The Effect of Selective Logging and Climate Change on Understory Bird Communities

A Thesis
submitted to
Indian Institute of Science Education and Research Pune in partial fulfilment of the requirements for the BS-MS Dual Degree Programme

by

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Date: April, 2026

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From May 2025 to Mar 2026

INDIAN INSTITUTE OF SCIENCE EDUCATION AND RESEARCH PUNE

Certificate

This is to certify that this dissertation entitled "**The Effect of Selective Logging and Climate Change on Understory Bird Communities**" towards the partial fulfilment of the BS-MS dual degree programme at the Indian Institute of Science Education and Research, Pune represents study/work carried out by Saranya Sundar at Center for Ecological Sciences, Indian Institute of Science, Bengaluru under the supervision of Dr. Umesh Srinivasan, Assistant Professor, Center for Ecological Sciences, Indian Institute of Science, during the academic year 2025-2026.

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This thesis is dedicated to Siddhesh, who among many other things lured me into joining IISER Pune for the “good food”.

Declaration

I hereby declare that the matter embodied in the report entitled “**The Effect of Selective Logging and Climate Change on Understory Bird Communities** ” are the results of the work carried out by me at the Center for Ecological Sciences, Indian Institute of Science, Bengaluru, under the supervision of Dr. Umesh Srinivasan, and the same has not been submitted elsewhere for any other degree. Wherever others contribute, every effort is made to indicate this clearly, with due reference to the literature and acknowledgement of collaborative research and discussions.

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Abstract

Climate change and anthropogenic land-use change are both processes that threaten natural ecosystems. These global change drivers do not act in isolation, but interact with each other to affect biotic communities in complex ways. This thesis aims to understand how communities respond to the synergistic effects of these global change drivers. Using a trait-based approach, this thesis looks at the responses of climate change and selective logging (extraction of a subset of economically beneficial timber) over a fifteen year period in an avian bird community at a mid-elevation site in the Eastern Himalaya. I compared functional diversity and trait distributions (of traits related to thermoregulation, foraging and diet) between primary and logged forest. In addition, I examined how functional diversity and trait values changed over a fifteen year period, to understand the differential effects of climate change in primary and logged forest. There was no evidence for a significant difference in average functional dispersion between intact and modified habitat although mean functional dispersion was marginally higher in primary forest. In addition, and contrary to expectation, functional dispersion and community-weighted body mass increased over time in logged forest. Increases in functional dispersion in logged forest over time might be because of (a) a decline in functionally similar species because of increased competition (b) upslope range shifts of species from lower elevations to mid-elevations that increases functional diversity at mid-elevations (because low-elevation communities tend to be more functionally diverse that higher elevation communities). An increase in community-weighted body mass could be because of an increase in abundance of a few species driving the increase in body mass at the community level. Similar changes were not observed in primary forest in either functional dispersion or body mass. This indicates that the effects of climate change on the average values and distributions of functional traits are likely not equal across a disturbance gradient; more studies should investigate the effects of climate change and land-use change and how they interact with each other rather than treating these two global change drivers in isolation.

Acknowledgments

I am grateful to many people without whom not only this thesis but also my academic (and personal) journey so far would not have been possible. First, I would like to thank Dr. Umesh Srinivasan for many things but most importantly an open door both literally and metaphorically, for the mentorship that taught me how to be a better scientist, for being understanding on countless occasions and for showing me what it means to be a kind and supportive mentor. I enjoyed my time in this research group, and this is in no small part thanks to all my lab mates Anisha, Kaling, Kunya, Pranav, Sarthak, Soumya and Tarun, some of whom became friends along the way. Thanks for all the ideas and suggestions that helped make this thesis better, for help with anything related to analysis when I was still figuring out how to use R and for always being approachable and entertaining all my little doubts. I also feel obligated to mention that when I first approached Umesh, he gave me the freedom to choose a question of my interest. While this was an exciting prospect, I was a nervous wreck, and Krishna helped me refine my vague, incoherent ideas into a question I finally considered worthy of proposing to Umesh.

This thesis would quite literally be impossible without the wonderful people at Eaglenest – Aman Bhaiya, Dema Di, Dinesh Bhaiya, Kancha Bhaiya, Kanchi Di, Mangal Bhaiya, Micah Bhaiya, Nockte Bhaiya, and Pankey Bhaiya, and many others who collected the data I am currently working on. Hearing the crazy field stories from the lab, I was excited to meet everyone in person and experience Eaglenest firsthand. My time at Eaglenest was short, regardless I made many memories I shall carry with me for the rest of my life. From the constant banter and laughter to the amazing food, the small lessons in Nepali, and even the work, it was all possible because of the people who were extremely welcoming, warm, and gracious. I also learnt field techniques and how the data I was working on was collected, for which I am again grateful to the field staff, who were extremely patient and never made any question seem too small to ask. They taught me so much about fieldwork, possible questions I could ask for a PhD if I were to return there, and life.

Countless mentors have shaped my academic journey so far. I would first like to thank Dr. Anand Krishnan. Very few mentors would let four bumbling undergrads visit the field to explore and come up with questions that interested them. It was during this time that I worked on amphibians for the first time (thanks to Abhijith) and learnt how to ask ecologically relevant questions. I also spent a summer in Prof. Rohini Balakrishnan's lab. Prof. Balakrishnan was always constructive in her criticism, and my time in the lab taught me to be more rigorous in my work. I learnt almost all the basics of programming in Prof. Balakrishnan's lab, thanks to Arpit, who walked me through writing good code (with comments). Lastly, a large part of this thesis is influenced by ideas and concepts I was first introduced to in my ecology courses at IISER, taught by Dr. Deepak Barua. I would also like to thank KVPY for funding.

My five years at IISER, which involved immense personal growth, would not have been possible if not for the wonderful people who surrounded me every single day. Medha – for being there with me through all the highs and lows and providing me a safe space to confide in without the fear of being judged (except when I deserved it). I will forever cherish the small, cute walks around campus that got us through exam seasons, as well as the amazing churro shop that was taken away from us not once, but twice! Berry for being in all my courses with me, supporting me as I figured out my academic niche, and always proofreading my emails (even if it just said, 'Thank you!'). All the "Cheaters": Berry, Chris, Kinjal, Maddy, Medha, Rajat and Vishnu, whose VCs kept me sane during thesis year and for constantly being the voice of reason when I was driving myself insane.

If there were one thing that I could predict with 100% certainty, it would be that when I entered my room after a long day of classes, I would find one of the three unlawful residents of B-914. Adheena, Mugdha, Vaishnavi – thank you for always providing me with a community of people I could laugh and cry with. Another thing I could predict with 100% certainty would be that the only other lawful resident of B-914 would not be in her room. Srijani – for being the best and most understanding roommate one could ask for and for single-handedly making sure I do not end college with a vitamin deficiency.

My time in Bangalore would have been relatively uneventful and unmemorable if not for Neha and Authisha. Thank you for keeping me alive through it all and ensuring every day was the Best Birthday Ever. You folks raised the bar for what I expect from a flatmate a little too high.

From my life before IISER, thank you, Monjima. I may not have been easy to deal with, but you always stuck around and stayed for me. Your openness and empathy for others taught me a couple of things, and I am a more thoughtful person because of it.

Finally, none of this would have been remotely achievable without the unwavering support of my family. Amma and Appa, I do not say this often enough, and I do not think any number of words can capture how indebted I am to you. Thank you for allowing me the space to grow and become the person I am today. As a woman wanting to pursue a career in field ecology, which often involves working in remote places, I can understand the many worries you may have had. Still, I cannot express how grateful I am that it never stopped you from letting me pursue my passion. I truly hope I made you happy. Siddhesh, thank you for always being in my corner, thank you for being the big brother every little sister could only hope for. Through all the fights and quarrels, the only thing I can remember is how much you taught me about life. Times may not have always been easy for you, but you always made sure to be there for me through it all, and for that, I am eternally grateful. My grandparents for not always understanding why I do what I do and why I care about it so much but still being happy and supportive of my choices. No matter where I am, how I am doing, I will always miss home.

Contributions

Contributor name	Contributor role
Saranya Sundar, Dr. Umesh Srinivasan	Conceptualization Ideas
Saranya Sundar, Dr. Umesh Srinivasan	Methodology
Saranya Sundar	Software
Saranya Sundar	Validation
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Dr. Umesh Srinivasan	Investigation
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Saranya Sundar, Dr. Umesh Srinivasan	Writing - review and editing
Saranya Sundar	Visualization
Dr. Umesh Srinivasan	Supervision
Dr. Umesh Srinivasan	Project administration
Dr. Umesh Srinivasan	Funding acquisition

This contributor syntax is based on the Journal of Cell Science CRediT Taxonomy[1].

I declare that the usage of Generative AI in this thesis did not extend beyond what is described in Section 4.6.1 of the 'Guidelines for Generative AI usage at IISER Pune', and accordingly, no attribution is required.

[1] https://journals.biologists.com/jcs/pages/author-contributions

Chapter 1: Introduction

1.1. Climate change in the Anthropocene

The current epoch we are living in is often referred to as the Anthropocene, and is characterised by profound human-induced changes in the earth's biosphere. When this era began is debated, with some believing it started in 1850 (Crutzen & Stoermer, 2021) with the industrial revolution, and some people believing that the anthropogenic effects on global climate long predate the industrial revolution, and had already accumulated substantial effects in the thousand years leading up to 1850 (Ruddiman, 2003). Debates about the start of the anthropocene may not be resolved; however, the adverse impacts of human-induced climate change on global biodiversity and community structure and dynamics that ultimately affect ecosystem functioning are unequivocal (Parmesan & Yohe, 2003; Grimm et al., 2013; Boukal et al., 2019; Nunez et al., 2019). Even in the absence of other global change drivers such as land-use change (LUC), rainfall and temperature trends alone are regarded as one of the key agents that threaten natural ecosystems by changing environmental conditions (McCain & Colwell, 2011; Martay et al., 2016). Understanding the impacts of climate change on biodiversity and ecosystems is imperative in order to be able to conserve and protect species from going completely extinct.

Biodiversity is not evenly distributed across latitudes. The tropics are more speciose, and there are multiple hypotheses for why this is the case (Pianka, 1966). One of the hypotheses is that of climatic stability which states that the tropics are relatively stable in terms of climatic conditions, allowing for higher rates of diversification, lower extinction rates and greater specialisation (Pianka, 1966; Rolland et al., 2014). In addition to this, some evidence exists to support the "out of the tropics" hypothesis, which posits that species generally originate in the tropics and then disperse polewards (Jablonski et al., 2006). The unfortunate reality of the current climate crisis is that the tropics are one of the most vulnerable regions to the warming (Sheldon, 2019). Most species in this region have narrow thermal niches owing to the relatively stable climatic conditions they evolved in (Janzen, 1967; Polato et al., 2018). Therefore, tropical species are not tolerant to extremes in temperature, and many species may not be able to adapt to the changing climate, or track suitable climatic niches through dispersal fast enough (Devictor et al., 2008). This means species will go locally, and potentially globally, extinct in one of the most biodiverse regions in the world, which could have implications for global ecosystem functioning.

Even within the tropics, mountains hold a disproportionate amount of biodiversity (Rahbek et al., 2019). Montane systems often serve as ecological "islands", and therefore, a lot of mountain ranges have a high degree of endemism (Kessler & Kluge, 2008). Most endemic species live sedentary lifestyles with low dispersal abilities and narrow climatic niches that render them vulnerable to the changing climate (Janzen, 1967; Şekercioğlu et al., 2008; Şekercioğlu et al., 2012). In addition, montane bird species undertake upslope range shifts in response to climate change, probably to track their preferred thermal niches (Peh, 2007; Girish & Srinivasan, 2022), but this means a smaller area of occupancy at the top when compared to the base of a mountain; therefore, these species may slowly be driven to extinction as their ranges become smaller and smaller because of upslope shifts (Colwell et al., 2008; Gasner et al., 2010). Among tropical montane birds, understorey insectivorous species tend to be the most vulnerable to global change drivers including climate change (Powell et al., 2015; Srinivasan et al., 2019).

Terrestrial ectotherms, the main prey for insectivorous birds, are particularly susceptible to climate impacts because of their inability to regulate body temperature (Huey et al., 2012). Some species may behaviorally regulate their body temperature, but even they may experience rapid changes in temperature in more open habitats. Among the tropical ectotherms that are at increased risk are the arthropod species that most insectivorous birds consume. Therefore, insectivorous bird species are likely to disproportionately face both direct (physiological) and indirect (prey availability) climate impacts.

Climate change (CC) is not the only anthropogenic process that threatens natural ecosystems. Alongside CC, another human-induced factor for rapid ecosystem and habitat change is LUC. Some evidence suggests that factors such as anthropogenic LUC and habitat degradation might play a larger role in the local extinctions of species than global phenomena such as CC, at least as of now (Dobson et al., 2021).

1.2. Anthropogenic land-use change as a threat to global biodiversity

Land-use change (LUC) is described as the use of land by anthropogenic activities that cause changes to natural habitats via the expansion of agriculture, plantation, and pasture and through activities such as selective logging and habitat fragmentation (Zvoleff et al., 2014). LUC is considered one of the greatest and most immediate threats to biodiversity (Sala et al., 2000; Jetz et al., 2007; Phillips et al., 2017; Dobson et al., 2021). Habitat alteration for human activities causes changes in the structure and function of ecological communities and may eventually lead to local extinctions at a faster rate than CC (Jetz et al., 2007; Dobson et al., 2021). Of particular importance are tropical forests, a habitat that hosts more than 50% of biodiversity (Dirzo & Raven, 2003), and where rates of forest clearance for conversion to different land-use types is among the highest (Lambin et al., 2003). About 68,000 km^2 was the estimated amount of forest land lost between 1990 to 2005 (Lindquist, 2012) with loss rates increasing by 3% every year (Hansen et al., 2013). It is therefore essential to understand the effects of this large-scale habitat degradation on local and global ecosystem functioning, biodiversity and community structure.

LUC varies in intensity, with some forms clearing the entire habitat to use it for agricultural or other purposes. In forests, less intense forms of land-use include selective logging, where although the entire forest is not clear-felled, a subset of commercially valuable trees are selectively removed from the forest. It was believed that such selective logging does not have a negative impact on forest biodiversity and ecosystem functioning (Dekker & De Graaf, 2003; Rametsteiner & Simula, 2003). While lower intensity LUC might be the least invasive and might best preserve the structure and function of the habitat, recent studies have provided evidence that selective logging at any intensity has adverse impacts on biodiversity (Santos et al., 2024; Ewers et al., 2024).

