± 0.01	0.10	0.36

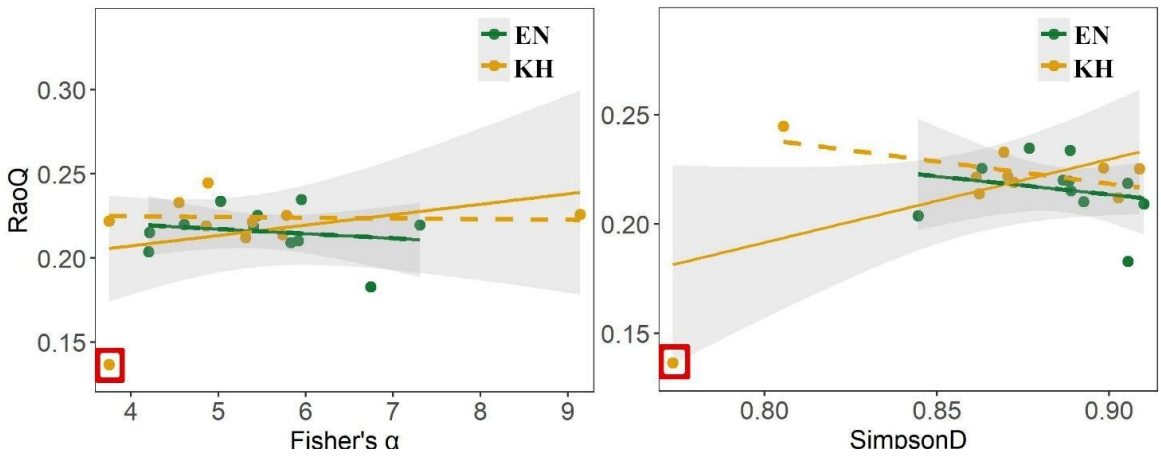


Figure 5.7: Relationship between functional diversity (Rao's Q) and taxonomic diversity (left: Fisher's α; right: Chao-corrected Simpson's D) in ant communities of Eaglenest (EN) and Khupi (KH). Green and yellow solid circles represent elevational communities in Eaglenest and Khupi, respectively. Solid lines represent the linear fit for all elevational communities sampled. The dashed yellow line represents a linear fit along Khupi after excluding an outlier elevational community, as marked by a red square. Note that functional diversity does not change as a function of increasing taxonomic diversity.

5.3.4 Guild-specific and composite elevational beta diversity

The composite functional beta diversity (FβD) increased moderately with elevational separation between communities in both Eaglenest and Khupi **(Figure 5.8A & Table 5.7)**. Both the additive components (turnover & nestedness) of composite FβD increased with elevational distance **(Figure 5.8B)**, with turnover (0.32: 88%) contributing considerably more than nestedness (0.04–0.05: 12%). The relationship between composite FβD and its additive components with elevational distance is similar in both Eaglenest and Khupi as inferred from the non-significant interaction coefficients.

Elevational responses of the individual guilds within each of the three functional axes differ considerably amongst each other **(Table 5.8)** and between slopes **(Table 5.9)**. However, the beta profiles are steeper in Khupi (7 of the 11 guilds exhibit a change in FβD which is >10% per km and also statistically significant at 95% level) than in Eaglenest (only 2 guilds).

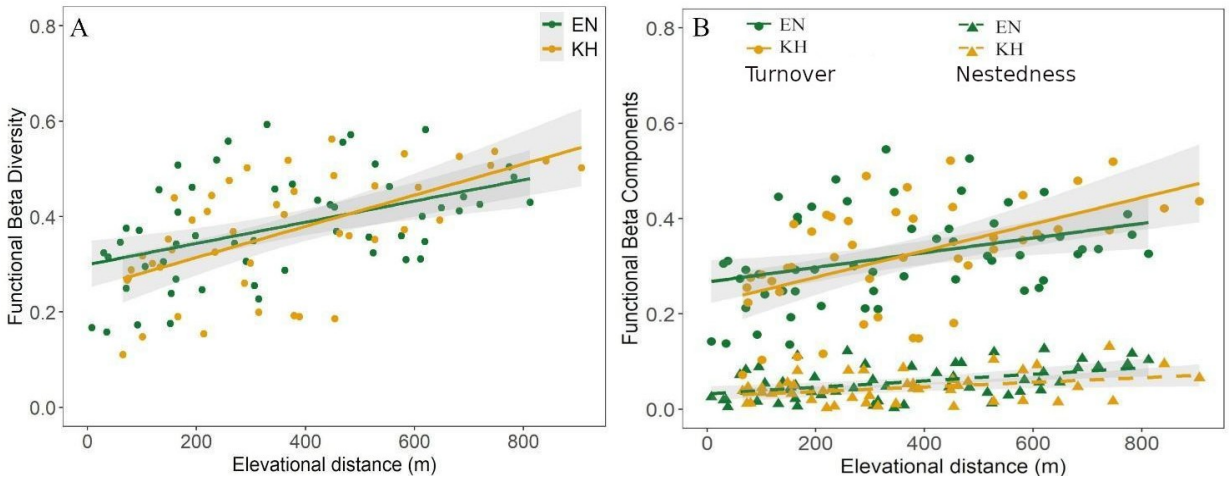


Figure 5.8: Composite functional beta diversity (A) and its additive components (B) in ant communities along Eaglenest (EN) and Khupi (KH). In panel A, green and yellow solid circles represent total functional beta diversity of elevational communities in Eaglenest and Khupi, respectively. Corresponding solid lines represent the modelled linear relationships between functional beta diversity and elevational distance between communities within Eaglenest (green line) and Khupi (yellow line). Panel B plots the contributions of the two components i.e. turnover and nestedness, to the observed functional beta diversity. Solid circles represent the contribution of turnover, while solid triangles represent the contribution of nestedness. Green and yellow points represent communities in Eaglenest and Khupi, respectively.

Table 5.7: Linear model summary of total ant functional beta diversity along with its components across elevation in Eaglenest (EN) and Khupi (KH). The table reports the estimate of slope ± SE (per km), R^2 and p-values within each slope. Interaction coefficients (Elevation × Transect) and p-values are included to assess whether there are significant differences in elevational patterns between slopes. Asterisks indicate levels of statistical significance ($p < 0.1^{*}$, $p < 0.05^{**}$, $p < 0.01^{***}$, $p < 0.001^{****}$).

Functional Beta	EN Slope ± SE	EN R^2	KH Slope ± SE	KH R^2	Interaction β	Interaction p
FβD (Total)	$0.22 \pm 0.06^{****}$	0.22	$0.33 \pm 0.07^{****}$	0.35	0.11 ± 0.09	0.24
Turnover	$0.15 \pm 0.06^{***}$	0.14	$0.28 \pm 0.07^{****}$	0.28	0.13 ± 0.09	0.15
Nestedness	$0.07 \pm 0.02^{****}$	0.20	$0.05 \pm 0.02^{**}$	0.12	-0.02 ± 0.46	0.46

In Eaglenest, the three thermal guilds have essentially flat elevational functional beta diversity profiles while in Khupi they show a linear increase with elevational distance **(Figure 5.9)**. Tropical-climate specialists exhibit the strongest change of the three guilds.

Along the trophic axis, omnivores and large predators in Eaglenest show increasing FβD with elevational distance while this change is seen in small and large predators in Khupi **(Figure 5.10 & Table 5.8)**.

Along the axis of competitive dominance, dominant and subordinate ant communities in Khupi are the only guilds in which FβD increases with elevational distance **(Figure 5.11)**.

Eight of eleven guilds we examined exhibited slope-specific differences **(Table 5.9)**. The three guilds which behaved the same way in Eaglenest and Khupi were opportunists and specialists along the competitive dominance axis, and herbivores in the trophic axes - they exhibited no change of FβD with elevational distance.

