Evaluating impacts of climate change and land-use land-cover change on birds of eastern Indian Himalaya, a global biodiversity hotspot



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Dedicated to the people of Etabe and Ahunli villages



Himalayan Cutia *Cutia nipalensis* seen performing several maneuvers in the forests of Dri. In that moment, Aliha and I sat down on the forest floor and admired it for a long time.

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Author Contributions

Aavika Dhanda completed all aspects of this thesis independently. She acquired funding, formulated ideas, conducted field work, collated and analysed the data, wrote first drafts, and generated final chapters with inputs from the co-authors.

Sonya M. Clegg (supervisor and co-author of Chapter 2, 3, and 4) provided guidance and intellectual inputs on all drafts, co-developed ideas and methodologies, and supported Aavika's funding applications.

Tim Coulson (co-supervisor and co-author of Chapter 2) provided guidance and intellectual inputs on drafts of Chapter 2, 3, and 4.

Micha-l T. Jezierski (co-author of Chapter 2) co-performed modelling

Author contributions are also mentioned at the end of each chapter

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Abstract

Tropical mountains provide a suite of ecosystem services relevant to global, continental, and regional scales. They also provide heterogeneous biotic and abiotic conditions to species in ecologically rich global biodiversity hotspots of the world. However, many tropical mountain regions are highly threatened due to anthropogenic activities, and at the same time, highly understudied. In my thesis, I studied bird communities of the eastern Indian Himalaya, a global biodiversity hotspot, undergoing anthropogenic pressures at varying scales. I assessed how ecological and evolutionary traits of species govern community-level responses to climate change and land-use land-cover change.

In **Chapter 1**, I present the General Introduction. In **Chapter 2**, using secondary data, I explored how climate change at a large spatial and temporal scale impacts the potential distributions of Muscicapids (Flycatchers), one of the largest terrestrial bird families in the region. I found that the habitat generalists were more sensitive to abiotic variables than the habitat specialists, and there was little to no phylogenetic signal detected within the family's response to climate change. I then shifted focus to examining the effects of land-use land-cover changes on the bird communities of Dibang Valley based on my field data. In **Chapter 3**, I applied multiple metrics to investigate the effects of microclimatic variations on the bird communities of four land-use land-cover types at a smaller spatial scale in Dibang Valley. I demonstrated that while taxonomic richness and phylogenetic richness were higher in the natural habitats, the functional richness was the highest in modified habitats. I also observed that the bird communities are tracking both their thermal and hygric niches in these habitats. Finally, in **Chapter 4**, I compared multiple aspects of the relationships between species diversity and forest vegetation, before and after the onset of small-scale disturbance. I found evidence for a rise of sub-canopy invertivores, although the overall species diversity was maintained. In General Discussion (**Chapter 5**), I summarise my broad findings and suggest future directions. This thesis elucidates that the responses in the eastern Indian Himalayan bird communities are quite intricate, the evaluation of which has implications for landscape conservation.

Chapter 1

General Introduction

Humans are altering the planet in a multitude of ways, generating wide-ranging effects on other species, biomes, ecosystem functions, and services. Arguably, one of the most ubiquitous anthropogenic effects is human-mediated climate change. Climate change is manifested as an increase in the frequency of extreme events such as intense snowfalls, floods, heavy rains, heat waves, droughts, and wildfires (Trenberth, 2011). Varied effects of climate change also result in severe changes in agricultural patterns and the resultant food crisis (Wheeler and von Braun, 2013), an increase in vector-transmitted human diseases (Kovats et al., 2001), and altered physiology, growth, reproduction and survival of species (Harley et al., 2012). Human-induced warming had increased by 1°C in 2017 and is expected to continue increasing at the rate of 0.20°C per decade (Intergovernmental Panel On Climate Change, 2023). The Intergovernmental Panel for Climate Change (IPCC) aims to hold the increase in global average temperature to below 2°C above preindustrial levels while continuing to hold temperature increase to 1.5°C above preindustrial levels by 2025 and 2030 (UNFCCC, 2022). These targets have been criticised as inefficient (Gupta et al., 2024), and will result in massive biodiversity losses, especially in the tropics (Price et al., 2024).