Selective logging is responsible for roughly 51% of anthropogenic disturbances in tropical forests (Hosonuma et al., 2012) and, like other forms of LUC, has been shown to reduce tropical forest biomass and subsequently reduces aboveground carbon storage capacity (Gatti et al., 2015). It also causes an increase in the proliferation of invasive species, slowing down forest regeneration and ecological succession (Gatti et al., 2015). Apart from their effects on local biotic communities, these processes also cause changes in the abiotic environment, with temperatures in degraded forest patches being higher than in primary or old-growth forests (Senior et al., 2017). Changes in forest structure and abiotic conditions lead to changes in forest microclimates, with microclimatic conditions being warmer and drier in selectively logged forests compared with primary forests (De Frenne et al., 2019; Santos et al., 2024). These changes greatly alter the buffering capacity of degraded forest ecosystems against global warming, and open forest patches deny species of refugia to evade increased sunlight and temperatures (De Frenne et al., 2019; Santos et al., 2024).

The multi-faceted changes in structure, microclimate and macroclimates of degraded forest patches have cascading effects on local biodiversity at higher trophic levels as well (Barnes et al., 2017; Aggarwal et al., 2023). The changing microclimatic conditions alter invertebrate communities in logged forest, thereby potentially causing changes in insectivorous bird communities that rely on invertebrates for food. Even more direct effects of human disturbance such as the destruction of nests, adversely affect bird populations in habitats where LUC is prevalent (Barnes et al., 2017).

Importantly, LUC and CC do not occur in isolation but interact with each other to affect biodiversity in ways that are not yet clearly understood. Therefore, it has become increasingly evident that research is needed to examine the joint effects of these global change drivers on species and ecosystems, and not as separate phenomena that both negatively impact biodiversity causing changes in species distributions and in their traits in isolation from one another.

1.3. Species traits and their distributions

CC and LUC affect species in multiple ways. For instance, they might result in changes in the distribution of species caused by species tracking their preferred climatic niche (Parmesan & Yohe, 2003) and changes in the phenology of life history events that depend on environmental cues such as temperature thresholds (Durant et al., 2007). CC and LUC can also result in changes in morphological traits and community trait distributions (Jirinec et al., 2021; Vázquez-Reyes et al., 2022). A trait is defined as "a well-defined, measurable property of organisms, usually measured at the level of an individual and used comparatively across species. A functional trait is one that strongly influences organismal performance" (McGill et al., 2006).

An example of a functional trait in plant species is leaf mass per area (LMA) a measure of the "leaf dry-mass investment per unit of light-intercepting leaf area deployed", (Wright et al., 2004) i.e., a thinner leaf blade would have lower LMA. High LMA leaves display lower nutrient concentrations, lower rates of respiration and photosynthesis, essentially meaning they display a slow return on investments and have longer lifetimes. But, high LMA might also confer low palatability and therefore, a resistance to herbivory (Wright et al., 2004). It is clear from this example that some traits have a direct influence on the fitness of an organism through the role they play in certain "functions" of the organism.

The most classic example of a change in a trait distribution is that of Darwin's finches on Daphne Major, an island in the Galapagos Archipelago. In their seminal paper, Grant & Grant, (2006) showed that in the absence of a competitor species, *Geospiza fortis* (Medium Ground-Finch), which usually prefer small seeds when they are abundant, turned to consuming larger seeds of *Tribulus* because of a reduction in the abundance of small seeds during a drought. The large seeds of *Tribulus* were a resource only the large billed population of *G. fortis* had access to, because the smaller billed population was unable to crack open the seeds to consume them. Subsequently, a shift in mean bill size to higher values was observed post the drought year of 1977. In contrast to this, in the drought years of 2003-2005, a competing species, *Geospiza magnirostris* (Large Ground-Finch), had established a stable population on Daphne Major. This large billed finch competitively excluded the smaller billed *G. fortis* from accessing large seeds, and therefore, the mean bill size of *G. fortis* decreased in the years during and after the drought (Grant & Grant, 2006). This is one of the clearest examples of how a change in environmental conditions alters resource availability and therefore, changes the distributions of traits that are important in acquiring resources.

The above example is of an extreme weather event impacting single species trait distributions, and therefore, the timescales of responses are short and immediate. When it comes to processes such as CC and LUC, the ability of a species to adapt to and persist in an altered, novel, environment depends on its functional traits (Angert et al., 2011; MacLean & Beissinger, 2017). Therefore, one can think of species' traits responding to global change drivers and subsequently, in a particular habitat CC and anthropogenic LUC bringing about changes in the trait distributions of ecological communities. This response has been observed in multiple taxa, from plants (Cornwell & Ackerly, 2009; Ding et al., 2012) to more recently in birds (Ausprey et al., 2022; Vázquez-Reyes et al., 2022). As mentioned earlier, amongst forest birds, understorey insectivores are particularly vulnerable to the effects of environmental change. Here, I aim to understand how community trait distributions for understorey insectivorous birds change over a fifteen-year period in two habitats, one being anthropogenically modified and another undisturbed.

1.4. Trait-based approaches in ecology

Trait-based approaches in ecology are useful in that they can help answer questions across all levels of organisation, be it at the level of the individual, population, community or ecosystem (Carmona et al., 2016; Fontana et al., 2021). Traits help in understanding species interactions (as seen above with the example of the Galapagos finches), which in turn allow inferences about trophic interactions, species coexistence and therefore community structuring and dynamics (Abdala-Roberts et al., 2019; Litchman et al., 2021). As CC and LUC can cause changes in community trait distributions, trait-based approaches can be used to track the effects these processes have on communities as a whole instead of individual species responses (Terseleer et al., 2014; Wieczynski et al., 2019).

Species' traits have been an integral part of the development of ecology as a field, although trait-based approaches as a defined paradigm emerged much later (Klausmeier et al., 2020). One can think of traits being parameters of classical ecological models such as the growth rate of a species in the Verhulst logistic population growth model or the Lotka-Volterra predator-prey model that uses the growth rate of prey, attack rate, mortality of predator, etc., (Klausmeier et al., 2020). However, the use of these approaches to study community assembly, using traits to understand dynamics at a level higher than individual or species populations, is a product of research done in the last two to three decades (Klausmeier et al., 2020; Fontana et al., 2021; Green et al., 2022).

An exponential increase in studies using functional traits to answer questions in ecology was observed from the year 2011 (Green et al., 2022), and this can be attributed to the rethinking of ecological fields from a trait-based perspective. Fields such as population and community ecology (McGill et al., 2006; Violle et al., 2012), biogeography (Violle et al., 2014) and conservation ecology (Cadotte et al., 2011) all increasingly started using trait-based research. It was also noted that an overwhelming number of studies use plants as their taxonomic focus, with about 35% of studies looking at plant traits, a consequence of trait-based research originally being used to study plant community assembly (Green et al., 2022). Therefore, life-history trade-offs in plants and abiotic and biotic filters for plant community assembly are very well researched (Westoby & Wright, 2006; Suding et al., 2008; Kattge et al., 2020), and despite the growing focus on other taxonomic groups, there is a lack of trait-based knowledge in non-plant communities and assemblages. Especially, in the face of CC and LUC, it is important to not only study changes to ecological communities in terms of altered species richness and diversity, but to also discern the factors that might be responsible for community disassembly (Ausprey et al., 2022), and develop predictive trait-based approaches that will allow an understanding of how community dynamics, and perhaps some aspects of community function, will shift under novel conditions (Yang et al., 2019; Boonman et al., 2022).

1.5. Functional diversity

The establishment of trait-based ecology as a distinct sub-field was followed by the establishment of functional diversity as a metric of biodiversity. Tilman (2001), defined functional diversity as "the range and value of those species and organismal traits that influence ecosystem functioning." This essentially means that functional diversity is defined based on species' function in communities/ecosystems and their traits as opposed to classical species' taxonomic identity. The easiest way to understand functional diversity as distinct from taxonomic diversity is to consider an illustrative example. Consider the diets of species in two communities of birds. Community A has eight species of insectivores and Community B has one species each of insectivore, granivore, frugivore, nectarivore and piscivore. Community A might have a greater taxonomic diversity, but in terms of the range of functions performed by the two communities and the number of resources used, it is clear that Community B has a higher dietary diversity. Therefore, functional diversity can be more informative than taxonomic diversity when it comes to answering questions about how diversity affects ecosystem functioning, which ultimately depends on traits, which in turn is tightly linked to the niche of a species (Cadotte et al., 2011).

The complex relationship between ecosystem processes and species' traits is not fully understood, but many ecosystem processes are results of the actions of organisms. One can think of these processes as the outcomes of functional traits of organisms mediating these actions and therefore community/ecosystem function. Summarising this range of functions in a single metric should give us a measure of diversity that informs us about particular ecosystem processes (Tilman, 2001). Functional diversity has immense potential in linking variation at the individual or species level to community-level patterns and processes; the source of such variation can be morphological, physiological or phenological. In addition to this, functional diversity also incorporates information about species interactions (Naeem et al., 2009).

Alongside functional diversity, it is also useful to introduce the term functional trait space. Functional trait space is defined as the "multidimensional space where the axes are functional traits. Individuals or species are placed in this space in coordinates given by their functional traits." (Carmona et al., 2016). Figure 1 is a conceptual diagram of functional trait space for a single trait and two traits and how to go from individual species trait distributions to community trait distributions.

The loss of biodiversity because of CC and LUC is far from a random process (Dirzo et al., 2014). It is known that species with certain traits including larger body sizes, longer life spans and lower reproductive rates are generally at higher risk of extinction, and this means that ecosystem functions linked to these traits might be impacted to a greater extent (Díaz et al., 2006).

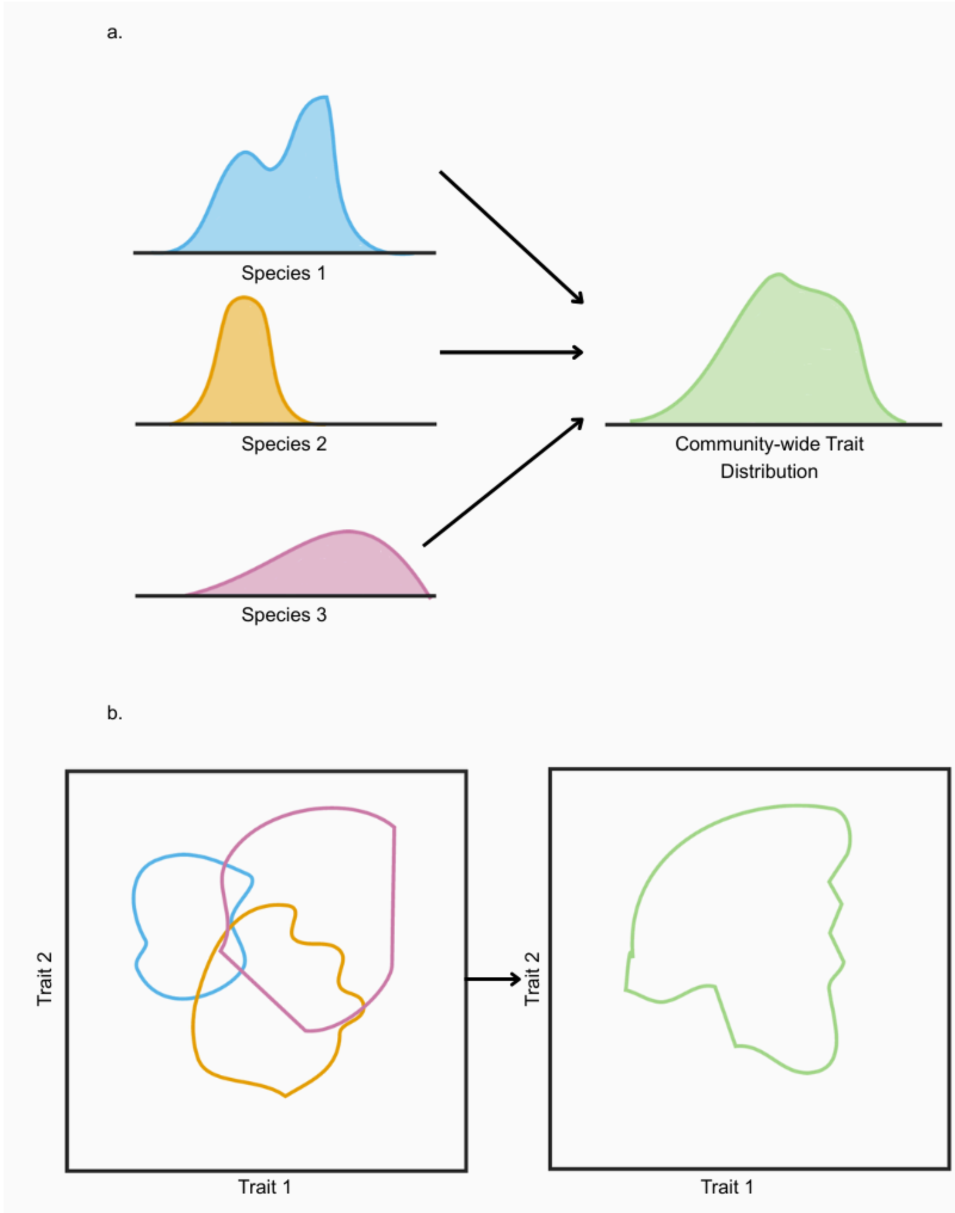

Figure 1. Illustration showing trait space in (a) a single trait e.g., bill length in three different species. The community-wide trait distribution is the weighted average of the individual species trait distributions with the weights being the abundances of species. The range of values of the trait i.e, bill length can be considered as the "trait-space" occupied by each individual species or the community as a whole, (b) two-dimensional trait space. The panel on the left shows the individual trait-spaces of three different species for two traits e.g., bill length and body mass. The panel on the right shows the community trait-space of a community consisting of the three species in the panel on the left. The area occupied by the polygon in each case is considered the trait-space occupied by the species or the community. Similarly, trait-space can extend to multiple dimensions with the addition of more traits.

1.6. Setting the stage

Old growth forests (primary forests hereafter for the sake of simplicity) and logged forests differ in two primary biotic and abiotic factors:

1. Abiotic factors: logged forest is generally warmer and drier than primary forest, and primary forests tend to have greater buffering capacity against temperature extremes (Senior et al., 2017; De Frenne et al., 2019; Santos et al., 2024)
2. Biotic factors: Arthropod density differs in primary and logged forests, with logged forests hosting more flying insects when compared with primary forests that host more foliage-dwelling arthropods (Aggarwal et al., 2023). In addition, logged forests might have a proliferation of invasives in the understory that alters vegetation structure (Gatti et al., 2015).

These differences in temperature and arthropod density essentially mean that the thermal environment as well as resources available for insectivorous birds differ between primary and logged forests. In turn, this means that the kinds of morphological traits, especially those related to thermal adaptation (e.g., body mass) and foraging and dietary habits (e.g., body mass, bill length, shape, wing length and foraging strategy), would be expected to differ in primary and logged forest.

1.7. Questions, hypotheses and predictions

The broader aim of this project is to examine how CC and LUC affect trait distributions in understory-midstory bird communities in the Eastern Himalaya. The more specific questions, hypotheses and predictions are as follows:

Questions

1. How do understory-midstory bird communities in primary and logged forest differ in their functional traits? In other words, how does LUC impact functional diversity?
2. How does the functional trait profile of understory-midstory bird communities in primary and logged forest change with time? In other words, how does CC alter functional diversity over time, and does the impact of CC on functional diversity differ in primary and logged forest?