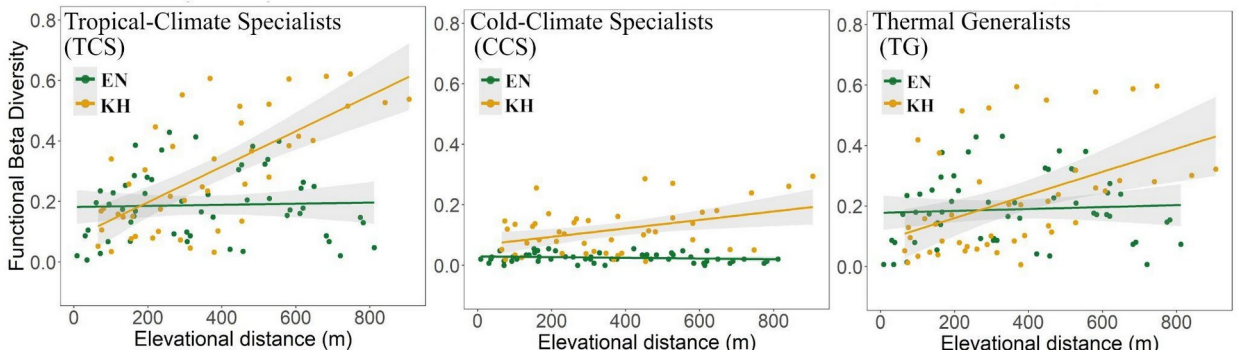


Figure 5.9: Functional beta diversity of individual ant thermal guilds along Eaglenest (EN) and Khupi (KH). Each green and yellow solid circle represent an elevational community in Eaglenest and Khupi, respectively. Green and yellow trend lines are the linear fits showing compositional change within each thermal guild with elevation (1000–2000 m). Abbreviations: TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists.

5.3.5 Phylogenetic signal in guild combinations

The Mantel test revealed a weak positive correlation between phylogenetic distance and functional Gower distance ($r = 0.087$; $p = 0.08$), suggesting weak phylogenetic structuring of the combined functional space (across the three functional axes) at the generic level. Therefore, phylogeny may not have a large influence over the observed elevational responses of ant guilds.

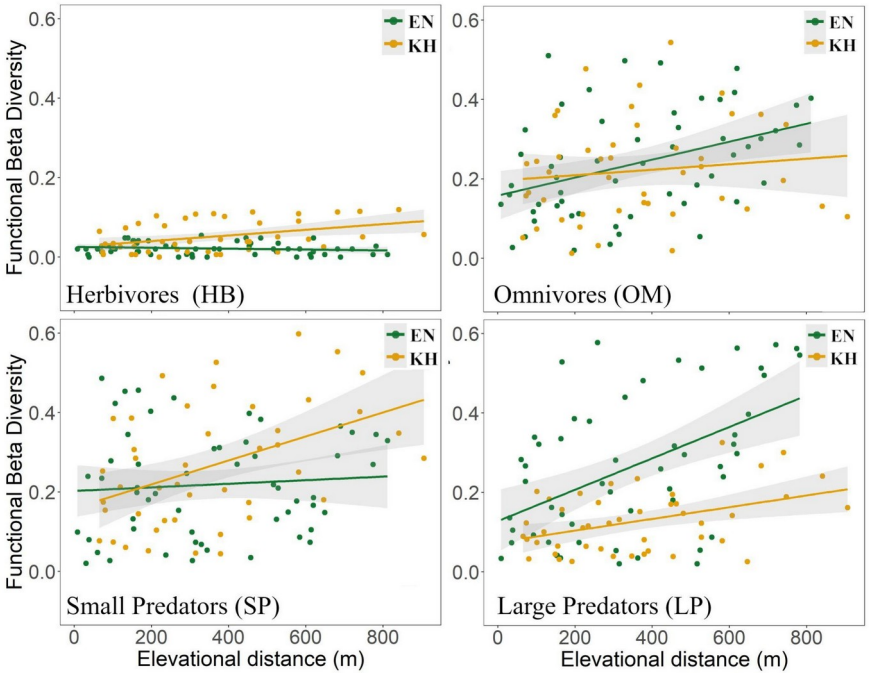


Figure 5.10: Functional beta diversity of trophic guilds along Eaglenest (EN) and Khupi (KH). Each green and yellow solid circle represent an elevational community in Eaglenest and Khupi, respectively. Abbreviations: Abbreviations: HB = herbivore, OM = omnivore, SP = small predator, LP = large predator.

Table 5.8: Elevational functional beta diversity of individual guilds in Eaglenest (EN) and Khupi (KH). The table includes slopes ± SE (per km) and R^2 values for profiles of all 11 guilds. TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders. *($p < 0.1^{*}, p < 0.05^{**}, p < 0.01^{***}, p < 0.001^{****}$).*

Functional axis	Guild	EN Slope ± SE	EN R^2	KH Slope ± SE	KH R^2
Thermal Niche	TCS	0.02 ± 0.07	< 0.01	0.59 ± 0.09****	0.48
	CCS	-0.01 ± 0.03	0.03	0.14 ± 0.03****	0.16
	TG	0.03 ± 0.08	< 0.01	0.38 ± 0.10****	0.22
Trophic Level	HB	-0.01 ± 0.02	0.03	0.07 ± 0.02****	0.17
	OM	0.23 ± 0.07***	0.15	0.07 ± 0.09	0.01
	SP	0.05 ± 0.08	0.01	0.35 ± 0.09****	0.19
	LP	0.42 ± 0.07****	0.29	0.15 ± 0.09*	0.18
Competitive Dominance	DM	0.02 ± 0.07	< 0.01	0.29 ± 0.08****	0.18
	SB	-0.01 ± 0.03	0.03	0.12 ± 0.03****	0.13
	OP	0.13 ± 0.07*	0.05	-0.04 ± 0.08	0.01
	SL	0.09 ± 0.07	0.02	-0.02 ± 0.09	< 0.01

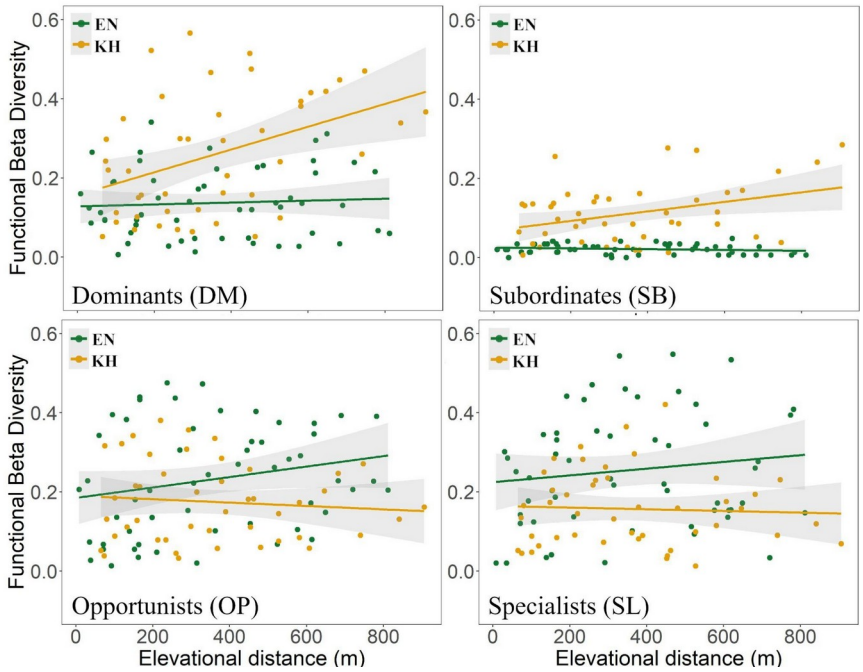


Figure 5.11: Functional beta diversity of each competition guild in Eaglenest (EN) and Khupi (KH). Green and yellow solid circles represent an elevational community in Eaglenest and Khupi, respectively. Abbreviations: DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders.