In addition to climate change, tropical biodiversity also faces the effects of habitat alteration, hunting, logging, fire, fragmentation, the emergence of pathogens, environmental stressors such as UV radiation, pesticides and pollutants, and outbreak of diseases- which at times may interact with each other (Laurance and Useche, 2009). While these events are likely to have profound impacts on several species, land-use/ land-cover change remains the most significant with many direct and cascading effects on ecological functions, biomass, species richness, and biotic interactions in tropical systems (Barnes et al., 2017).

Climate change impacts on biodiversity: higher sensitivity in the tropics

Human-induced climate change can affect biodiversity at individual, population, community, ecosystem, and biome scales, giving rise to one, or a combination of species responses to evade local or global extinction. Broadly, these responses may be phenological, for

example, adjustments in the breeding period in passerine birds (Charmantier et al., 2008; Both et al., 2009) or advancements in butterfly emergence stage (Diamond et al., 2011); physiological, for example, accumulating tolerance to warmer climate (Bennett et al., 2019) or undergoing elevational or latitudinal range shifts and distribution changes. The latter appears to be a particularly obvious and frequently-studied response, with examples known from a wide range of taxa spanning plants (Kelly and Goulden, 2008), fish (Comte et al., 2013), butterflies (Rödder et al., 2021), and birds (Kirchman and Van Keuren, 2017).

The prevailing research suggests that the patterns of climate-induced range shifts and distribution changes are expected to follow an upward trend. For instance, the Arctic birds are predicted to track their climatic niches latitudinally with no trend in southward movement (Brommer et al., 2012). Such poleward movement of species is expected to increase species richness in the temperate latitudes (Hiddink and ter Hofstede, 2008), and also lead to increased population density towards the poles (Virkkala and Lehikoinen, 2014). However, regions in the higher latitudes have largely been at the epicentre of climate change research, findings from which may not adequately reflect the processes occurring at the lower latitudes (Sheldon, 2019). For instance, several tropical bird species are now demonstrating multi-directional distributional shifts determined by their temperature and precipitation tolerances (VanDerWal et al., 2013), deviating from the common assumption that range shifts are solely poleward or uni-directional and based on temperature alone (Parmesan and Yohe, 2003). The distribution changes in tropical species can thus be disparate and at times be highly idiosyncratic compared to species in the higher latitudes.

Distribution changes and range shifts in tropical species can be nuanced and region-specific, which may be overlooked by global patterns. Tropical terrestrial vertebrates, for instance, are likely to be thermal specialists (Chan et al., 2016), and could potentially have limited ability to exist outside of their current distributions (Kellermann et al., 2009). Moreover, tropical regions hold many hotspots with disproportionately high numbers of

range-restricted endemics that are projected to lose their suitable ranges in greatly variable patterns (Malcolm et al., 2006). These species are also often found in data-deficient parts of the world (Cayuela et al., 2009). Thus, it is crucial to model the impacts on tropical species at regional and local scales instead of relying on global models, findings from which are generally biased towards the heavily studied systems in the higher latitudes (Bitencourt et al., 2016). In addition to climate change, species in the tropical regions are also anticipated to have synergistic impacts with other human-induced threats such as land-use/ land-cover change, which is immediate and extreme, hence amplifying the complexities of making accurate predictions using global models.

Effects of land-use land-cover changes on tropical systems

Land-use land-cover (henceforth LULC) change in the tropics is caused due to various activities such as cash cropping, slash-and-burn agriculture, selective logging, and deforestation occurring at different spatial scales, and have negative impacts on the regional hydrological and atmospheric processes. Small-scale conversion of tropical forests to agricultural lands by the traditional method of slashing-and-burning (swidden agriculture), alters local evapotranspiration and runoff rates (Tinker et al., 1996). Large-scale intensification of agriculture affects the biogeochemical cycles, amounts of emissions of trace gases, and proportion of atmospheric gases like CO2, CO, N2O, NO, and CH4 stored in tropical soils and vegetation (Keller and Matson, 1994). In Malaysian Borneo, palm oil plantations are estimated to emit three times the volatile organic compounds as compared to tropical rainforests (Fowler et al., 2011). Conversion of forests to agricultural plantations transforms the original characteristics of microclimatic conditions such as air temperature, wind speed, light intensity, and relative humidity, which also have subsequent negative effects on the overall ecosystem functioning (Anamulai et al., 2019). Selectively logged forests are estimated to have more heterogeneous and hotter air temperatures than intact forests in Malaysian Borneo (Blonder et al., 2018). Native forests provide lower temperatures and higher relative humidity as compared to open pasture lands and plantations in the

tropical mountains of Ecuador (Trávez and Guarderas, 2023). LULC change thus alters abiotic conditions and deteriorates habitat quality at both regional and local scales, which has consequences for biodiversity.