Hypotheses and Predictions

1. Comparison of traits in primary and logged forest

1.1. Body mass

Large bird species might face disadvantages with logging, likely because smaller species (a) need less absolute amounts of food, and (b) are better adapted to warmer habitats (Srinivasan, 2013; Srinivasan & Quader, 2019). Therefore, on average, species in logged forest bird communities should be smaller than those in primary forest communities.

Prediction: Body mass will be higher in primary forest than in logged forest.

1.2. Bill morphology

In the Eastern Himalaya, logging leads to a proliferation of bamboo in the forest understory, and bamboo specialist bird species tend to have very different bill morphologies reflecting different strategies for foraging in bamboo (Srinivasan et al., 2025). Therefore, bill morphologies would be different in the two habitats, with morphological uniqueness being higher in logged forest because of the unique bills that bamboo specialists possess.

Additionally, sallying (a foraging strategy where bird species catch flying insects in short bursts of flight from a perch) bird species, likely are more in abundance in logged forest because of the higher density of flying arthropods, and therefore, bill morphologies in logged forest might be dominated by those of sallying bird species more (i.e., generally broader and flatter bills). Although, this trend might be masked by the bamboo specialists who have very different bill morphologies.

Predictions:

1. Morphological uniqueness will be greater in logged forest when compared with primary forest
2. Bills in logged forest would be flatter and broader when compared with those in primary forest.

1.3. Wing morphology

The presence of greater density of flying arthropods in could lead to a higher abundance of sallying bird species and consequently to hand-wing index (HWI - a measure of pointedness) being higher in logged forest because studies in the past have shown a correlation between HWI and flight efficiency (Sheard et al., 2020) although these proxies should be used with caution (Yang et al., 2025).

Prediction: HWI will be higher in logged forest when compared with primary forest.

2. Comparison of traits across time in primary and logged forest

There are two primary hypotheses when it comes to what changes we would expect in individual traits and functional diversity with time. One is that the trait distributions and functional diversity changes with time because of CC which alters resource availability. The other is that despite the changes in resource availability and CC, trait distributions and functional diversity will remain more or less constant with time. The explanations for why these two different hypotheses exist are given below:

2.1. Changing trait distributions

Mean annual temperatures have risen in both primary and logged forest because of CC over the last fifteen years, and therefore, the trait distributions of birds in these habitats are also likely to have changed. The impacts of CC in logged forest are likely to be more pronounced. From previous work, we know that temperatures in logged forest are on average 2°C warmer than in primary forest, and the difference in maximum temperatures between the two habitats can be as high as 5.85°C (Srinivasan & Wilcove, 2021).

Therefore, because the impacts of CC are more pronounced in logged forest, trait distributions are expected to change faster in logged forest when compared with primary forest especially because primary forest tends to buffer against thermal extremes, which logged forest cannot do because because of the more open canopy (Senior et al., 2017; De Frenne et al., 2019; Santos et al., 2024).

Some species face resource shortages in logged forest and as a consequence of altered resource availability coupled with the pace at which resources change because of poor buffering capacity of logged forest. This could lead to bird trait distributions changing more rapidly in logged forest as a consequence of arthropod communities changing more rapidly and also, temperature changes being more rapid. On the other hand, salliers might fare better in logged forest because of the higher density of flying arthropods (Aggarwal et al., 2023).

Predictions:

1. Functional diversity will be negatively correlated with time.
2. The rate of decrease in functional diversity will be greater in logged forest when compared with primary forest.
3. Body mass will decrease in both primary and logged forest with time, the rate of decrease in logged forest will be higher.
4. Bills in logged forest would become flatter and broader compared with those in primary forest.
5. HWI would increase in logged forest with time but remain constant in primary forest.

2.2. Constant trait distributions

In response to CC, species are expected to track their preferred climatic niches and shift their distributional ranges. Temperature-induced range shifts caused by CC can cause the geographic distribution of species to change in two ways (a) latitudinally (i..e, move polewards) or (b) elevationally (i.e., move upslope) to track preferred thermal niches. The upslope movements of species along elevation gradients have been documented across various montane systems in multiple taxa (Menéndez et al., 2014; Schai-Braun et al., 2021; Zu et al., 2021). Particularly in the Himalaya, there is evidence of range shifts from plants (Salick et al., 2019), and birds (Girish & Srinivasan, 2022).

These upslope movements of birds from lower elevations to higher elevations results in the species composition of the community at any particular elevation changing, as some species “enter” from lower elevations and others “leave” for higher elevations. Various abiotic and biotic factors determine whether a species can survive at a particular elevation. Therefore, species that move to a particular elevation from lower elevations that are similar in functional trait-space to those species that have moved further upslope are likely to fill the “unutilised” niches and survive at that elevation, suggesting that functional replacement could be a mechanism of CC effects on biodiversity. This would essentially mean that functional trait-space and functional diversity remain more or less constant with time because of this functional replacement.

Prediction: The functional trait space of species declining in abundance at a given elevation will show significant overlap with that of species increasing in abundance at that elevation in both habitat types.

Chapter 2: Methodology

2.1. Data collection

Fifteen years of mist netting data (2011 to 2025) were collected in Eaglenest Wildlife Sanctuary, Arunachal Pradesh (Figure 2). In each year, mist netting was conducted during summer months of April and May representing the early breeding season of these bird species. Plots were chosen in 2011 based on semi-quantitative data regarding the level of timber extraction in the area, obtained through interviews with former logging managers and by assessing the vegetation structure of the forests at that time, correlating tree densities with data recorded during the interviews (Srinivasan, 2013; Srinivasan et al., 2015). This led to the establishment of three primary forest plots and three logged forest plots centered at an elevation of 2000m ASL (Figure 2). The total area sampled for birds was nine hectares each in primary and logged forest.

Primary forest plots differed significantly from logged forest plots in terms of vegetation structure, tree density and several abiotic factors. The primary forest plots were either never or very minimally logged with less than one tree removed per hectare and tree densities ranging 168 to 192 trees/hectare. This is in contrast to logged forest plots, which had tree densities ranging 76 to 110 trees/hectare and were intensively logged until 2002 after which logging was stopped in these forests (Srinivasan, 2019; Srinivasan & Wilcove, 2021). The halting of logging in these historically intensively logged forest patches led to the proliferation of fast-growing invasive native bamboo species, considerably altering vegetation structure. Specifically, logged forest had a bamboo density of 0.94 stems/m^2 $\pm$ 0.22 SE (standard error), while primary forest had a bamboo density of 0.37stems/m^2 $\pm$ 0.07 SE (Srinivasan & Wilcove, 2021). The understory of logged forest patches is now dominated by bamboo which restricts the growth of forest tree seedlings and saplings, causing vegetation structure to remain unchanged in the fifteen year time period. The intensive logging coupled with the invasion of native bamboo species means that logged forest tend to have open and drier habitats with logged forest being on an average 2°C (95% CI = [1.91°C, 2.10°C]) warmer than primary forest and differences in maximum temperatures between the forest types reaching as high as 5.85°C [5.42°, 6.29°C] (Srinivasan & Wilcove, 2021).

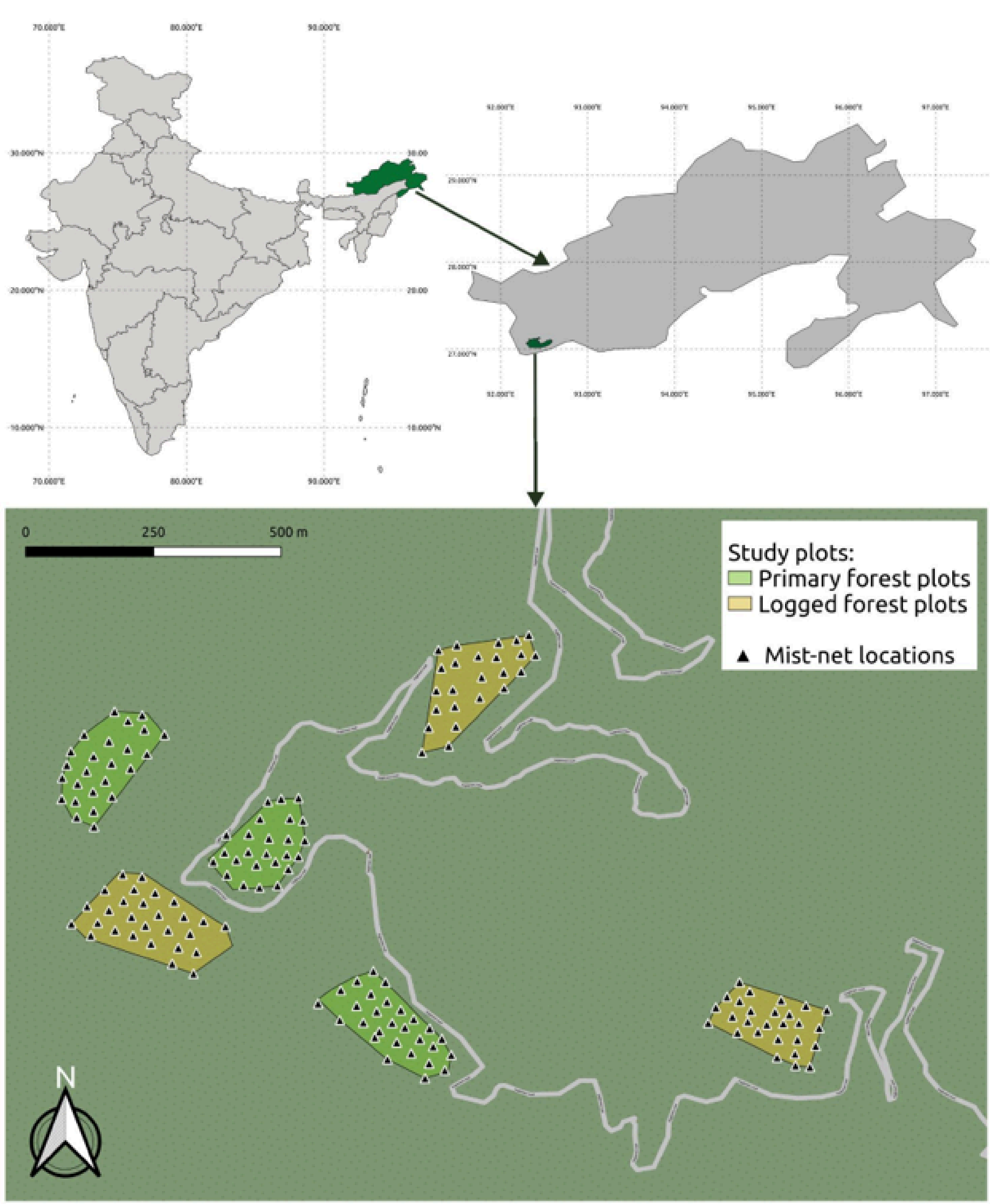

Figure 2. Map of India showing location of Arunachal Pradesh and Eaglenest Wildlife Sanctuary in Arunachal Pradesh. Map of plots sampled with the primary forest plots represented in green and logged forest plots represented in yellow. The black dots represent mist net locations. From supporting information in Bharadwaj et al. (2025).

In each plot, 24-28 mist nets were set up systematically in a grid-based design (Figure 2). Mist nets consisted of four shelves and were 12m in length, 2.4m high and 16mm mesh size (Srinivasan & Quader, 2019). Birds caught in these nets are mostly understory or midstory species with very few captures of canopy species. Each plot was sampled every year over a fifteen year period for three consecutive days from 0500 to 1200 hours, in April and May (protocol in Srinivasan, 2013). Nets were checked every 20 to 30 minutes. Birds caught in the nets were first weighed to the nearest 0.01g, ringed and released. Ringing of birds involves attaching a small metal ring to the tarsus (analogous to an anklet) with a unique number for each individual. Therefore, a capture history for each individual caught in these mist nets is obtained, allowing estimation of annual survival for different species in primary and logged forest and approximate population sizes of species using mark-recapture data. Only 6.4% of the birds that were first caught and ringed in a particular forest type were then recaptured in a different forest type, indicating high independence of populations between habitats (Srinivasan & Wilcove, 2021).

2.2. Data cleaning and curation

Data collected from the field was entered into an Excel spreadsheet and then cleaned using an R script (R Core Team, 2025). Ring numbers assigned to two or more species were excluded from the analysis, forming only a small subset of the data (212 individual entries out of 12802 entries, ~ 1.7%). Trait data were obtained from the AVONET bird trait dataset, a global dataset comprising morphological, ecological, and other traits (Tobias et al., 2022). Using this global bird trait dataset, morphological traits of interest were extracted, which were:

1. Body mass: plays an important role in thermoregulation. Mean body mass was the only trait obtained from mist netting data collected in the field, rather than from the AVONET dataset.
2. Bill-related traits such as bill length, bill depth and bill width: these are traits related to the diet of the birds.
3. Tarsus length and wing length: traits that pertain to the foraging habits of these birds.
4. Hand-wing index (HWI): a measure of flight and dispersal ability.

These morphological traits for AVONET were measured on museum samples. This may not be ideal, as the samples were originally collected from various countries and not specifically from Eaglenest Wildlife Sanctuary (although most museum specimens were collected in India, with ~34% of the specimens being from India). Additionally, the same trait values would be used for primary and logged forest, as the AVONET dataset does not differentiate between habitat types but was created to have a global repository of bird traits. However, because the study focuses on community trait values, the species-specific differences in traits values between primary and logged forest are likely to be obscured by patterns that arise at the community level.

A subset of the original AVONET dataset was created, comprising only species from the Eastern Himalaya in the mist netting dataset. Each trait was averaged across species, resulting in an "average species-trait matrix" for the Eastern Himalayan bird community (see Figure A1 in the appendix). The measured body mass from mist netting data was also averaged for each species and added to this average species-trait matrix. The AVONET bird trait dataset did not contain any morphological trait data for the following four species: *Brachypteryx cruralis* (Himalayan Shortwing), *Zoothera salimalii* (Himalayan Thrush), *Tachyspiza virgata* (Besra) and *Liocichla bugunorum* (Bugun Liochicla). These species were subsequently excluded from our analysis, assuming they would not significantly affect community trait values, as they had very low captures over the fifteen years. *Brachypteryx cruralis* was the species with the highest captures (7 total captures, including both habitat types) among the four species.

Additionally, raw counts of species captured in each year in each habitat type were computed. This was done for a specific habitat type by calculating the total number of unique captures per year, disregarding plot-level identity (see Figure A2 in the appendix). Therefore, the result was a matrix of raw capture counts for each habitat type. The year 2020 was excluded from analysis because no sampling took place in that year because of nation-wide lockdown brought about by the COVID pandemic. Raw counts served as proxies for the abundances of these species. These counts were not effort-standardised by time spent sampling because this standardisation assumes a linear relationship between the amount of time sampled and the number of individuals caught in mist nets, when in reality, the relationship actually saturates with effort. However, analysing these counts assumes relatively equal sampling effort across years and in each habitat, as well as relatively constant recapture probabilities across years and habitats.