Table 5.9:Guild-specific beta diversity profiles in Eaglenest (EN) and Khupi (KH). The table includes interaction coefficients (β ± SE) and p values for all 11 ant guilds linked along three functional axes. TCS = tropical climate specialists, CCS = cold climate specialists, TG = thermal generalists; HB = herbivore, OM = omnivore, SP = small predator, LP = large predator; DM = dominants, SB = subordinates, OP = opportunists, SL = specialists/competition avoiders. *($p < 0.1^{*}, p < 0.05^{**}, p < 0.01^{***}, p < 0.001^{****}$).*

Functional axis	Guild	Interaction β	Interaction p
Thermal Niche	TCS	$0.57 \pm 0.11^{****}$	< 0.001
	CCS	$0.15 \pm 0.04^{****}$	< 0.001
	TG	$0.35 \pm 0.12^{***}$	< 0.01
Trophic Level	HB	$0.08 \pm 0.02^{****}$	< 0.001
	OM	-0.16 ± 0.11	0.16
	SP	$0.27 \pm 0.12^{**}$	< 0.05
	LP	$-0.27 \pm 0.11^{**}$	< 0.05
Competitive Dominance	DM	$0.26 \pm 0.10^{**}$	0.01
	SB	$0.13 \pm 0.04^{***}$	< 0.01
	OP	-0.18 ± 0.11	0.11
	SL	-0.11 ± 0.11	0.35

5.4 Discussion

Studies of ant communities across spatial gradients have consistently revealed a large role of microhabitat heterogeneity in influencing functional diversity patterns (Muluvhahothe et al., 2021; Nascimento et al., 2022; Pérez-Sánchez et al., 2023). Recent studies conducted across elevational gradients have shown variability in functional diversity patterns between slopes (Muluvhahothe et al. 2021) and even within elevational bands due to differences in vertical foraging stratum (Leahy et al., 2022), leaf litter depth (Silva et al., 2011) or soil organic and inorganic content (Fichaux et al., 2021; Munyai & Foord, 2012). However, broad-scale environmental factors are expected to dominate across larger spatial spans due to the likelihood of sampling greater environmental heterogeneity (Boet et al., 2020). But, at local scales, the relative contributions of environmental and biotic filters can be highly variable. The steep elevational gradients in the eastern Himalayas compress broad-scale environmental heterogeneity (comparable to a tropic-to-temperate latitudinal extent) over exceptionally short distances. Therefore, both broad-scale environmental filters and fine-scale microhabitat heterogeneity may be reflected in the functional responses of ant communities with elevation.

5.4.1 Change in the relative abundance of guilds with elevation

Thermal Niche Axis

Contrary to our expectations, we found weak structuring of thermal guilds across elevation in Eaglenest. However, along Khupi, tropical-climate specialists reduced substantially towards higher elevations as expected, while thermal generalists and cold-climate specialists dominated at higher elevations. The lack of an elevational response in Eaglenest, despite sampling the same elevational span as Khupi, could suggest the role of other factors in influencing the distribution of thermal guilds. For instance, higher solar radiation (characteristic of south-facing slopes like Eaglenest) may allow continued activity of ant communities at higher elevations and has been linked to the lack of change in the heat tolerance thresholds of terrestrial ectotherms (Sunday et al., 2019)

The response of ant communities to temperature change with elevation can often be complex, with different components of the thermal response (e.g., tolerance and sensitivity) driven by variables such as microclimate and vegetation rather than just elevation. For example, thresholds of heat tolerance (CT_{max}) in ants are correlated with the vertical stratum occupied, while cold tolerance

(CT_{min}) closely tracks elevation (Leahy et al., 2022). A recent study from the Indian subcontinent examining multiple thermal response components (thermal breadth, maximum and minimum tolerance) in arthropod communities (including ants) found that topographic and microclimatic factors were key drivers of thermal responses along two mountain slopes (Khaliq et al., 2025). Therefore, differences in the elevational responses of thermal guilds between Eaglenest and Khupi may reflect substantial contributions of factors other than elevation.

Trophic Level Axis

Differential trophic structuring base has been shown in canopy arthropods that directly depend on the distribution of host trees (Schowalter et al., 2025). However, the evidence for resources differentially influencing trophic structure in ground-dwelling arthropods may be context-dependent.

Communities with trophic groups spanning several trophic levels (herbivores, omnivores, detritivores, predators) have been shown to exhibit similar elevational responses, e.g mid-elevation peak in abundance in Colorado (Uhey et al., 2021). However, this study was conducted in an arid montane system where moisture and temperature severely limited diversity at lower and higher elevations, respectively. Therefore, the convergence in elevational patterns of different trophic guilds may be related to abiotic factors, rather than the distribution of resources on which each guild depends. However, a later study by the same group revealed differences in elevational patterns of trophic guilds spanning all arthropods along forested and open grassland elevational gradients in the same system (Uhey et al., 2022).

We found divergent elevational responses of trophic groups, with a significant decline in the proportion of omnivores at higher elevations in both Eaglenest and Khupi. Predatory ants, on the other hand, increase in proportion at higher elevations in both sites. Carnivory is reported to dominate at higher elevations in ant communities, especially above the tree line, owing to reduced primary productivity (Guariento & Fiedler, 2021). Predatory arthropods tend to have relatively small population sizes (Pilar et al., 2020), which may explain their prevalence and wider elevational ranges in resource-poor higher elevations above the tree line (Uemori et al, 2022). Our study was restricted to forested habitats well below the tree line in the eastern Himalayas. Therefore, we

cannot attribute changes in trophic elevational profiles to large-scale differences in habitats (trees vs. grass). Nevertheless, a similar increase in the proportion of predatory ants has been reported independently along three tropical gradients sampled below the tree line (Moses et al. 2023, but see Binkenstein et al., 2018).

On separating the larger and the smaller predators, we observed an increasing prevalence of the larger genera towards higher elevations in Eaglenest, while the small predators show no significant change. A stacked bar-plot from a previous study in Eaglenest (Marathe et al., 2021) shows the same functional form for small predators but an apparently decreasing abundance profile for the larger species. However, the larger predators showed a significant decrease with elevation in Khupi in our study (like in Marathe et al. 2021), while the proportion of smaller predators increased with elevation. We note that our study showed an increase with elevation of the overall proportion of predators in both Eaglenest and Khupi.

The smaller predators may dominate at higher elevations in Khupi because the available area is relatively limited on approaching the ridge at 2100 m. Besides, smaller body size is linked to smaller range sizes in insects and vertebrates largely due to reduced dispersal abilities (Biedermann, 2003). On the other hand, our transect in Eaglenest terminates 1800 m, much below the ridge located at 3200 m and may therefore support the relatively large ranges that large predators may require. Complexity of vegetation is also known to influence whether larger or smaller arthropods dominate (Stanska et al., 2018). Bottom-up effects such as a reduction in overall arthropod prey abundance may also influence large predatory ants more than smaller predatory ants; the smaller predators are also known to feed on small-sized soil detritivores (e.g. collembola) that remain abundant at high elevations.

Competitive Dominance Axis

We found no change in the proportion of competitive guilds with elevation in Eaglenest. However, in Khupi, we observed a reduction in the proportion of dominants towards higher elevation as predicted. In turn, subordinates increased in relative abundance at higher elevations. We note that despite the increase in proportion the subordinates remained a smaller proportion of each community at all elevations.