Tropical forests offer stable habitat conditions which is critical for the survival of several species. Vegetation structures such as canopies, epiphytes, ground vegetation, and tree holes provide mean thermal buffering of up to 4℃, thereby protecting species which may not survive in warmer ambient temperatures of non-forested areas (Scheffers et al., 2014). Thermal buffering provided by high canopy cover also mitigates the impacts of heat exposure on understory species of subtropical Asian ants that have high vulnerability to habitat disturbances (Lee et al., 2021). Moreover, microhabitats of understorey vegetation provide foraging opportunities to specialist species dependent on leaf litter, for example, ground-dwelling babblers in Malaysian rainforests (Mansor et al., 2019). Species with such specialised traits are likely to be more susceptible to changes whereas those with generalised traits are expected to persist.

Persist, disperse, or perish: responses to change and consequences for community patterns

Broadly, species can exhibit any of the three types of responses to human-induced climate change and LULC change- to adapt and acclimate (persist), to adapt and migrate (disperse), or to go extinct (perish) - the choice of which is often determined by their ecological and evolutionary traits. Thermal specialists in the tropics, already close to their upper thermal limits, are incapable of adapting and expanding their ranges to increased warming due to climate change (Overgaard et al., 2014). Rainforest species often lack genetic variation necessary for adapting and acclimating to warmer and drier environments (van Heerwaarden and Sgrò, 2014). Many tropical species also lack the evolutionary capacity to undergo morphological trait change as a means to adapt to climate change, and are thus likely to go extinct (Onstein et al., 2018). These highly specialised species also have multiple trophic interactions with other species, further increasing the complications

of persisting or dispersing if the other species that they depend upon cannot adapt at the same rate (Moreira et al., 2018). Additionally, species with low dispersal capacity are extremely sensitive to forest fragmentation (Metzger et al., 2009), and are unlikely to disperse geographically to track their climatic niches (Urban et al., 2013). Climate change and LULC change are hence a catastrophe for tropical specialist species, but can be an opportunity to thrive for generalists.

Species with higher tolerances can adapt successfully. Generalist species that use a wider range of resources, have wider thermal tolerances and niches, can expand their distributions following forest disturbances (Pinotti et al., 2015), are expected to withstand the impacts of both climate change and LULC change (generalization hypothesis) (Sweeney and Jarzyna, 2022). Although climate change and LULC change occur at different spatial and temporal scales, both events may favour species with similar traits (Williams and Newbold, 2020). For instance, in the Neotropics, species that prefer drier climates have higher chances of persisting through both land use and climate changes, whereas those preferring wetter climates have lower chances of surviving forest loss and climate change (Frishkoff et al., 2016). The persistence, dispersal, or extinction of certain species and not of others, can alter the overall community patterns with consequences for regional and local biodiversity.

Responses to change can lead to rearrangement of species community, and losses of functional diversity and phylogenetic diversity in the tropics. For example, in Panama, community composition is over-represented by drought-tolerant species of trees as climate change is expected to benefit species with similar traits (Feeley et al., 2011). The presence of such "winning" traits can result in high losses of functional diversity in a community since ecologically-nuanced or unique traits are lost indefinitely (Barbet-Massin and Jetz, 2015). The replacement of specialists by generalist species following the loss of native forests results in biotic homogenisation (Morante-Filho et al., 2016). Furthermore, it is expected that closely related species occupying similar niches will exhibit similar responses to climate change (niche conservatism hypothesis), resulting in phylogenetic clustering of

communities (presence of closely related species) across the tropics and the subtropics (Voskamp et al., 2022). These responses can have additional consequences in heterogeneous regions, such as the tropical mountains where species generally have narrower thermal tolerances, lower dispersal capacities, (Janzen, 1967), higher cryptic diversity, higher speciation rates, and much greater species accumulation rates, all of which contributes to amplifying the variability in observed patterns due to environmental changes (Polato et al., 2018).