2.3. Indices based on taxonomic identity

These diversity indices do not consider traits, but instead consider species taxonomic identity and their relative abundance in the community to determine diversity. The diversity index we used to compare primary and degraded habitats was the Shannon diversity index. Consider p_i is the relative abundance of the i^{th} species in a community that has a total of S species (Shannon and Weaver, 1949). The Shannon diversity index is measured as:

$$H = -\sum_{i=1}^{S} p_i ln(p_i)$$

A standardisation performed on this diversity metric is to use species evenness or equitability. Evenness allows us to compare communities that have different numbers of species and also allows to form certain ecological inferences such as how resources are partitioned (an evenness value close to one indicates an even community where potentially almost all niches are utilised). This allows us to corroborate results from the functional diversity analysis.

Pielou's evenness is calculated as the Shannon diversity index H normalised by the natural logarithm of the total number of species S (Pielou, 1966) i.e.,

$$J = \frac{H}{ln(S)}$$

2.4. Community-weighted means of trait distributions

Community-weighted means (CWMs) help in quantifying changes in trait distributions in the face of environmental perturbations. Therefore, CWMs prove to be a valuable tool by summarising the effects that global change drivers have on a single trait, but across species.

Before defining CWM, a few terms that need to be defined are:

1. Relative abundance: The proportion of individuals of a particular species to the total number of individuals in the community. For a community with a total of S species, relative abundance of species i is defined as

$$p_i = \frac{unique\ captures\ of\ species\ i}{total\ unique\ captures\ across\ all\ S\ species}$$

2. Mean trait value: The mean trait value for a species i is the average value of all individual measurements of traits for the species i. Suppose species i has a total of n individuals in the community

$$\theta_i = \frac{\sum_{x=1}^{n} \theta}{n}$$

   I obtained this data from the AVONET dataset.

For a particular trait (e.g., bill length), a CWM is defined as

$$CWM_j = \sum_{i=1}^{S} p_{ij}\theta_i,$$

where for a community with S species, p_{ij} represents the relative abundance of the i^{th} species at time t_j and θ_i the mean trait value (e.g., mean bill length) for species i. It should be noted that CWM_j is the community-weighted mean for the community at time t_j. Even if community species composition in terms of species identity does not change over time, the CWM can change because 1) the relative abundances of species in the community change, altering the species-specific contributions to of average trait values, 2) the average trait values themselves change with the relative abundance of species remaining unchanged, or 3) both species-specific relative abundances and average trait values change. CWMs can also change when community composition changes, altering p_{ij} and adding or excluding θ_i via the addition or removal of species. Here, I assume that the average trait value of individual species remains constant over the fifteen years and across habitat types. However, because of changes in community composition as a response to CC and LUC, community-weighted trait distributions would be expected to show changes.

There are certain disadvantages to using a community-weighted mean to summarise responses to environmental perturbations. Such metrics are relatively information-poor in allowing inferences on whether a few influential species drive changes in the mean or whether the community as a whole is changing (Gaüzère et al., 2019). Such metrics also ignore intra-specific variability by considering a single averaged trait value per species. However, regardless of these caveats, CWMs provide a simple and interpretable measure that allow us to infer relationships between traits and their changes with LUC and CC.

Traits chosen for CWM analyses were body mass, bill length culmen, bill width normalised by bill length, bill depth normalised by bill length, tarsus length, wing length, and HWI. The final set of traits was chosen by (a) ecological expectations for why these traits might be expected to respond to anthropogenic LUC and CC (see introduction and section 2.2), and (2) by examining pairwise correlations between each pair of traits. The correlation was checked using the *pairs* function in R (R Core Team, 2025). All morphological traits are obviously correlated with each other to a certain extent (see Figure A3 in the appendix). Traits related to body size such as body mass and wing length might be expected to be highly correlated. But because there was a strong biological consideration to include them they were considered regardless of this high correlation. Bill width and bill depth were normalised by bill length. The reason for this normalisation instead of normalising by body mass is that Eastern Himalayan bird species have diverse bill morphologies. For example the *Paradoxornis* *ruficeps* (White-breasted Parrotbill) and the *Pomatorhinus ferruginosus* (Black-crowned Scimitar-Babbler) are very similar in terms of body mass. However, the parrotbill has a finch-like wedge shaped bill for tearing into bamboo and the scimitar-babbler has a long hook shaped bill for probing in bamboo sheaths. In this case, for instance, body size is not the trait that is most correlated with bill width or bill depth. Normalising by bill length allows to account for bill size and therefore, will enable inferences that are to a certain degree independent of bill size when commenting on how bill width or bill depth have changed with LUC or CC.

Once the final set of traits to be considered for future analysis was determined, I computed the CWMs of the seven traits under consideration for each year and in each habitat type. This was done by first computing a year-wise species-trait matrix that filters through the capture history for the last 15 years and then creates an average-trait matrix that includes only the species that were caught in a particular year separately for each habitat type. Once this yearly species-trait matrix was computed the CWM was calculated for each trait for that year per habitat type. These were then compared across habitat types and for how they changed over time.

2.5. Functional diversity using Rao's entropy

Rao's quadratic entropy (*Q*) is one of the many ways to measure functional diversity (Botta-Dukát, 2005). *Q* is a measure of functional dispersion that quantifies how closely clustered or how far apart communities are in terms of their traits. For instance, an overdispersed community with a high *Q* value would be one where all the species are very different from each other in terms of their trait values and an underdispersed community with a low *Q* value would be one where all species are extremely similar to each other. In specific Rao's quadratic entropy is defined as

$$FD_Q = \sum_{i=1}^{S-1} \sum_{j=i+1}^{S} d_{ij} p_i p_j, \text{ where}$$

In a community with S species, p_i represents the relative abundance of species i and p_j represents the relative abundance of species j, d_{ij} is the distance or difference between the mean trait values of species i and j (Botta-Dukát, 2005). The distance metric used for this study was Euclidean distance. All traits were all normalised by range in trait values across species:

$$\theta_i = \frac{\theta_i - \theta_{min}}{\theta_{max} - \theta_{min}}$$

This was done to ensure that all the traits contribute the same weights to the calculation of Q and that the calculations were not affected by the units and scale in which each of these traits are measured.

The reason for choosing Rao's entropy over other functional diversity measures is that most other measures of functional diversity do not account for species abundances in the community, which is an important consideration for studies of this nature. Other metrics such as Convex Hull Volume, Mean Dissimilarity, Functional Attribute Diversity, FD, FD_{LD} do not incorporate species abundances. While FD_{var} (variation in functional diversity) does account for species abundance, it is simply the community-weighted variance and therefore, considers only one trait at a time and severely restricts the utility of this index (Naeem et al., 2009).

In addition to the functional diversity, morphological uniqueness in bill characteristics was also computed using this metric because a higher value of Q essentially indicates overdispersion or more morphologically unique bill types compared with a lower Q that indicates similarity in the morphological traits in the bills of the species in the community. For this calculation, only bill characteristics i.e., bill length culmen, bill width and bill depth were taken into consideration.

Rao's entropy (Q) was calculated using the *fundiversity* (Gruson & Grenié, 2022) package in R (R Core Team 2025)

2.6. Linear models

Once I calculated year-wise CWMs for each trait in each habitat, year-wise overall Q and the year-wise Q in only bill characteristics for both habitats, the quantification of differences between these habitat types and across time were evaluated using linear models. Two sets of linear regressions were performed.

1. ANOVA to quantify differences in trait space and functional diversity between habitats:
   This linear regression used a single categorical predictor variable, habitat, with two levels: primary and logged. This allowed us to check for the effects of anthropogenic LUC alone on the traits and functional diversity of these species. Therefore, the model was constructed as follows:
   $$lm(trait/rao's\ entropy \sim habitat\ type)$$

2. Multiple regression to quantify changes in trait space and functional diversity over time in the two habitats:
   This linear regression used two predictors: habitat (categorical) and time (continuous, in years) and an interaction term between the two. The model was constructed as follows:
   $$lm(trait/rao's\ entropy \sim habitat\ type\ +\ year\ +\ habitat\ type{:}\ year)$$

All linear models were run in R (R Core Team 2025) and coefficients from the output of these models indicated the direction and magnitude of the effects of habitat type and time on these response variables.

2.7. Visualising trait-space overlap

The second set of hypotheses, that elevational range shifts in response to CC can cause species with similar traits to replace those lost from the community leading to unchanged trait distributions over time was also tested.

As a first step, only species that were caught more than twenty-five times in both primary and logged in the 15 years were considered for analysis. Once the dataset was filtered, a linear regression was run to estimate the effect of time on the abundances of these species. The linear regression with two predictor variables was run with habitat type (categorical), time (continuous, in years) and an interaction term between the two. Therefore, the linear model was set up as follows:

$$lm(species\ abundance \sim\ habitat\ type\ +\ year\ +\ habitat\ type{:}\ year)$$

After obtaining the slopes for each species from the linear regressions, a distribution of these slopes was plotted. The distribution of the slopes in these species represented the interspecific variation in the change in abundances of these species across time. An arbitrary cut off of 30 percentile was used to classify species into increasing in abundance (species that were above the 70th percentile of the slope distributions) or decreasing in abundance (below the 30th percentile of the distribution with negative slopes).

Once the species that were increasing and decreasing most in abundance were identified, overlap between functional trait spaces was checked using PCA plots, the code for which was written on R (R Core Team 2025).

Chapter 3: Results

3.1. Comparison of functional diversity and individual traits across habitats

There was no evidence for a statistically significant difference in functional diversity between habitats, although it was on average higher in primary forest (ANOVA: β(*Q*) = 0.021; 95% CI = [-0.004, 0.045]; R^2 = 0.10; Figure 3).

Year-wise Shannon diversity was computed for both habitat types. This was then used to compare the average diversity between the two habitats. It was found that the Shannon diversity in primary forest was higher when compared with logged forest (ANOVA: β(*shannon entropy*) = 0.141; 95% CI = [0.052, 0.231]; R^2 = 0.29; Figure 4). Pielou's evenness was also computed and it was found that similar to Shannon diversity, the evenness was higher in primary forest (ANOVA: β(*evenness*) = 0.028; 95% CI = [0.011, 0.044]; R^2 = 0.32; Figure 5).

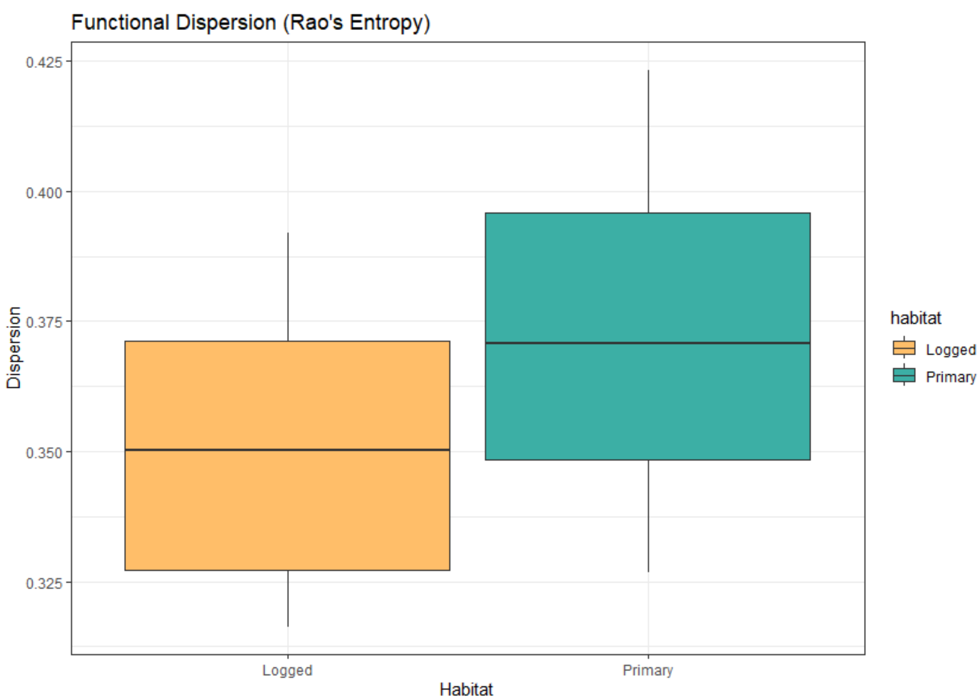

Figure 3. Boxplot comparing functional dispersion in primary and logged forest. The horizontal line represents the mean with whiskers spanning the 95% confidence intervals.

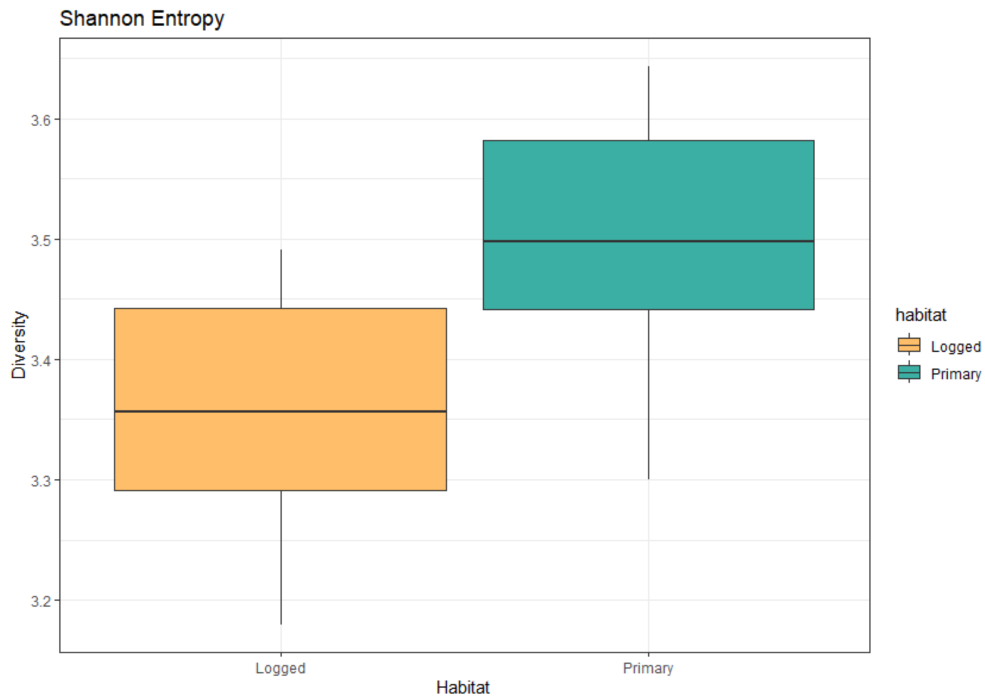

Figure 4. Boxplot comparing Shannon diversity in primary and logged forest. The horizontal line represents the mean diversity across years with the whiskers spanning the 95% confidence intervals.