Differing responses and other compensatory factors may weaken competition, thereby allowing subordinates to survive or even replace dominants (Arnan et al., 2018). Studies have reported mixed patterns regarding the relative proportion of dominants along productivity gradients, with some reporting a decline in sites with lower productivity (Guariento & Fiedler, 2021) and others an increase (Arnan et al., 2018). Dominant ant taxa in the Mediterranean possess much lower thermal tolerances compared to subordinates, enabling the latter to flexibly increase foraging times both daily and seasonally to avoid direct competition (Retana & Cerdá, 2000; Boet et al., 2020). Besides, a lack of access to carbohydrate-rich diets at higher elevations (otherwise abundant at lower elevations) has been linked to reduced activity and aggression of dominants (Contala et al., 2024). The dominance-discovery tradeoff suggests that subordinate groups have faster resource discovery rates but perform poorly at defending them, while dominants are slower at discovery but aggressive at defense (Fellers, 1987; Pearce-Duvet et al., 2011). Other factors such as microhabitat complexity, presence of parasitoids and levels of disturbance or invasion, have been shown to favour subordinates (Parr & Gibb, 2017).

Another explanation for the reduction in the preponderance of dominants at the highest elevations in Khupi is related to its lower diversity. The dominance–diversity hypothesis predicts a reduced occurrence of dominant groups in low-diversity communities (Whittaker, 1965). A global analysis in ant communities confirms the predictions of the dominance-diversity rule in native ant communities (Arnan et al. 2018).

5.4.2 Relationship between guild and taxonomic alpha diversities

Functional and taxonomic diversity form complementary axes of biodiversity and may respond differently to environmental and biotic filters along elevational gradients (Nunes et al., 2016; Zhao et al., 2022). Studies have revealed contrasting patterns: both congruence and decoupling of this association across taxa and habitats (Swenson, 2011). Contrary to our expectations of congruency under the niche complementary hypothesis, we observed no association between functional alpha diversity and taxonomic alpha diversity along both Eaglenest and Khupi. While generic diversity changed across the elevational gradient **(Figure 3.3)**, **Figure 5.7** shows that functional diversity (Rao’s Q) is independent of the taxonomic diversity index. This suggests functional redundancy in

communities with high diversity i.e., functional space does not shrink even as taxonomic diversity reduces.

Functional redundancy has been documented in multiple insect groups (Cardoso et al., 2011; Mori et al., 2015; Nunes et al., 2016; Castro et al., 2020), plants (de Bello et al., 2017; Wang et al., 2025) and bats (Cisneros et al., 2014). On the other hand, some studies have reported a positive correlation between functional and taxonomic diversity in mammals (Chakravarty et al., 2021; Kohli et al., 2022) and birds (Dehling et al., 2014; Pernice et al., 2025).

Microhabitat complexity and spatial scale can modify the relationship between functional and taxonomic diversity along elevational gradients. In ant montane communities of South Africa, taxonomic and functional diversity responded to different environmental factors and exhibited a weak association with each other (Muluvhahothe et al. 2018). Taxonomic diversity was more influenced by large-scale macroclimatic factors such as seasonality, while functional diversity was driven by small-scale microhabitat differences between the northern and southern slopes. However, the strength of the association between the two diversity facets depends on the spatial scales at which they are measured. At the local microhabitat level, functional diversity has been shown to correlate positively with taxonomic diversity in spider communities (Cardoso et al. 2011). However, this relationship weakens at larger spatial scales, which may suggest the role of several other factors that differentially influence these two complementary facets of diversity.

We observed no difference in the overall functional diversity between Eaglenest and Khupi. This may be due to the coarse resolution at which we measured both functional and taxonomic diversity. We quantified functional diversity along three trait axes at the generic level. The low taxonomic resolution in our study may limit our ability to capture sufficient functional and taxonomic variation within communities and across elevation. Investigators have cited multiple reasons for weaker changes in functional diversity across geographic and environmental gradients relative to taxonomic diversity (Graco-Roza et al., 2022; Teittinen & Virta, 2021). Most datasets naturally measure fewer traits than the number of species recorded. Hence, taxonomic composition inherently appears more diverse than functional diversity. The resolution and type of trait measured, along with differing challenges of measuring traits across taxa, compounds these issues. Furthermore, only a limited set

of all mathematically possible trait combinations is biologically viable or “fit” enough to pass through dispersal, environmental and biotic filtering mechanisms that assemble communities. Therefore, in most communities, it is more likely that we observe functional redundancy due to a combination of both methodological and biological constraints.

5.4.3 Guild-specific and composite functional beta diversity

As expected, we observed an increase in total functional beta diversity with elevational distance in both Eaglenest and Khupi. The magnitude of change in total functional beta diversity and its components were similar along both mountain slopes. Turnover accounted for 88% of the total functional beta diversity, with a smaller contribution from nestedness **(Figure 5.8).** Previous studies on ant communities have shown substantial contributions from both functional turnover and nestedness to the total functional beta diversity (Bishop et al., 2015; Nunes et al., 2020). Other studies found greater functional nestedness at higher elevations, attributing it to the filtering by harsher climate at higher elevations, while competition and niche specialisation may encourage greater functional turnover at lower elevations (Machac et al., 2011; LaManna et al., 2022). Nevertheless, these contributions are known to shift across elevation in ant communities depending on the sampling season (Nunes et al. 2020).

Several studies have examined multi-trait (composite) functional beta diversity along elevational gradients and have compared them to individual trait- or guild-specific patterns. (Swenson, 2011; Binkenstein et al., 2018; Bishop et al., 2015; Ding et al., 2019). Examining guild-specific responses allows us to identify traits or functions that dominate community assembly across elevation, which may be obscured in composite trends that may average opposite trends or include unresponsive traits. In our study, individual guilds differed substantially in composition with increasing elevational separation, even though the composite response was moderate in both Eaglenest and Khupi. Nonetheless, some studies find convergence in the elevational responses of multiple traits, which is also reflected in the composite trends (Read et al., 2014; Ding et al., 2019).

We found an increase in the prevalence of predatory ants in both Eaglenest and Khupi. However, this increase was driven by only large predators in Eaglenest, whereas both small and large predators contributed, albeit unevenly, to the signal in Khupi. Lumping different guilds from the

same taxon can result in incorrect conclusions regarding elevational patterns of functional traits. In the neotropics, Mancini et al., (2019) reported that understory bats, but not open-space bats, contributed to the composite increase in body mass with elevation. On the other hand, open-space bats were responsible for an increasing elevational trend in wing-span, with no contribution from understory bats. The net result was a moderate change in body mass and wing-loading for the bat community.

Divergent elevational responses among individual guilds may reflect the differing selection pressures acting on each. Pollinator communities of wasps increased in body size and reduced seasonal duration of activity at higher elevations due to greater sensitivity to thermal (abiotic) stress and resource constraints. However, predatory wasps showed no such change in activity across seasons (Uemori et al., 2022). The composite pattern of functional beta diversity where pollinator, predatory and parasitoids were examined as a unit showed no elevational association, despite clear elevational trends within each of the three guilds. Not only did we find contrasting responses among individual guilds along the elevational gradient, we also noted differences in both the proportion and strength of responses between the two mountain slopes. In contrast to our findings, Muluvhahothe et al. (2018) find differences in composite functional beta diversity between the north- and south-facing slopes in South Africa. But this study did not examine the individual (trait-specific) responses of the seven morphological traits measured. Therefore, it is unclear which traits respond most sensitively to microhabitat differences between the two slope aspects, or even, what proportion of traits respond along each slope.

Only a subset of traits may drive functional beta diversity patterns across elevation. In our study, seven out of eleven guilds contributed substantially to the composite functional beta diversity pattern in Khupi, while only two guilds (omnivores and large predators) in Eaglenest had comparable beta diversity profiles. A recent study in elevational spider assemblages found an increase in the functional beta diversity at higher elevations. However, only two traits (body size, ballooning frequency) out of several morphological and behavioral traits examined contributed to the total change in functional composition between low and high elevation assemblages (Malumbres-Olarte et al. 2025). In freshwater communities, traits related to dispersal may be the primary drivers of divergent beta diversity profiles (Jamoneau et al., 2022). Another study that

examined functional beta diversity in relation to foraging, reproduction and life-history of Andean birds found only a few traits relating to elevational range size, migration and nesting sites correlated with elevational differences in the functional composition of communities (Altamirano et al., 2020). In fact, multivariate (composite) functional beta diversity patterns may be dominated by a few evolutionary labile traits as revealed in plant communities of the Swiss Alps (Ndiribe et al., 2014). Leaf traits that drove functional turnover showed low phylogenetic signals, reinforcing the notion that assembly processes may often act directly on specific trait combinations (ecology) rather than on lineages (phylogeny).

5.4.4 Role of microhabitat complexity and topography

Microclimatic and topographic factors can serve as crucial filters that select for specific functions in communities, leading to differing elevational trait responses along similar macroclimatic spans. In a temperate montane system, understory microclimatic variation within just 59 m of elevational gradient paralleled the temperature gradient across ~2.7° of latitude (McNichol et al., 2024). To provide context, the complete latitudinal span of Arunachal Pradesh is approximately 3°. While microclimatic variability is not well measured in tropical systems (but see Jia et al. 2024), we can perhaps expect comparable, if not finer, microclimatic variability in the latter.

In seasonally dry tropical forests of Central America, elevation rather than slope aspect, contributed to greater dissimilarity in the functional strategies of trees at higher elevations in response to greater fluctuation in water availability (Méndez-Toribio et al., 2017). Trees inhabiting drier slopes produced heavier seeds (greater desiccation tolerance) than light-seeded trees on wetter slopes (X. Tang et al., 2025). Functional traits in soil invertebrates, like Collembola, were found to be influenced by differing moisture regimes across slopes, with drier slopes fostering greater variability in body size of springtails compared to more humid slopes (Hishi et al., 2022). While traits related to desiccation tolerance may be linked to microclimatic conditions, other traits such as tree height may respond to macroclimatic conditions. Shorter trees, reflecting conservative growth strategies, are known to dominate at higher elevations to survive cold stress and strong winds (Apaza-Quevedo et al., 2015; Báez et al., 2022; L. Tang et al., 2022). However, in the Western Himalayas and Western Ghats, plant height and specific leaf area differ more between slope aspects, rather than with elevation (Thakur & Chawla, 2019; Maheshwori et al., 2025). Therefore,

differences in the sensitivity of traits to microclimate and macroclimate warrants further investigation.

In our study, eight of eleven guilds exhibited differing abundance and compositional profiles between Eaglenest and Khupi. While some studies have shown disproportionate contributions of individual traits to dissimilarity, few have explicitly examined the role of differing contexts (topographic and microclimatic) in the variability in the contributions of individual trait responses to the total functional beta diversity (Lajoie & Vellend, 2015; Spasojevic et al., 2016).We show pronounced differences in the proportion and identity of guilds that contribute towards similar composite beta diversity patterns. More guilds (7 of 11) exhibit a stronger response with elevation in Khupi compared to Eaglenest (2 of 11). Even between different sampling years, there may be notable differences in the responses of guilds which requires further investigation. A study conducted a decade earlier in Eaglenest reported similar relative abundance profiles for small (cryptic) predators as our study, but not for large (specialised) predators. On the other hand, the proportional decrease in large (specialised) predators along another mountain slope (Khupi) resembled the pattern previously reported from Eaglenest (Marathe et al., 2021).

Ant colonies, with largely fixed nesting sites, behave similarly to sessile plants (Andersen et al. 1995, and both are known to respond more sensitively to microclimatic filters compared to mobile mesofauna (Barton et al., 2024; Heydari et al., 2021). Therefore, it is important to elucidate the role of microclimatic heterogeneity in shaping diversity patterns of ant communities across varying spatial scales.

5.5 Conclusion

Exploring whether and how communities segregate functionally along elevational gradients provides insights on the role of environmental factors and resources availability in influencing assembly patterns. By examining elevational functional diversity patterns between slopes, we highlight the importance of both broad-scale climatic and small-scale microclimatic differences producing the variable responses of trophic, thermal and competitive guilds. Our results underscore the necessity of accounting for local factors while assessing the generality of ecological processes governing community structure and function in (especially topographically complex) montane ecosystems.

Concluding Remarks

Montane landscapes, with their complex topography and climatic gradients, provide a great system to evaluate the role of environmental and geographic factors that govern distributional patterns. Our investigations in a globally important biodiversity hotspot showed that elevation-driven patterns can be modified other factors: landscape topography and associated microclimatic variables. Crucially, the observed contributions of macroclimatic and microclimatic factors differed depending on the facet of diversity examined and the scale of investigation.

Studies of elevational gradients have either focused on single transects within a region, or mixed distinct elevational communities from different mountain slopes. These studies have been essential to understand the role of macroclimatic factors (closely linked to elevation) in driving richness and compositional turnover of communities. However, the complex terrain of montane landscapes can modify local climatic conditions, influencing floral and faunal distribution between neighbouring slopes. Plants and ground-dwelling arthropods are especially known to respond sensitively to localised changes in climate.

The principal drawback of this study was the absence of species-level identity of ants, in large part due to constraints of time (due to Covid lockdown) and due to the large sample of ants that we obtained in this rich landscape. This is the obvious issue that needs to be remedied. Many taxa remain undescribed from eastern Himalayas, even for a family like ants that are relatively better described at the global scale. Improved tools and aids to species identification of the lesser known taxa will help in building a more comprehensive understanding of the ant fauna in the region.

Our study of ant communities from two mountain slopes differing in aspect, inclination and elevational limits revealed the importance of microhabitat in determining ant community composition in both taxonomic and functional space. This is especially vital while studying ectotherms or life forms with limited dispersal. Future investigations could measure multiple abiotic climate variables at each sampled quadrat to capture microhabitat-level changes within and across elevation. In general, slopes across a mountain range will differ from each other in multiple topographical attributes. Teasing them apart will not always be easy finding accessible slopes which differ in just one or two topographic variables is a challenge.

Investigating responses of multiple taxa can help in elucidating general mechanisms that shape diversity, independent of taxon-specific mechanisms. This study, along with previous studies from the research group, show that certain features of observed patterns remain unchanged across different taxa, while other features differ. Sampling multiple taxa across seasons would reveal whether shared (similar) patterns between differing taxa (e.g. moths and ants) are temporally stable and generalisable across different seasons. There is evidence to suggest that ants respond to seasonality, exhibiting differences in beta diversity patterns and contributions of turnover/nestedness (Nunes et al., 2020). Therefore, examining phenology and the role of seasonality in ants would additionally reveal how they respond to changes across temporal (annual) scales.

Interpreting these shared and divergent responses along various facets of diversity (taxonomic, functional, phylogenetic) would help reveal key drivers of distributional patterns in communities. Integration of phylogenetic diversity into functional frameworks will lead to a better understanding of the relative roles of environmental filtering and competitive exclusion. Functional frameworks can be further improved by measuring individual and colony-level traits as recommended by the Global Ants Database (Gibb et al., 2017), though measuring colony-level traits would require a lot of resources in that terrain. Associating functional guilds to ant taxa, even at the generic level, also requires a lot more of work, throughout the Indian subcontinent. Building and integrating trait, phylogenetic and natural history information is a necessary next step towards understanding the assembly and function of faunal and floral communties. This is especially crucial in the Himalayan region, a highly biodiverse yet sparsely documented part of the world.