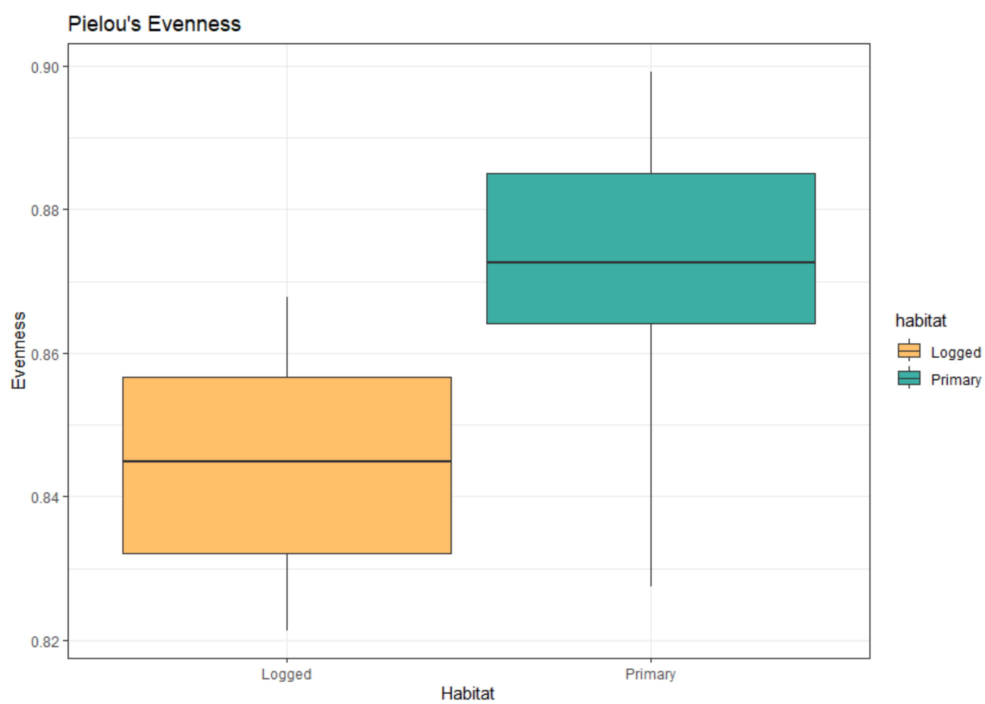

Figure 5. Boxplot comparing Pielou's evenness in primary and logged forest. The horizontal line represents the mean evenness across years with the whiskers spanning the 95% confidence intervals.

Morphological uniqueness in bill characteristics (bill length culmen, bill depth and bill width). Contrary to our expectations, there was no evidence for difference in bill uniqueness between the habitats (ANOVA: β(*bill uniqueness)* = 0.089; 95% CI = [-0.304, 0.483]; R^2 = 0.008; Figure 6).

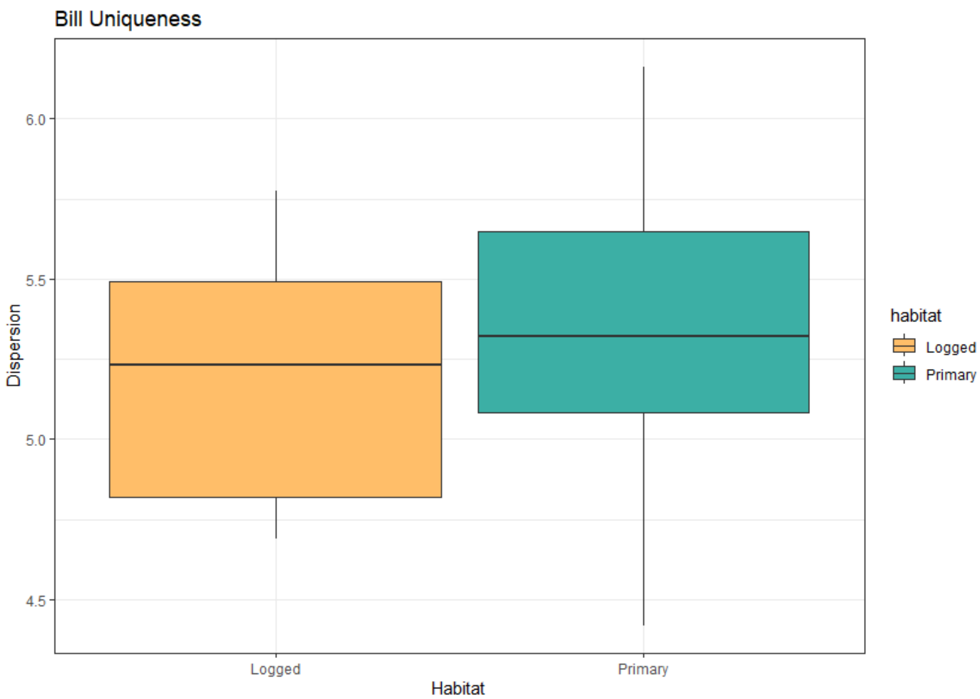

Figure 6. Boxplot comparing bill uniqueness between primary and logged forest. The horizontal line represents the mean with the whiskers spanning the 95% confidence interval.

Contrary to our expectations there was no evidence for difference in body mass between the two habitats (ANOVA: β(*body mass)* = 0.88; 95% CI = [-0.49, 2.24]; R^2 = 0.06; Figure 7a). Similarly, there was no evidence for difference in bill length between primary and logged forest (ANOVA: β(*bill length)* = 0.18; 95% CI = [-0.24, 0.61]; R^2 = 0.029; Figure 7b). There was no evidence for a statistically significant difference in bill width (normalised by bill length) and bill depth (normalised by bill length) in primary and logged forest: ANOVA: β(*bill width/bill length)* = 0.0046; 95% CI = [-0.001, 0.010]; R^2 = 0.11; ANOVA: β(*bill depth/bill length)* = -0.001; 95% CI = [-0.008, 0.006]; R^2 = 0.003 (Figure 7c & 7d) .

Community-weighted wing length was higher in primary forest when compared with logged forest (ANOVA: β(*wing length)* = 1.41; 95% CI = [0.10, 2.72]; R^2 = 0.16; Figure 7e). There was no evidence for statistically significant difference in tarsus lengths between the two habitat types (ANOVA: β (*tarsus length)* = -0.26; 95% CI = [-0.63, 0.11]; R^2 = 0.07; Figure 7g).

HWI for bird communities was expected to be higher in logged forest because sallying species might prefer logged forest because of the higher abundance of flies. However, the results show that primary forest bird communities have a higher community-weighted HWI when compared with logged forest (ANOVA: β(*hwi)* = 0.76; 95% CI = [0.52, 1.00]; R^2 = 0.62; Figure 7f).

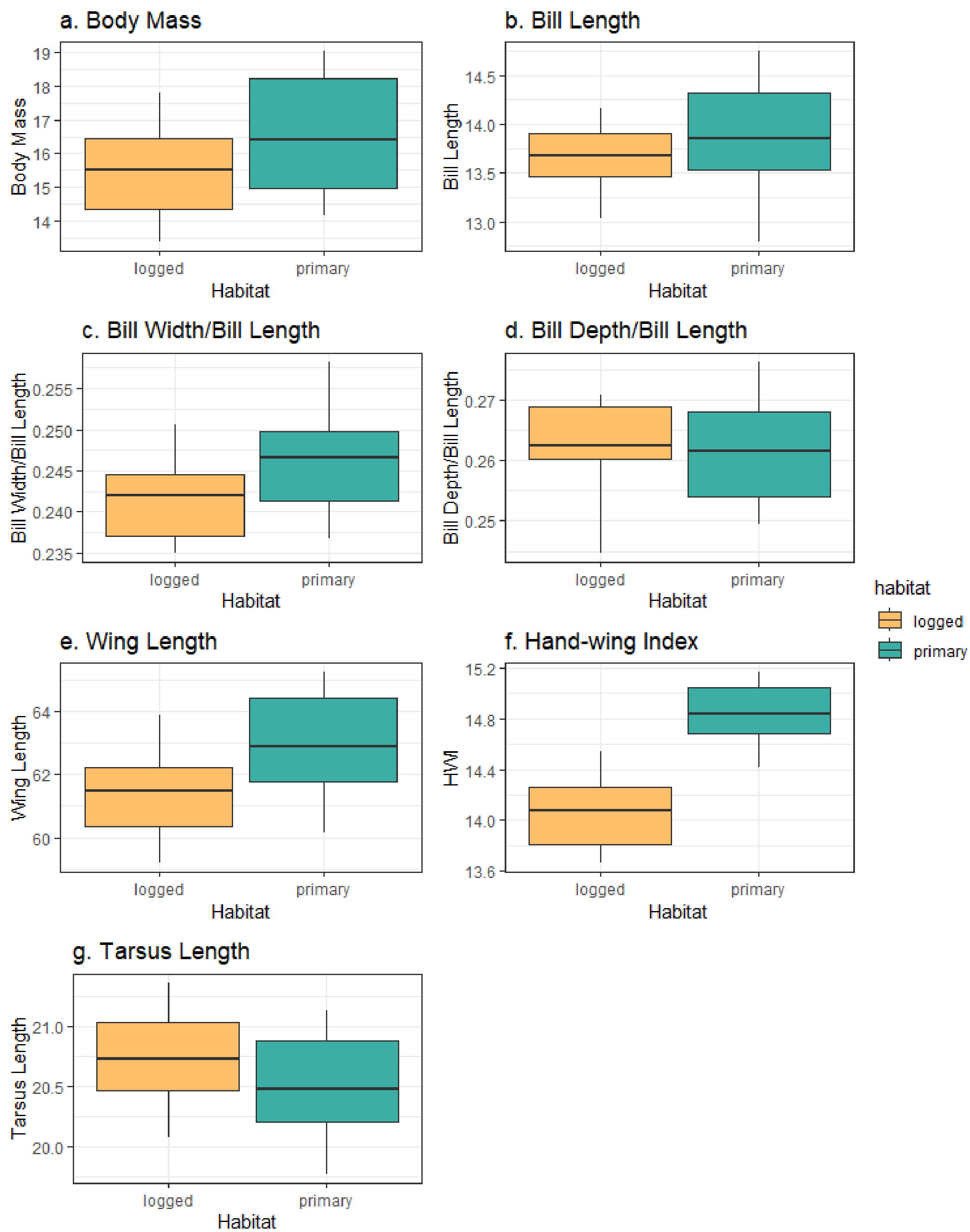

Figure 7. Community-weighted means for seven functional traits in primary and logged forest. Boxplot horizontal line indicates the mean and whiskers span the 95% confidence intervals. Boxplot was constructed using community-weighted means across years i.e., each point used to calculate the mean and confidence intervals was a community-weighted mean of a particular trait for a particular year.

3.2. Trends in functional diversity and functional traits over time

Contrary to our expectations, functional dispersion increased in logged forest with time but showed no evidence for change in primary forest (β(slope logged) = 0.004; 95% CI = [0.001, 0.008]; β (slope(primary-logged)) = -0.002; 95% CI = [-0.007, 0.003]; R^2 = 0.32; Figure 8).

Results indicate that the Shannon diversity is increasing in primary forests and logged forest but neither of these results are statistically significant (β(slope logged) = 0.003; 95% CI = [-0.011, 0.016]; β (slope(primary-logged)) = 0.010; 95% CI = [-0.099, 0.030]; R^2 = 0.38; Figure 9). Again, similar to the trend for Shannon diversity, there was no evidence for change in Pielou's evenness with time in both primary and logged forest with primary forest showing a weak positive correlation with time and logged forest showing essentially no trend (β(slope logged) = 0.001; 95% CI = [-0.002, 0.003]; β (slope(primary-logged)) = 0.001; 95% CI = [-0.002, 0.005]; R^2 = 0.40; Figure 10).

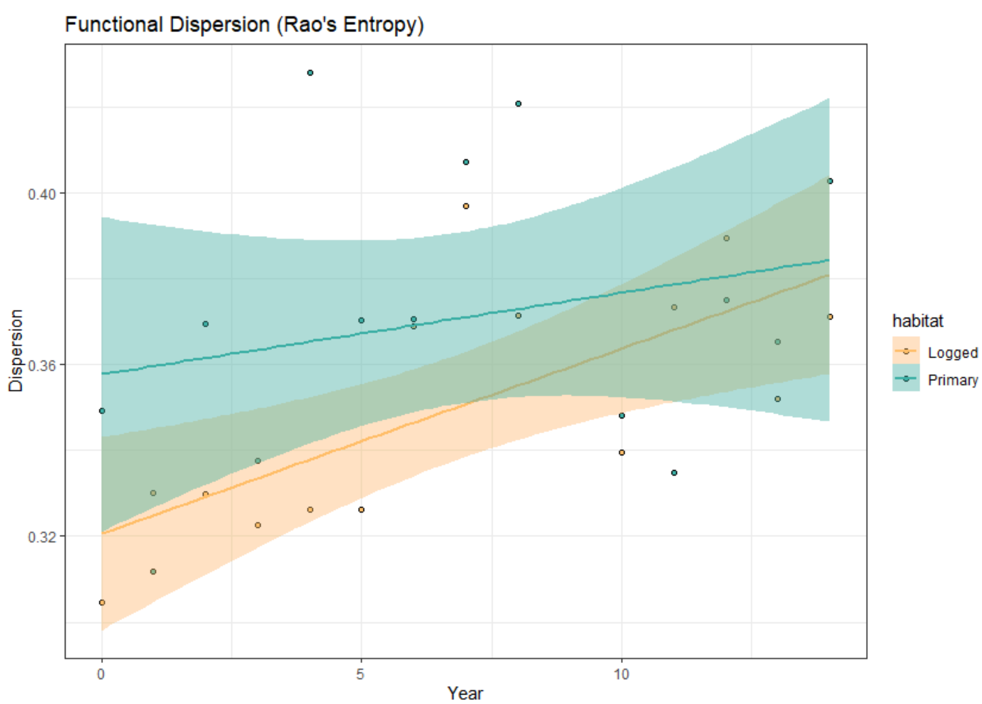

Figure 8. Linear regression for Rao's entropy over time. The solid line represents the best fit line according to ordinary least squares with the shaded regions representing the 95% confidence intervals around the line.

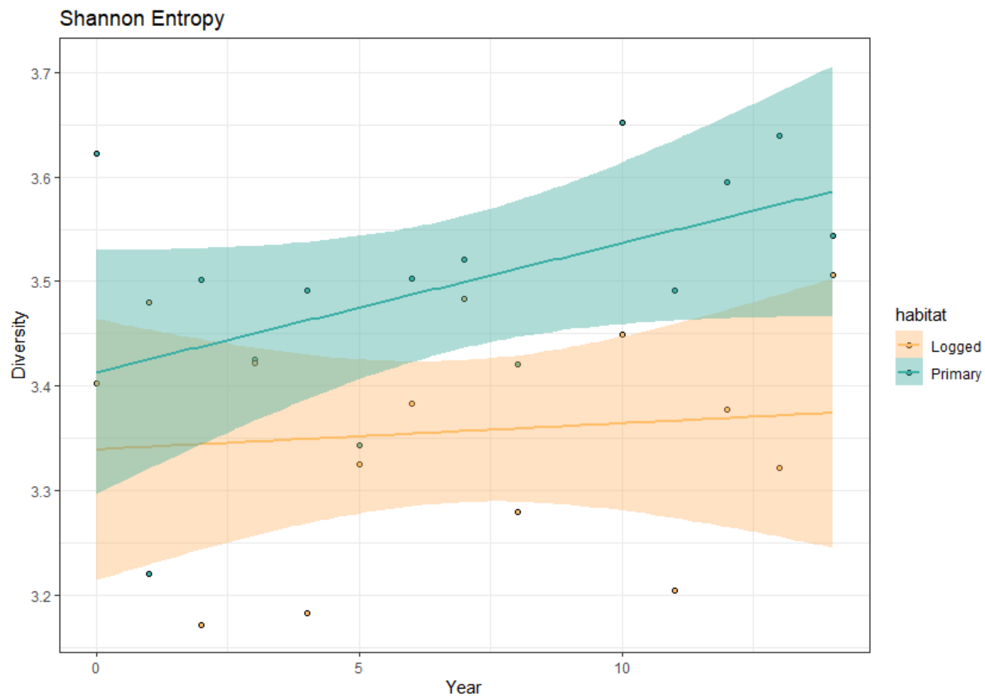

Figure 9. Linear regression for Shannon diversity with time. The solid line represents the best fit line according to ordinary least squares with the shaded regions representing the 95% confidence intervals around the line.

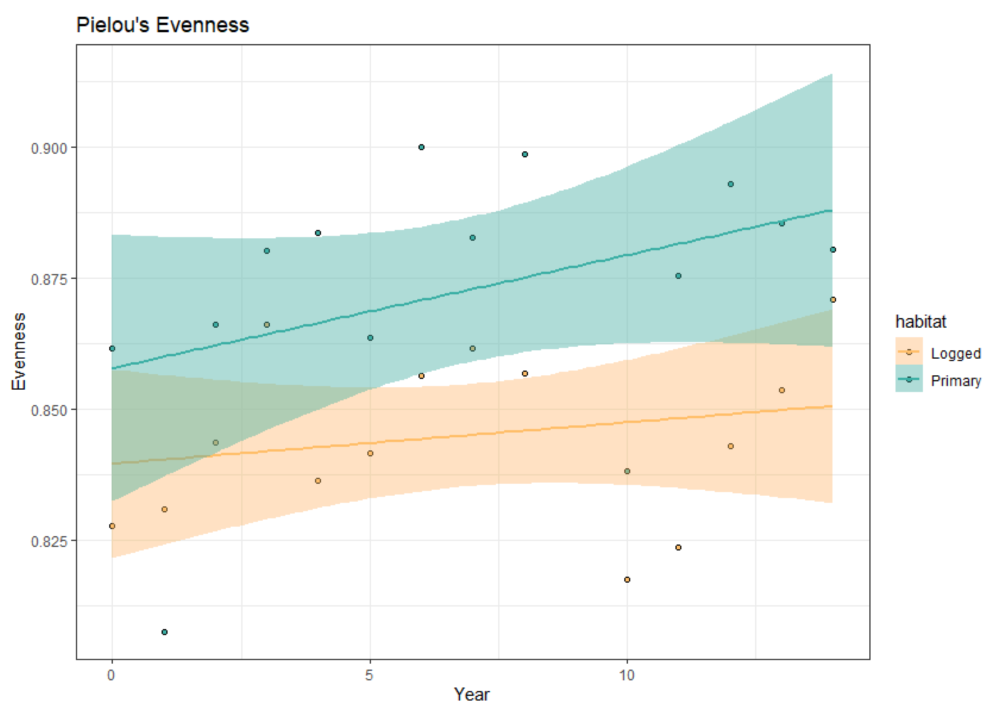

Figure 10. Linear regression for Pielou's evenness with time. The solid line represents the best fit line according to ordinary least squares with the shaded regions representing the 95% confidence intervals around the line.

There was no evidence for change in bill uniqueness with time in both primary and logged forest (β (slope logged) = 0.044; 95% CI = [-0.017, 0.105]; β(slope(primary-logged)) = -0.006; 95% CI = [-0.091, 0.080]; R^2 = 0.15; Figure 11).

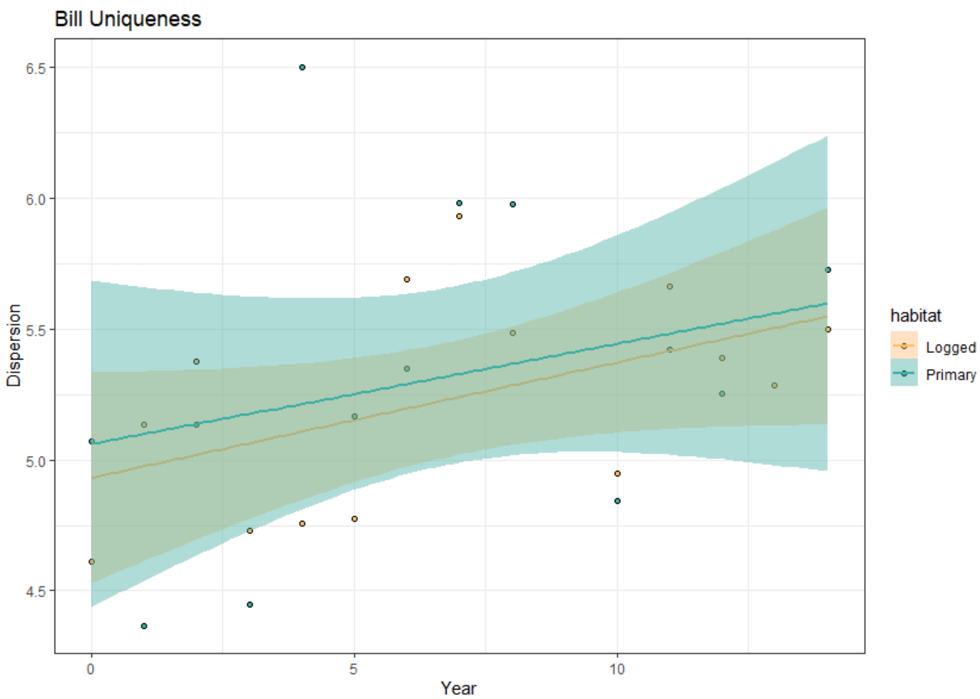

Figure 11. Linear regression for bill uniqueness over time in primary and logged forest. The solid line represents the best fit line according to ordinary least squares with the shaded regions representing the 95% confidence intervals around the line.

Similar to trends in functional dispersion, some morphological traits showed temporal trends in logged forest but not in primary forest. A few exceptions to these trends were the changes in bill width and bill depth relative to bill length in primary forest. The major results are summarised below. Contrary to our expectations, community-weighted body mass increased over time in logged forest and showed a weak but non-significant positive trend in primary forest as well (β(slope logged) = 0.229; 95% CI = [0.031, 0.426]; β(slope(primary-logged)) = -0.091; 95% CI = [-0.371, 0.188]; R^2 = 0.29; Figure 12a). Community-weighted bill length showed a non-significant positive trend in both primary and logged forest (β(slope logged) = 0.033; 95% CI = [-0.032, 0.098]; β(slope(primary-logged)) = 0.026; 95% CI = [-0.065, 0.118]; R^2 = 0.19; Figure 12b).

Surprisingly, bill width (normalised by bill length) and bill depth (also normalised by bill length) showed significant temporal trends; in primary forest, bill width decreased while there was no evidence for statistically significant change in logged forest (β(slope logged) = 0.000; 95% CI = [-0.005, 0.001];

β(slope(primary-logged)) = -0.001; 95% CI = [-0.002, 0.000]; R^2 = 0.30; Figure 12c). Bill depth decreased in primary forest and showed no evidence for change in logged forest (β(slope logged) = 0.001; 95% CI = [0.000, 0.002]; β(slope(primary-logged)) = -0.002; 95% CI = [-0.004, -0.001]; R^2 = 0.28; Figure 12d).

There was an increase in community-weighted wing length in logged forest but no statistically significant change in primary forest with time (β(slope logged) = 0.224; 95% CI = [0.032, 0.416]; β (slope(primary-logged)) = -0.121; 95% CI = [-0.392, 0.151]; R^2 = 0.35; Figure 12e). HWI showed showed an extremely weak non-significant negative trend in logged forest (β(slope logged) = -0.020; 95% CI = [-0.059, 0.018]; β(slope(primary-logged)) = 0.020; 95% CI = [-0.034, 0.075]; R^2 = 0.64; Figure 12f). Similar to wing length there was an increase in community-weighted tarsus length in logged forest but no statistically significant change in primary forest (β(slope logged) = 0.061; 95% CI = [0.005, 0.117]; β(slope(primary-logged)) = -0.048; 95% CI = [-0.127, 0.031]; R^2 = 0.24; Figure 12g).

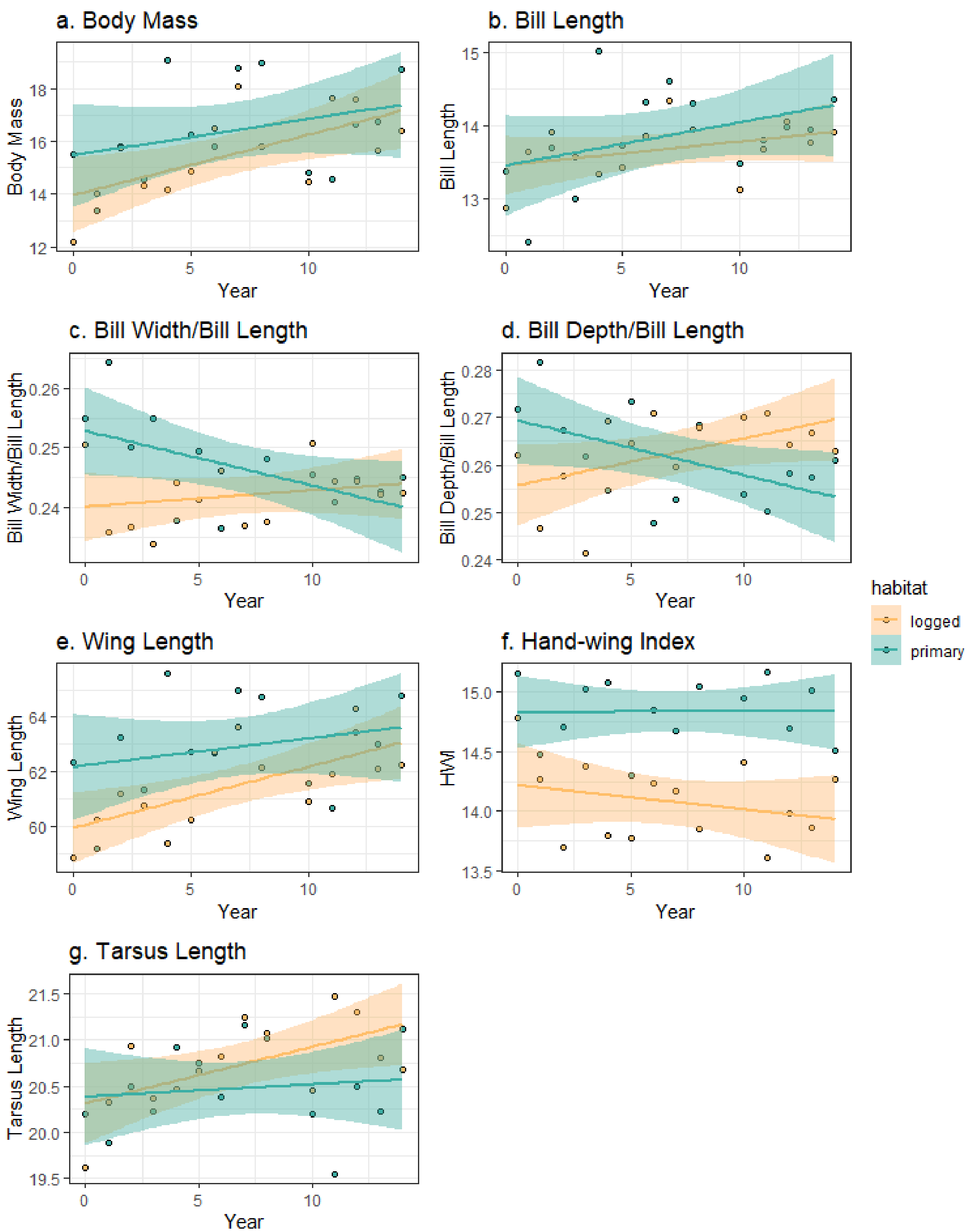

Figure 12. Linear regressions for individual traits over time. The solid lines represent the best fit lines according to ordinary least squares for respective habitat type and the shaded region represents the 95% confidence interval around the line.

3.3. Overlap in trait space at 2000m ASL for species increasing and decreasing in abundance

Apart from the natural cycles in population, some species at 2000m ASL show drastic reductions in population size over the fifteen year periods while other species have considerably increased in their abundance. The time-series of raw counts versus time for a selected subset of species can be found in the supplementary information (Figure S1).

In primary forest, the 30th percentile and 70th percentile spanned zero (30% quantile = -0.256; 70% quantile = 0.087) therefore, species below the 30th percentile were considered to be decreasing at this elevation in primary forest and species above the 70th percentile were considered to be increasing at this elevation in primary forest. Similarly, in logged forest as well, the 30th and 70th quantile spanned zero (30% quantile = -0.008; 70% quantile = 0.230) therefore, species below the 30th percentile were considered to be decreasing at this elevation in logged forest and species above the 70th percentile were considered to be increasing at this elevation in logged forest. The histograms for distribution of rate of change of species abundances over time in the two habitat types (Figure S2 & Figure S3) and tables that list the species (Table S1 & Table S2) can be found in the supplementary information.

A PCA shows that there is a high degree of overlap between functional trait space between species increasing and decreasing in abundance in both primary and logged forest (Figure 13).