APPENDIX I

Key to subfamilies of ant genera from Arunachal

There are ten subfamilies of ants reported from India. The key below allows for identification of nine subfamilies reported in Arunachal with a brief note on the tenth subfamily, Leptanillinae.

1a. Single reduced segment between mesosoma and gaster (Fig A01) 2
1b. Two reduced segments between mesosoma and gaster (Fig A02) 10

2a. Front and top face of petiole distinct with rear face fused to front face of gaster through most of its length; at most a shallow impression between the two (Fig A03) 3
2b. Petiole with distinct front & rear faces at the very least 4

3a. Second gastral tergite strongly convex; gastral apex almost pointing forward (Fig A04) ..... part Proceratiinae
3b. Second gastral tergite is only slightly curved ..... Amblyoponinae

4a. A distinct impression (even if slight) between the first and second gastral segment (Fig A05) 5
4b.Gaster outline uniform (Fig A06) 8

5a. Pygidium flattened with a row of setae ..... part Dorylinae
5b. Pygidium rounded without setae 6

6a Frontal lobes highly reduced/absent with antennal sockets fully exposed (Fig A07) ..... part Proceratiinae
6b. Frontal lobes expanded; at least partially covering the antennal insertions (Fig A08) 7

7a. Prora present (Fig A09). Coxae of hind leg with tooth (Fig A10) ..... Ectatomminae
7b. Prora absent (Fig A11) ..... part Ponerinae

8a. Mandibles long and placed largely parallel to each other from base to apex (Fig A12) ..... part Ponerinae
8b. Mandibles sub-triangular (Fig A13) or elongate triangular (Fig A14) 9

9a. Abdominal apex with a circular (acidopore) opening fringed with hair ..... Formicinae
9b. Abdominal apex with a slit-like opening; never fringed with hair ..... Dolichoderinae

10a. Frontal lobes absent (Fig A07). Eyes absent or reduced to a single ommatidium ..... part Dorylinae
10b. Frontal lobes may be present. Eyes are always conspicuous 11

11a. First thoracic segment flexibly articulating with second thoracic segment (Fig A15). Median portion of the clypeal area not extending in between antennal sockets (Fig A17) ..... Pseudomyrmicinae

11b. First thoracic segment fused with second thoracic segment (Fig A16). Median portion of the clypeal area extending in between antennal sockets (Fig A18) ..... Myrmicinae

Note on Leptanillinae: 12-segmented antenna with both petiole and post petiole. Species are usually less than 3 mm and resemble small myrmicines except antennal insertions are completely exposed.

Key to ant genera of Arunachal Pradesh

Subfamily: Formicinae

1a. Mandibles slender and blade-like; almost as long as the length of the head (Fig A19) ..... *Myrmoteras*

1b. Mandibles subtriangular 2

2a. Antennal sockets situated close to the posterior clypeal margin (Fig A20) 3

2b. Antennal sockets well behind the posterior clypeal margin (Fig A21) 5

3a. Maxillary palps 2-4 segmented ..... *Pseudolasius*

3b. Maxillary palps 6-segmented 4

4a. Setae on head and mesosoma distinctly paired (Fig A22) ..... *Nylanderia*

4b. Setae on head and mesosoma not distinctly paired ..... *Lasius*

5a. Petiole is low with a rounded dorsal face (Fig A23) ..... *Oecophylla*

5b. Petiole is distinct and upright (Fig A24) 6

6a Pair of spines present on the petiole and usually on the mesosoma (Fig A25) ..... *Polyrhachis*

6b. Spines absent on the petiole and the mesosoma ..... *Camponotus*

Subfamily: Ponerinae

1a. Mandibles long and placed largely parallel to each other from base to apex (Fig A12) 2

1b. Mandibles elongate triangular (Fig A13) or subtriangular (Fig A14) 3

2a. Posterior margin of the head curves inwards medially forming a crease down the centre of the head (Fig A26) ..... *Odontomachus*

2b. Posterior margin of the head forms a continuous arc medially. Crease lines absent (Fig A27) ..... *Anochetus*

3a. Metatibia with a single pectinate spur (Fig A28) 4
3b. Metatibia with a large pectinate spur and a smaller simple spur (Fig A29) 6

4a. Mandibles elongate-triangular (Fig A13) ..... *Emeryopone*
4b. Mandibles sub-triangular (Fig A14) 5

5a. Subpetiolar process with a sharp posteroventral angle and an anterior fenestra (Fig A30) ..... *Ponera*
5b. Subpetiolar process without a sharp posteroventral angle or an anterior fenestra (Fig A31) ..... *Hypoponera*

6a Pretarsal claws of hind legs pectinate (Fig A32) ..... *Leptogenys*
6b. Pretarsal claws of hind legs simple (Fig A33) 7

7a. Petiole armed dorsally with a pair of spines (Fig A34) ..... *Diacamma*
7b. Petiole unarmed (Fig A35) 8

8a. Petiolar scale notched (Fig A36) ..... *Odontoponera*
8b. Petiolar scale not notched 9

9a. Propodeal spiracle small and round (Fig A37) ..... *Brachyponera*
9b. Propodeal spiracle slit-shaped (Fig A38) ..... *Ectomomyrmex*

Subfamily: Myrmicinae

1a. Post petiole attached to dorsal face of first gastral segment (Fig A39) ..... *Crematogaster*
1b. Post petiole attached to the anterior face of the gaster (Fig A40) 2

2a. Antennal scrobe running below the eye (Fig A41) ..... *Catalaucus*
2b. Antennal scrobe absent or running above the eye (Fig A42) 3

3a. Antenna with 4-6 antennal segments ..... *Strumigenys*
3b. Antenna with 8-12 antennal segments 4

4a. Median portion of clypeus concave and bidentate (Fig A43) ..... *Mayriella*
4b. Median portion of clypeus nor armed 5

5a. Antenna with 2-segmented club (Fig A44) 6
5b. Antenna with a 3- (Fig A45) to 4-segmented club or without a club 7

6a Minor workers: Head distinctly rectangular with 10 segmented antennae ..... *Solenopsis*
6b. Minor workers: Head not rectangular ..... *Carebara*

7a. Antenna with 11 segments 8
7b. Antenna with 12 segments 15

8a. Head below eye with a longitudinal ridge distinguishable from background (Fig A46) ..... *Myrmecina (in part)*
8b. Head below the eye without a longitudinal ridge (Fig A47) 9

9a. Antennal sockets fully exposed. Clypeal margin with ≥ 3 denticles (Fig A48) ..... *Pristomyrmex*
9b. Antennal sockets partially or fully concealed. Anterior clypeal margin with 0-2 denticles 10

10a. Lateral portion of clypeus sharply raised in front of antennal sockets (Fig A49) ..... *Tetramorium (in part)*
10b. Lateral portion of clypeus in front of antennal sockets not raised (Fig A50) 11

11a. Posterodorsal margin of the petiole forms a rim (Fig A51) ..... *Vollenhovia (in part)*
11b. Posterodorsal margin of the petiole does not form a rim 12

12a. Anterior margin of clypeus with a single long seta at the midpoint ..... *Monomorium (in part)*
12b. Anterior margin of clypeus without a single long seta at the midpoint 13

13a. Anterolateral corners of pronotum sharply defined (Fig A52). Mandible with two teeth, a large denticle and a series of small denticles (Fig A53) ..... *Lophomyrmex*
13b. Anterolateral corners of pronotum undefined 14

14a. Median clypeal carina absent. Antenna 11-segmented ..... *Leptothorax*
14b. Median clypeal carina absent/present; antennae 12-segmented. A single species from the region (Korea) possesses 11-segmented antennae; but with carinate clypeus ..... *Temnothorax (in part)*