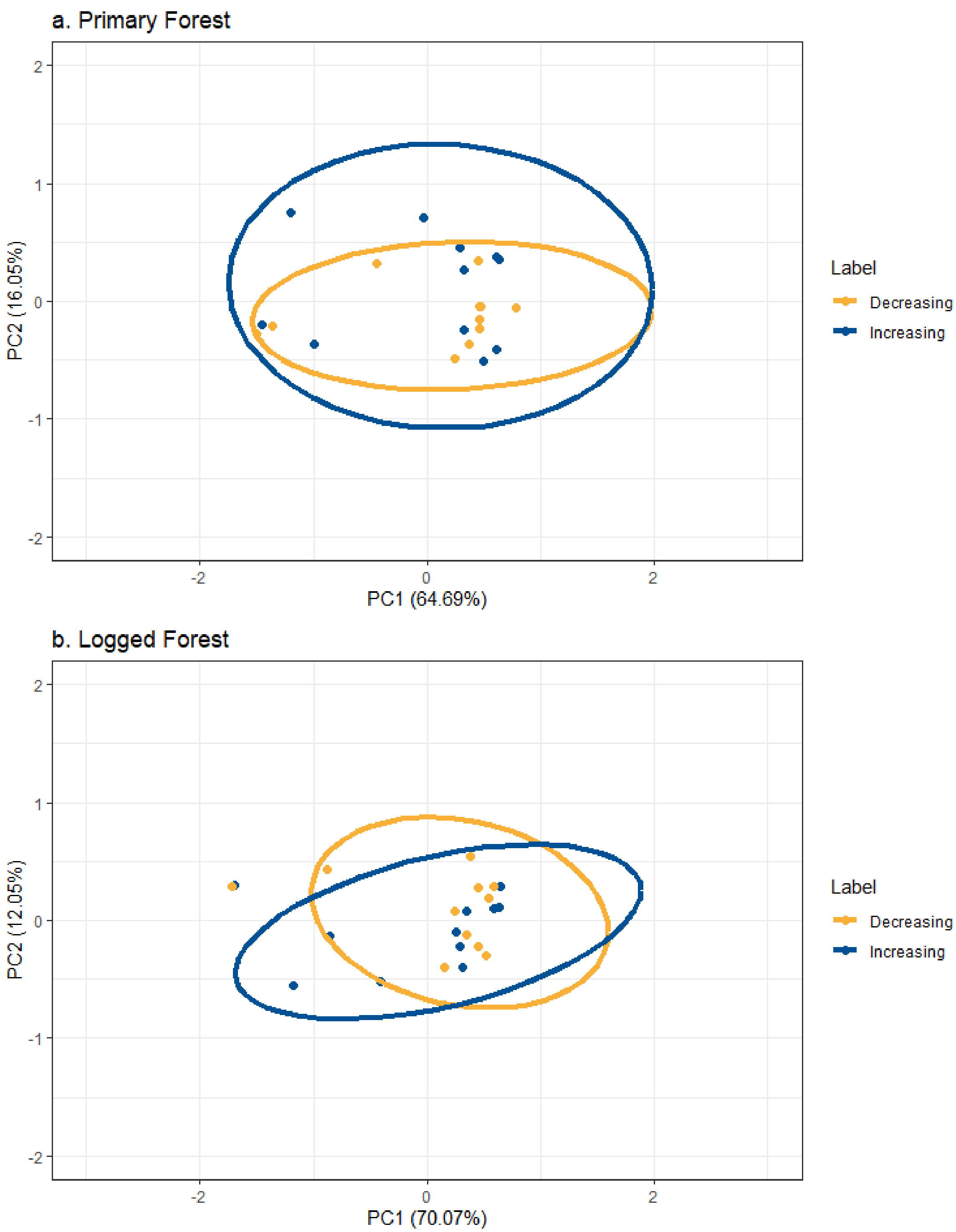

Figure 13. PCA plots show overlap in functional trait space for species that are increasing in abundance and decreasing in abundance in the two habitat types: (a) primary forest, (b) logged forest.

Chapter 4: Discussion

I report differences in functional diversity and trait distributions between primary and logged forest at a mid-elevation site in the Eastern Himalaya. I found no evidence for differences in functional dispersion (a measure of functional diversity) between the two habitat types. Similarly, I found no evidence for a difference in bill uniqueness with habitat. There was also no evidence for significant difference between habitat types for most functional traits including body mass, bill length, bill width relative to bill length, bill depth relative to bill length and tarsus length. The exceptions to these trends were community-weighted wing length and HWI, both of which were higher in primary forest bird communities. I found that functional dispersion, body mass, wing length and tarsus length increased over time in logged forest but show no evidence for change in primary forest. In addition to this, bill width and bill depth normalised by bill length both decreased in primary forest but did not change in logged forest. There was no evidence for change in other body traits and bill uniqueness over time in both habitats. Finally, I found that functional trait-space is overlapping for species that are decreasing and increasing in abundance at 2000m ASL in both primary and logged forest habitats.

Because of the poor goodness of fit for the linear models that use only habitat as a predictor variable, we cannot make any conclusive inferences about the nature of relationship between functional diversity, body traits and bill uniqueness to habitat type.

The Shannon diversity of primary forest is higher when compared with logged forest. This was expected as logged forest is homogenised in vegetation structure and has fewer microclimates for species to occupy thereby reducing the number of different species that can co-exist in logged forest. In addition to this logged forest also has fewer resources meaning that it would have greater competition thereby competitively excluding some species that could have survived in undegraded forest patches. In terms of evenness, it was found that primary forest also has a more equitable community when it comes to abundances of species. This high degree of evenness in primary forest could mean that it is primary forest has better cycling of resources and the niches in primary forest is more evenly occupied but it must be noted that logged forest itself has a high degree of evenness ~0.84 and therefore, both primary and logged forest bird communities are even in their communities.

Both Shannon diversity and Pielou's evenness do not change with time in either habitat type. This is interesting particularly because there is a turnover in species community composition over the fifteen year period and this not being reflected in either diversity or evenness metric probably means upslope range shifts are appropriately compensating for species lost at this elevation.

Contrary to my expectations, functional dispersion did not differ between the primary and logged forest (Figure 3) and showed a significant increase in logged forest with time (Figure 8). It is often assumed, and has sometimes been shown, that functional diversity decreases with time in anthropogenically modified habitats (Ernst et al., 2006; Flynn et al., 2009; Mouillot et al., 2013). At 2000m ASL in the Eastern Himalaya, increasing functional dispersion in logged forest bird communities was surprising. I have two hypotheses for why the functional dispersion might increase in logged forest over time:

a. Species loss is typically a non-random process (Dirzo et al., 2014) and in habitats where high functional similarity exists between species in a community, it is possible that species that are redundant in their functions are lost because of an increase in competition under resource-limited conditions (Brandl et al., 2016). This could cause an increase in functional dispersion because the average pairwise distances between species traits increases. An increase in functional originality (defined as "the isolation of a species in functional space occupied by a particular community" by Mouillot et al. (2013)) has been documented in an assemblage of coral reef fish in response to anthropogenic stressors. This increase in functional originality as documented by Brandl et al. (2016) was because of the decrease in functionally similar species susceptible to loss of coral habitat and an increase in the number of unique species that have traits that make them well-adapted to anthropogenic disturbance. This hypothesis can be tested by looking at how functional redundancy and functional originality of the bird community varies with time.
b. Trends in functional diversity in birds and other taxa along elevation gradients has been well documented, with most studies finding that functional diversity decreases with increasing elevation (Dehling et al., 2014; Spasojevic et al., 2014; Ding et al., 2019). This is probably because of lower elevation communities being structured more by competition which leads to an overdispersion in traits (Fleming, 1979) and communities at higher elevations being structured by abiotic filtering leading to trait clustering (Webb et al., 2002). Because logged forest poorly buffers against temperature extremes (Senior et al., 2017; Santos et al., 2024), it might be expected that climate warming will impact logged forest at a faster rate, mimicking low-elevation temperatures more. I hypothesise that upslope range shifts by low-elevation species towards 2000m ASL in response to increasing temperatures might be causing low-elevation species to preferentially occupy logged rather than primary forest. Because species from lower elevations that are likely already more overdispersed in their trait-spaces, move upwards into logged forest, this could be increasing functional diversity at mid-elevation. To test this, first it is necessary to (a) first establish how functional diversity varies with elevation in the Eastern Himalaya and then (b) to collect long-term elevation data to accurately

understand upslope range shifts of these species, and (c) differences in relative abundance of low-elevation species in primary and logged forest.

Similarly, contrary to my expectations, there was no evidence for change in body mass CWMs in primary forest but an increase in logged forest. While most research in the past have reported declines in body mass with warming and in disturbed habitats (Sheridan & Bickford, 2011; Paquette et al., 2014; Messina et al., 2021) these studies are restricted to individual species or averages of species-specific body mass declines, although Messina et al. (2021) also showed that some insectivorous bird species are increasing in body mass over time in logged habitat when compared with an unlogged site. Even previous studies from the same study region have reported declines in some species-specific body masses in logged forest (Bharadwaj et al., 2025). I hypothesise that while species-specific body masses might be declining in the study region, the increase in CWM for body mass might be being driven by the increase in abundance of a few large species. These large species although are not adapted to the warmer climates of logged forest, they are better thermoregulators and might be better adapted to the variation in temperature in logged forest especially in winters when poor buffering capacity of logged forest causes temperatures to drop and leads to the death of small bodied bird species. This can be tested by examining how much each individual species contributes to the overall trend in CWM and in what direction by the framework set up by Gaüzère et al. (2019).

Despite an established difference in arthropod communities between the two habitats, with primary forest hosting more foliage dwelling arthropods and logged forest more flying arthropods (Aggarwal et al., 2023), I found that community-weighted HWI is higher in primary forest. Traits such as HWI might have lower values in fragmented/disturbed habitats, with medium HWI, small body size and large range sizes being correlated with bird species that can persist in fragmented habitats (Han et al., 2025). Han et al. (2025) also hypothesise that larger values of HWI in undisturbed habitats might arise from specialist species that require large areas of continuous habitat. Therefore, this trait associated with high flight efficiency (Weeks et al., 2022), might be advantageous in continuous habitats with fewer obstacles. A more probable reason for the lower HWI in logged forest is that the invasion of bamboo in the understory selected for species that hop or crawl rather than fly. This could have led to the reduction of HWI in logged forest and the unchanging HWI is probably a signature of the constant vegetation structure in logged forest.

Surprisingly, while neither functional dispersion nor trait values changed with time in primary forest, bill width and bill depth (relative to bill length) declined. But a similar change was not observed in logged forest. In primary forest, community-weighted bill traits could change because of changes in arthropod communities over the fifteen year period. To investigate this, further long-term arthropod data and information on bird species' diets would be required. A similar change might not be observed in logged forest potentially because of the stronger abiotic filter imposed by logging, leading to a more temporally homogenised arthropod community composition and in turn, a more temporally homogenised set of bill traits in the bird species that feed on these arthropods. A more thorough examination of arthropod communities in both primary and logged forest might reveal why this trend in bill morphologies exists. This could also be the function of something other than diets of these bird species and the arthropods they consume, for example, recently there has been more research about the thermoregulatory potential of the bird bill.

The bird bill is also a thermoregulatory organ, and can be used to either conserve or dissipate heat depending on environmental conditions (Greenberg et al., 2012). It is possible that the lack of long-term changes in bill size in logged forest habitat might be because these bird species use their bill to dissipate excess heat in the warmer conditions of the logged forest. Species in primary forests are likely not to face harsh heat stress and warming compared with the species in logged forest. Therefore, it is possible that temporal trends in bill morphology might be more correlated with diet in primary forest as opposed to the thermoregulatory role of the bill in logged forest. This might explain changes in bill morphology in primary forest but not in logged forest. Similar to changes in body mass in logged forest, tarsus length and wing length also increased in logged forest. This is most likely because of the correlation between body mass and the two traits under consideration (see Appendix Figure A3). It could also be because of the thermoregulatory potential of the wing and tarsus similar to bills that allows species with larger wings (Jirinec et al., 2021) and tarsi to persist in logged forest (Ryding et al., 2024).

I expected changes in functional diversity and functional traits with time even in primary forest but there was no evidence for changes in functional diversity with time in these habitats. This could potentially be because, although primary forest has a functional diversity that is only marginally higher than logged forest, even if functionally diverse bird communities move upslope and establish themselves in primary forest, it is not changing the overall functional diversity. Evidence already exists for upslope range shifts in bird species in the Eastern Himalaya (Girish & Srinivasan, 2022). The PCA (Figure 13) was a preliminary analysis that shows that for primary forest, the functional trait-space is overlapping for both species, increasing in abundance at 2000m ASL and decreasing in abundance at 2000m ASL and the trait-space for species increasing in abundance is not overdispersed. This supports the hypothesis that functional diversity is not changing with time even though communities are changing because of the pre-existing high functional diversity. But, the same overlap in trait-space was seen for logged forest as well when ideally, the trait-space for species increasing in abundance (entering 2000m ASL) should be more dispersed. The PCA analysis might not correctly identify species that are entering and leaving 2000m ASL as it can only determine if a species is decreasing or increasing in abundance at that elevation. A more refined analysis could be using long-term elevation data to accurately determine upslope range shifts and checking if these species undertaking upslope range shifts actually preferentially enter logged forest or show no preference for habitat type.

Previous work in regards to trait distributions have overwhelmingly suggested that species' responses to environmental change depend on their traits and trait distributions (MacLean & Beissinger, 2017; Pacifici et al., 2017), and that global change drivers can also cause changes in trait distributions (Vázquez-Reyes et al., 2022; Kang et al., 2025). Here, using a trait-based approach, I show that there are differing impacts in an intact and an anthropogenically modified habitat that are likely caused because of climate change and its interaction with human disturbance. An increase in functional dispersion in logged forest over time could mean that logged forest has better conservation potential for functional diversity. However, it is likely that the increase in dispersion in logged forest is occurring because of the faster impacts of climate change and warming in these habitats as compared with primary forest that offers a greater buffering capacity against the warming, although this mechanism is yet to be investigated. This indicates that likely climate effects are not equal across disturbance gradients and more studies should investigate the effects of climate change and land-use change and how they interact with each other rather than treating these two global change drivers in isolation.

Supplementary Information

Changes in community composition at 2000m ASL

The time-series of raw counts against time for a few common species that have decreased and increased in abundance are presented in Figure S1.

From the time-series of the four species it is clear that the Black-throated Parrotbill and Snowy-browed Flycatcher are decreasing in abundance at this elevation albeit, at different rates in the two habitat types. Similarly, the White-gorgeted Flycatcher and White-spectacled Warbler are increasing in abundance in both habitat types at this elevation but at different rates.

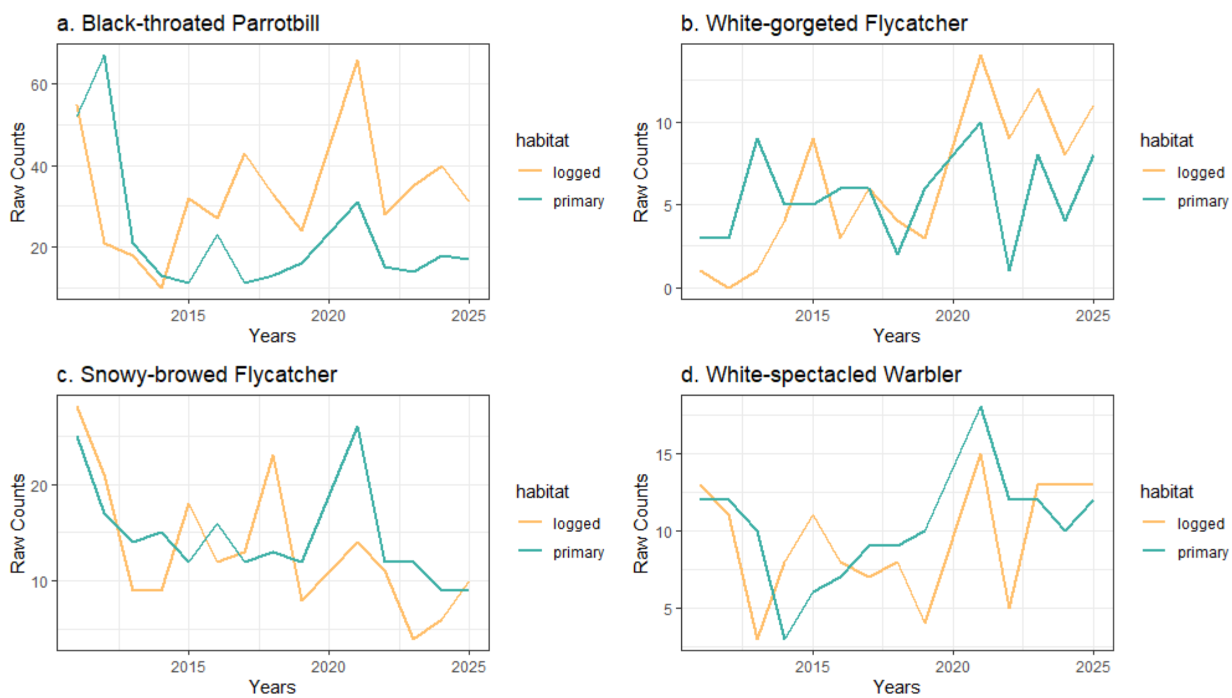

Figure S1. Time-series of four species in primary and logged forest at an elevation of 2000m ASL. Species a and c) Both Black-throated Parrotbill and Snowy-browed Flycatcher are decreasing in the two habitat types. Species b and d) White-gorgeted Flycatcher and White-spectacled Warbler show evidence of increase in the two habitat types.

These are just the most representative examples of increase or decrease in abundance at this elevation in the two habitat types. Most species display such trends with time. Many interesting questions about natural cycles in populations and the phase difference in these cycles between primary and logged forest arise but these are out of the scope of the present thesis.

Rate of change in species raw counts with time

Below are two figures representing the distribution of rate of change in species abundances with time

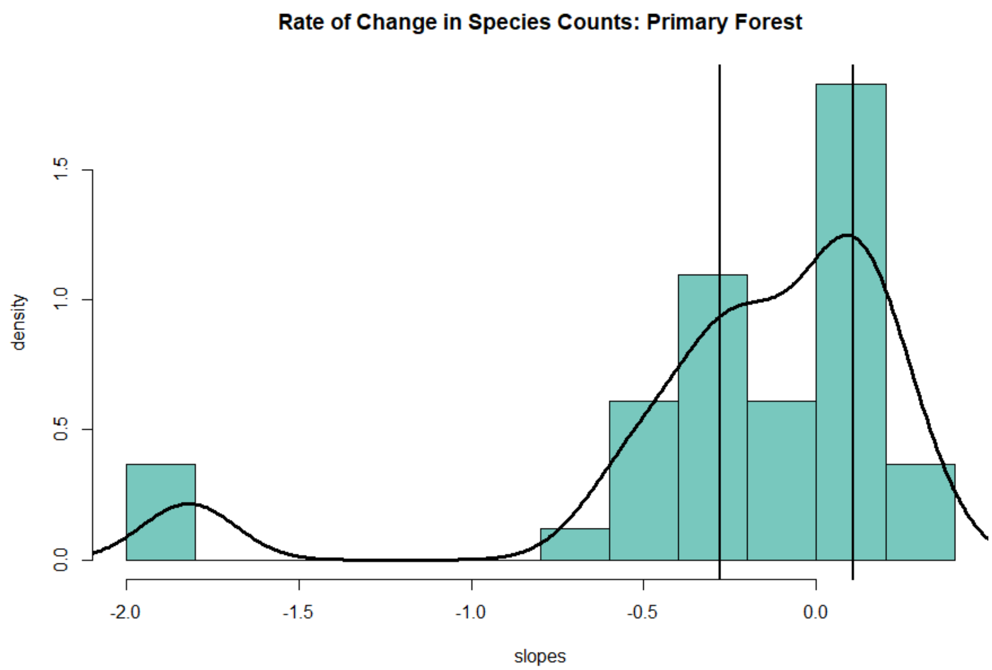

Figure S2. Histogram of slopes of species raw counts against time (30% quantile = -0.256; 70% quantile = 0.087), the vertical lines representing the 30th and 70th percentile and the solid curve representing the density curve.

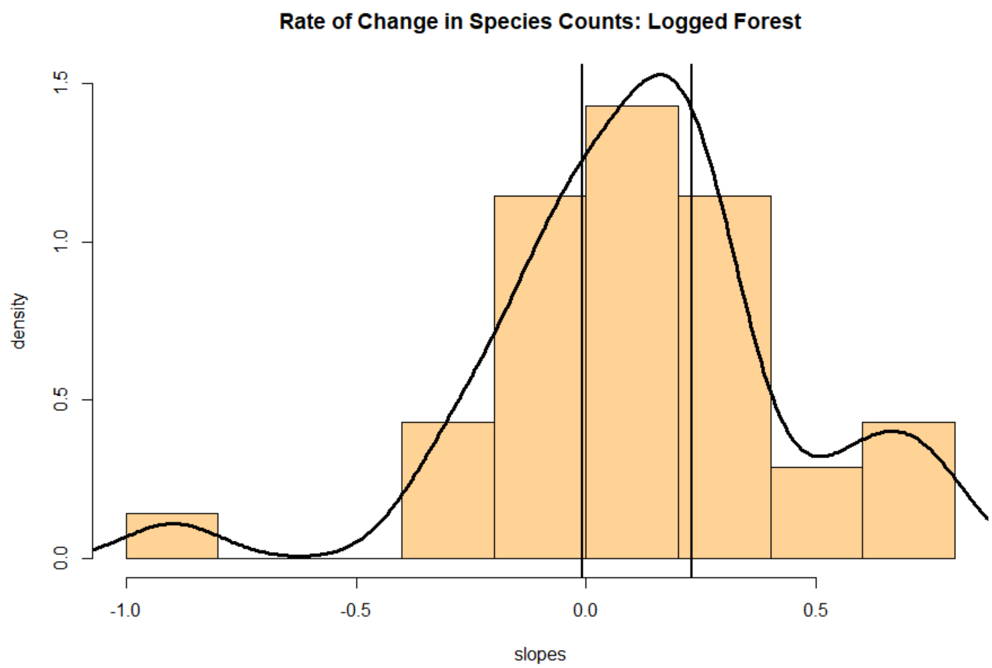

Figure S3. Histogram of slopes of species raw counts against time (30% quantile = -0.0084; 70% quantile = 0.2297), the vertical lines representing the 30th and 70th percentile and the solid curve representing the density curve.

S.No.	Species	Trend	Rate of Change
1.	White-spectacled Warbler	Increasing	0.28
2.	White-browed Piculet	Increasing	0.28*
3.	White-throated Fantail	Increasing	0.18
4.	Whiskered Yuhina	Increasing	0.17
5.	Green-tailed Sunbird	Increasing	0.14
6.	Beautiful Sibia	Increasing	0.13
7.	White-gorgeted Flycatcher	Increasing	0.12
8.	Golden Babbler	Increasing	0.12
9.	Black-crowned Scimitar-Babbler	Increasing	0.11
10.	Slender-billed Scimitar-Babbler	Increasing	0.11
11.	Slaty-bellied Tesia	Increasing	0.09
12.	Gray-bellied Tesia	Decreasing	-0.26
13.	Rusty-fronted Barwing	Decreasing	-0.28
14.	White-breasted Parrotbill	Decreasing	-0.30
15.	Blyth's Leaf Warbler	Decreasing	-0.31
16.	Black-faced Warbler	Decreasing	-0.33
17.	Rufous-bellied Niltava	Decreasing	-0.44
18.	Whistler's Warbler	Decreasing	-0.44
19.	Snowy-browed Flycatcher	Decreasing	-0.52
20.	Rufous-winged Fulvetta	Decreasing	-0.53
21.	Yellow-throated Fulvetta	Decreasing	-0.63
22.	Black-throated Parrotbill	Decreasing	-1.82

Table S1. List of species increasing and decreasing in abundance in primary forests. * indicates a statistically significant slope.

S.No	Species	Trend	Slope
1.	White-gorgeted Flycatcher	Increasing	0.77
2.	Black-throated Parrotbill	Increasing	0.72
3.	Golden Babbler	Increasing	0.67
4.	White-tailed Robin	Increasing	0.59
5.	Rusty-fronted Barwing	Increasing	0.52
6.	Chestnut-crowned Laughingthrush	Increasing	0.33
7.	Yellow-throated Fulvetta	Increasing	0.31
8.	White-browed Piculet	Increasing	0.29
9.	Lesser Shortwing	Increasing	0.27
10.	Golden-breasted Fulvetta	Increasing	0.25
11.	Beautiful Sibia	Increasing	0.23
12.	Rufous-winged Fulvetta	Decreasing	-0.01
13.	Black-crowned Scimitar Babbler	Decreasing	-0.05
14.	Whiskered Yuhina	Decreasing	-0.06
15.	Streak-breasted Scimitar Babbler	Decreasing	-0.08
16.	Red-flanked Bluetail	Decreasing	-0.09
17.	Green-tailed Sunbird	Decreasing	-0.15
18.	Rufous-capped Babbler	Decreasing	-0.19
19.	Gray-headed Canary-Flycatcher	Decreasing	-0.21
20.	Whistler's Warbler	Decreasing	-0.29
21.	Gray-bellied Tesia	Decreasing	-0.33
22.	Snowy-browed Flycatcher	Decreasing	-0.90

Table S2. List of species increasing and decreasing in abundance in logged forests. * indicates a statistically significant slope.

Appendix

	species	Body.Mass	Beak.Length_Culmen	Beak.Length_Nares	Beak.Width	Beak.Depth	Tarsus.Length
1	Aberrant Bush Warbler	9.73	13	6.575	2.825	2.475	21.175
2	Alpine Thrush	77.3025	25.06	14.75	5.3	5.66	36.16
3	Ashy-throated Warbler	5.464285714	8.92	4.225	2.6	2.12	18.06
4	Ashy Drongo	48.83538462	25.44285714	16.67857143	9.29047619	8.415	18.60952381
5	Barred Cuckoo-Dove	250.97	22.06	9.475	3.34	4.22	21.9
6	Bay Woodpecker	159.7533333	45.68181818	33.69	8.963636364	10.61818182	26
7	Beautiful Sibia	38.5131	24.88	14.4	4.68	5.08	30.76
8	Besra	105	NA	NA	NA	NA	NA

Figure A1. The first eight rows and first eight columns of the average species-trait matrix.

	species	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020
1	Aberrant Bush Warbler	0	0	0	0	0	0	0	0	0	NA
2	Alpine Thrush	0	0	1	0	0	0	0	0	0	NA
3	Ashy-throated Warbler	4	0	0	3	0	0	0	0	0	NA
4	Ashy Drongo	0	0	0	1	1	0	0	0	0	NA
5	Barred Cuckoo-Dove	0	0	0	0	0	0	0	0	0	NA
6	Bay Woodpecker	1	0	1	0	0	0	0	0	1	NA
7	Beautiful Sibia	4	3	0	5	4	2	9	4	3	NA
8	Besra	1	0	0	0	0	0	0	0	0	NA
9	Black-crowned Scimitar-Babbler	5	1	2	1	0	3	1	6	0	NA
10	Black-eared Shrike-Babbler	0	0	1	0	0	0	0	0	1	NA
11	Black-faced Warbler	4	10	7	12	3	3	8	1	3	NA
12	Black-throated Parrotbill	52	67	21	13	11	23	11	13	16	NA

Figure A2. Raw counts matrix for primary forest till the year 2020.

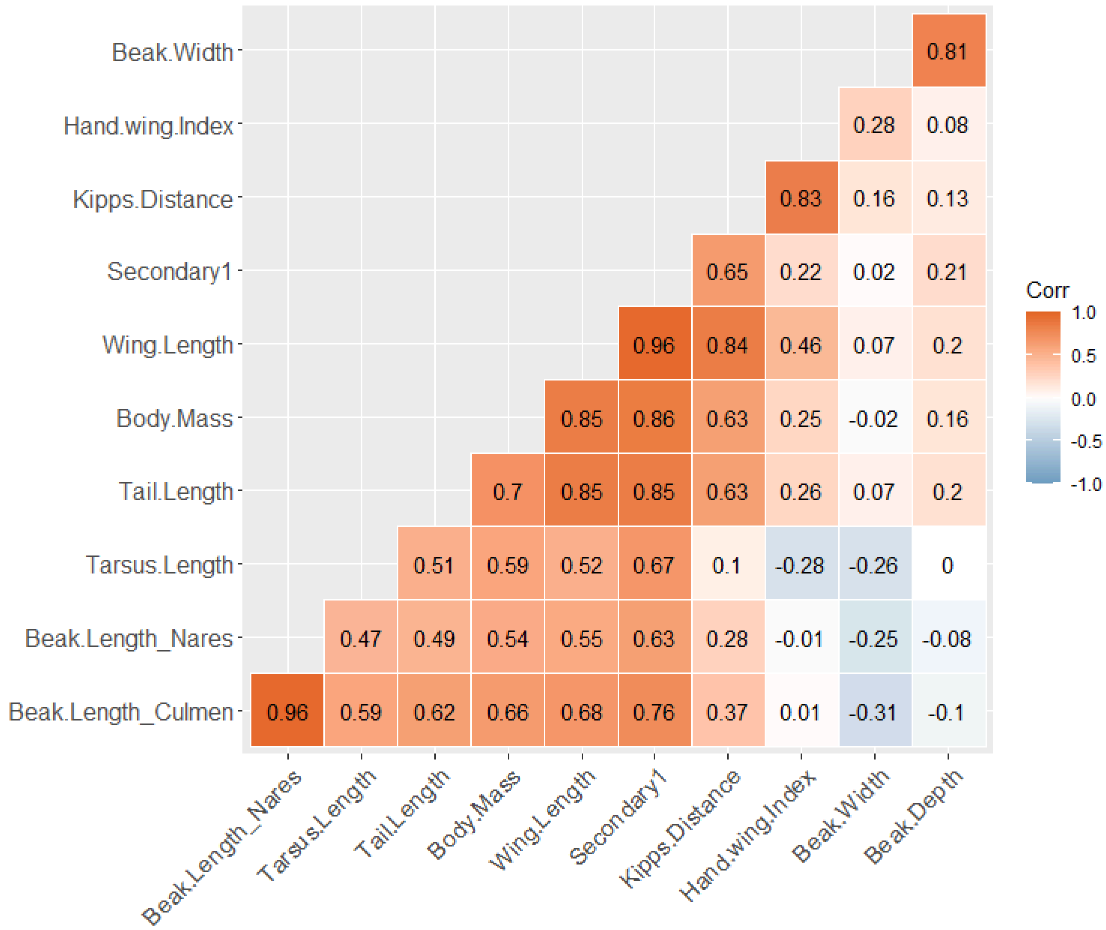

Figure A3. Correlation matrix for all morphological traits considered provided in AVONET. Bill depth and bill width are both normalised by bill length culmen.

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