15a. Head below eye with a longitudinal ridge distinguishable from background (Fig A54) 16
15b. Head below eye without a longitudinal ridge distinguishable from background Fig A47) 17
16a. Longitudinal ridge not touching the eye (Fig A46). Petiole sessile (Fig A55) ..... *Myrmecina (in part)*
16b. Longitudinal ridge touching the eye (Fig A54). Petiole stalked (Fig A56) ..... *Vombisidris*

17a Lateral portion of clypeus sharply raised in front of antennal sockets (Fig A49) ..... *Tetramorium (in part)*
17b. Lateral portion of clypeus in front of antennal sockets not raised (Fig A50) 18

18a. Middle portion of the masticatory margin edentate (Fig A57) ..... *Pheidole* (major worker
18b. Middle portion of the masticatory dentate 19

19a. Posterodorsal margin of the petiole forms a rim (Fig A51) ..... *Vollenhovia (in part)*
19b. Posterodorsal margin of the petiole does not form a rim 20

20a. Propodeal spines absent (Fig A58) ..... *Monomorium (in part)*
20b. Propodeal spines present as either tiny denticles or more well developed (Fig A59) 21

21a. Masticatory margin with 5-6 teeth ..... *Temnothorax (in part)*
21b. Masticatory margin with 7 or more teeth 22

22a. Masticatory margin with 1-3 denticles between preapical and 3rd large tooth (Fig A60) ..... *Pheidole* (minor)
22b. No denticles between the preapical tooth and 3rd large tooth (Fig A61) ..... *Aphaenogaster*

Subfamily: Dorylinae

The 2021-2022 ant dataset from Arunachal has Ooceraea and Cerapachys. However, the key includes three other genera from Arunachal Pradesh which are Aenictus, Parasyscia and Syscia. Few other genera have been reported from geographically proximal regions such as Sikkim and Yunnan province of China. However, they have been excluded from this key for simplicity.

1a. Scale of petiole greatly reduced with an overhanging abdomen (Fig A68) 1
1b. Scale of petiole with a prominent front and rear face without an overhanging abdomen (Fig A69) 2

2a. Five gastral segments visible in dorsal view ..... *Technomyrmex*
2b. Four gastral segments visible in dorsal view ..... *Tapinoma*

3a. Dorsal and rear faces of the propodeum meet at a sharp angle (Fig A70) 4
3b. Dorsal and rear faces of the propodeum rounding into each other (Fig A71) 5
4a. Petiole dorsolaterally flattened (Fig A72) ..... *Ochetellus*
4b. Petiole not dorsolaterally flattened (Fig A73) ..... *Dolichoderus*

5a. Eyes placed at mid-length of head (Fig A74) ..... *Iridomyrmex*
5b. Eyes placed below mid-length of head (Fig A75) ..... *Philidris*

Subfamily: Dolichoderinae

India has reported eight ant genera from this subfamily. However, without adequate description from the Indomalayan region with the last key made in 1903, this key is restricted to six genera for which there was some reliable morphological information.

1a. Scale of petiole greatly reduced with an overhanging abdomen (Fig A68) 1
1b. Scale of petiole with a prominent front and rear face without an overhanging abdomen (Fig A69) 2

2a. Five gastral segments visible in dorsal view ..... *Technomyrmex*
2b. Four gastral segments visible in dorsal view ..... *Tapinoma*

3a. Dorsal and rear faces of the propodeum meet at a sharp angle (Fig A70) 4
3b. Dorsal and rear faces of the propodeum rounding into each other (Fig A71) 5

4a. Petiole dorsolaterally flattened (Fig A72) ..... *Ochetellus*
4b. Petiole not dorsolaterally flattened (Fig A73) ..... *Dolichoderus*

5a. Eyes placed at mid-length of head (Fig A74) ..... *Iridomyrmex*
5b. Eyes placed below mid-length of head (Fig A75) ..... *Philidris*

Subfamily: Amblyoponinae

The key below allows identification of all four genera, from this subfamily, that have been reported in India.
1a. No gap between inner margins of mandibles and anterior clypeal margin (Fig A76) ..... *Prionopelta*
1b. Gap between inner margins of mandibles and anterior clypeal margin 2

2a. Apex of mandible round (Fig A77) ..... *Mystrium*
2b. Apex of mandible sharp (Fig A78) 3

3a. Frontal lobes projected anteriorly to form anteromedial portion of the head (Fig A79) ..... *Myopopone*
3b. Frontal lobes not forming the anteromedial portion of the head (Fig A80) ..... *Stigmatomma*

Subfamily: Proceratiinae

1a. Sternite of second gastral segment not reduced and clearly visible in lateral view with abdomen not distinctly curved downwards and apex pointing posteriorly (Fig A81) ..... *Probolomyrmex*

1b. Sternite of the second gastral segment highly reduced and slightly visible in lateral view with abdomen strongly curved downwards and apex pointing anteriorly (Fig A82) 2

2a. Apical antennal segments strongly bulbous ..... *Discothyrea*

2b. Apical antennal segments large but not strongly bulbous ..... *Proceratium*

I have not included identification keys for Ectatomminae and Pseudomyrmicinae since each consists of a single genus, *Stictoponera* and *Tetraponera* respectively, in India.



Fig A01



Fig A02



Fig A03



Fig A04



Fig A05



Fig A06



Fig A07

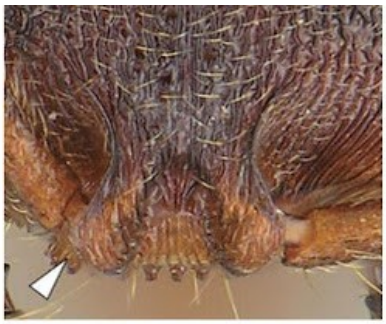


Fig A08

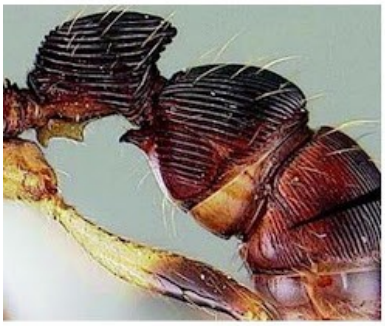


Fig A09



Fig A10



Fig A11



Fig A12



Fig A13



Fig A14



Fig A15



Fig A16



Fig A17



Fig A18



Fig A19



Fig A20



Fig A21



Fig A22



Fig A23



Fig A24



Fig A25



Fig A26



Fig A27



Fig A28



Fig A29

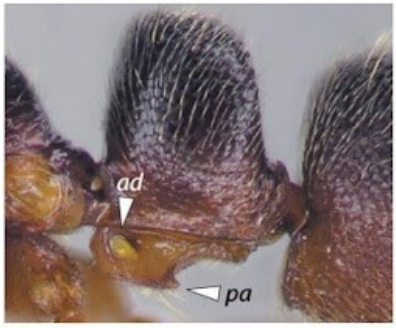


Fig A30



Fig A31



Fig A32



Fig A33



Fig A34

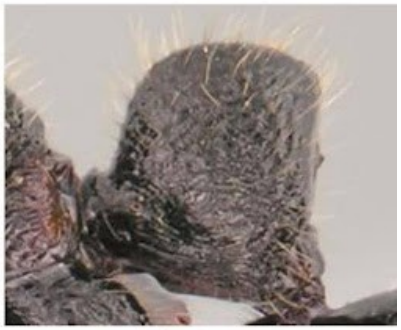


Fig A35



Fig A36



Fig A37



Fig A38



Fig A39



Fig A40



Fig A41



Fig A42



Fig A43



Fig A44



Fig A45



Fig A46



Fig A47



Fig A48



Fig A49



Fig A50



Fig A51





Fig A52

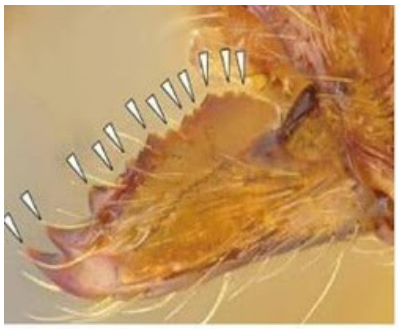


Fig A53



Fig A54

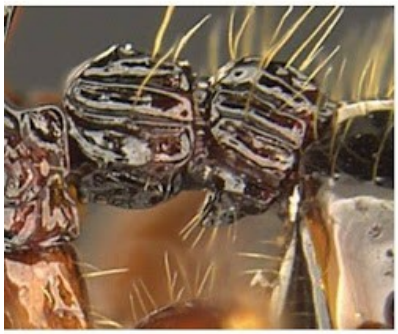


Fig A55



Fig A56

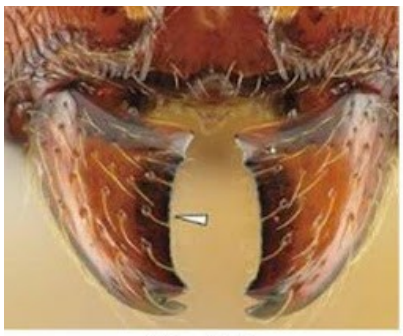


Fig A57



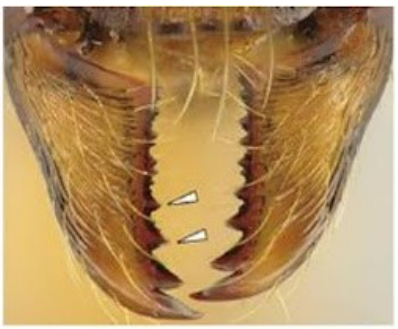
Fig A58



Fig A59



Fig A60



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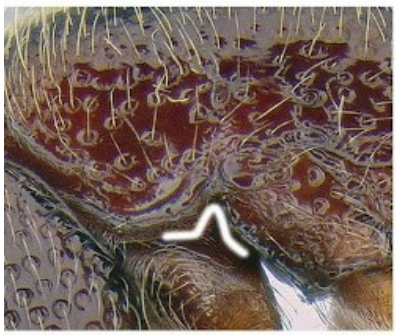


Fig A62



Fig A63

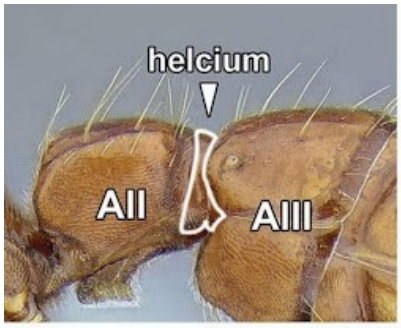


Fig A64

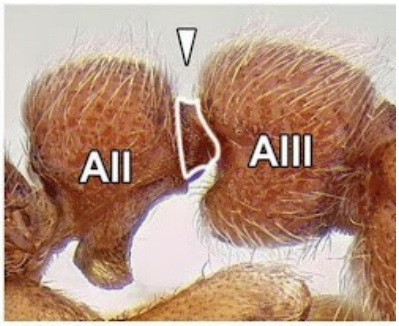


Fig A65



Fig A66



FigA67



Fig A68



Fig A69



Fig A70



FigA71



Fig A72



Fig A73



Fig A74



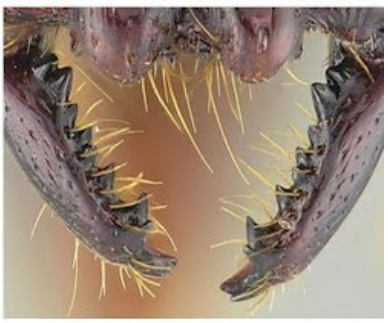
FigA75



Fig A76



Fig A77



FigA78



Fig A79



Fig A80

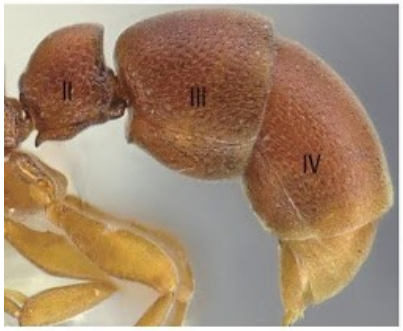
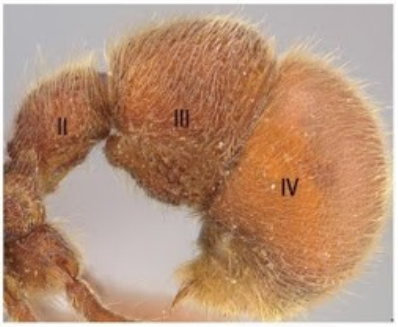


Fig A81



FigA82

APPENDIX II

Ant morphometry

Species concepts and species delimitation refer to the theoretical and operational definitions of species respectively (Queiroz et al. 2007). The aim of species delimitation is to determine the species boundaries given a group of individuals using multiple lines of evidence.

I have generated morphological and genetic data (1.5 kb mtDNA) for three ant genera which can be used for species delimitation. In this section, I shall discuss how the morphological data was obtained.

We chose ant genera based on two criteria:

1. Total body length equal to or greater than 4 mm. Larger ants for better PCR success of barcoding genes.
2. Occupies most of the elevational gradient in at least Eaglenest or Khupi, if not both sites. Greater morphological variation expected on sampling a larger environmental gradient.

Based on these two criteria and the resources available (time and funds), we narrowed down to three ant genera — *Odontomachus*, *Stictoponera* and *Aphaenogaster*.

One individual per quadrat was imaged using Radical Scientific RSM-9A. Each specimen was placed laterally in a shallow groove on an acrylic-based platform, with its head on the left side and the abdomen on the right side when viewed from the top. Using a pair of forceps, one of each leg was carefully removed without damaging or deforming the ant. Similarly, a single antenna and mandible were removed. Each of the five appendages were carefully placed on the hook-like surface of white velcro that could be rotated along a longitudinal axis. Along with the appendages, other body parts of each ant individual were measured in the lateral, dorsal and full-face view. A grid sheet of 1.0 mm resolution was placed in the background for scaling.

The specimen and the calibration grid were imaged at the same magnification. Since it was not possible to place the specimen and the grid at the same distance from the lens, the focal length was

adjusted between images to bring each into focus. This ensured that both the specimen trait and the grid images were acquired at identical scale, allowing the grid image to be used for accurate scaling of the specimen trait image. Dimensions of all images taken were 640 × 480 pixels.

All images were renamed to include information regarding the genus, the unique specimen identifier, whether it was a grid image or a trait image and the name of the trait, if latter. I created a csv file with two columns consisting of the file names of the trait images alongside corresponding calibration images. I used a python script written by Arjun Dhati, a project student in the lab, to output the scale for each trait image based on its calibration (grid) image. The script placed landmarks on intersections of grids on the calibration image and measured all pairwise distances, including diagonal distance, between these landmarks in pixel units. I sorted all outputted pairwise distances and set a filter to include only distances less than 1.4 of the smallest distance. These lengths correspond to 1.0 mm. The average of the filtered lengths was considered the scale(px/mm) of each trait image.

The number of landmarks needed for each trait was predefined in an R script, along with the landmarks required for estimating linear and area measurements. For each genus, images of each trait were digitized in a singlebatch using the same landmark configuration to maintain consistency across specimens of a given genus. The measurements for a representative subset of trait images were manually verified using GIMP, an image editingsoftware. For images where the discrepancy in measurement was more than 10%, landmarks were re-selected. The script ensured that image-specific scale obtained from the python script was used to convert all measurements from pixels to mm.

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CHAPTER 1

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CHAPTER 4

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CHAPTER 5

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