Climate change, LULC change, and bird communities in eastern Indian Himalaya

The Himalaya, a mountain range in South and East Asia, is one of the global biodiversity hotspots of the world (Mittermeier et al., 2011). The climate in the Himalaya is changing at a face pace and from 1982-2006, the annual average mean temperature in the region increased by 1.5 ℃ while the annual average precipitation increased or decreased with local variations (Shrestha et al., 2012; Choudhury et al., 2019). Maximum air temperature in the Himalayan mountain range is predicted to increase by a rate of 0.3 to 1.0℃ per decade under the worst-case climate change emission scenario (Dimri et al., 2018). Such rapid warming is expected to have profound negative effects not only on millions of humans depending on this ecosystem but also on several Himalayan species (Xu et al., 2009). For instance, Himalayan birch *(Betula utilis)*, is predicted to undergo an elevational shift and replace high-elevation alpine species (Schickhoff et al., 2015). Furthermore, rising temperatures and decreasing snowfall have drastically altered vegetation in the high altitudes forcing Himalayan blue sheep *(Pseduois nayaur)* to descend and raid crops, and subsequently attract snow leopards to lower altitudes to depredate livestock (Aryal et al., 2014). Climate change is thus expected to not only alter the Himalayan ecosystem but also species-human relationships.

Second to climate change, deforestation and concomitant LULC change are the biggest threats to species of the Himalayan region. Unprecedented deforestation in the Indian

Himalaya is largely unregulated and it is estimated that only 10% of land area under dense forest will remain intact by the year 2100 (Pandit et al., 2007). Also, continuing construction of hydropower dams on Indian Himalayan river basins will result in additional loss of thousands of hectares of forest cover (Pandit and Grumbine, 2012). Forest disturbances and fragmentation are also altering species niches and community structures in unexpected patterns. Several examples of altered community composition from a wide range of taxa following habitat fragmentation are seen across the Himalaya, for example, plants (Bisht et al., 2022), insects (Bhardwaj et al., 2012), and birds (Basnet et al., 2016).

The Indian Himalayan Region is divided into western and eastern Himalaya, each harbouring disparate patterns of species distribution and diversity. Specifically, bird richness is comparatively higher in the warm, wet, and largely aseasonal climatic region of the eastern Indian Himalaya than in the cold, dry, and relatively more extreme climatic region of the western Indian Himalaya (Price et al., 2011). Thus, birds in the aseasonal eastern Indian Himalaya have narrower niches and are far more sensitive to changing temperatures than their western Himalayan counterparts (Srinivasan et al., 2018a). Distinct abiotic and biotic factors have contributed to high endemicity and diversity in the eastern Himalaya, making it one of the earth's most biologically valuable ecoregions (Olson and Dinerstein, 1998).

Avian studies in the eastern Indian Himalaya have highlighted the essential role of habitat and climatic variability in driving community patterns at varying scales. For instance, bird species richness peaks mid-elevation and then drops abruptly after 2000 meters above sea level as evapotranspiration, plant species richness, and shrub density decline (Acharya et al., 2011). At a much smaller scale, primary forests which provide heterogeneous and complex vegetation attributes, are responsible for maintaining high species richness (Chettri et al., 2005). Notably, understorey and sub-canopy foliage are critical in sustaining overall bird diversity (Acharya and Vijayan, 2017). Additionally, the microclimatic changes following selective logging determine the long-term survival of birds in the region (in pre-print, Bharadwaj et al., 2023).

Arunachal Pradesh state, the largest by land area and part of the eastern Himalaya, has the highest percentage of forest cover in India (Lele and Joshi, 2008). The biodiversity of Arunachal Pradesh is far from being completely catalogued with many new animal and plant species being regularly described, e.g. Arunachal Macaque *(Macaca munzala)* (Sinha et al., 2005), Bugun Liocichla *(Liocichla bugunorum)* (Athreya, 2006), blue-eyed litter frog *(Leptobrachium waysepuntiense)* (Sondhi and Ohler, 2011), pit viper *(Trimeresurus arunachalensis)* (Captain et al., 2019), catfish *(Mystus prabini)* (Darshan et al., 2019), freshwater crab *(Abortelphusa namdaphaensis)* (Mitra, 2020), and plant species, *Impatiens siangensis* (Gogoi and Borah, 2015), and *Henckelia collegii-sancti-thomasii* (Borah et al., 2019).

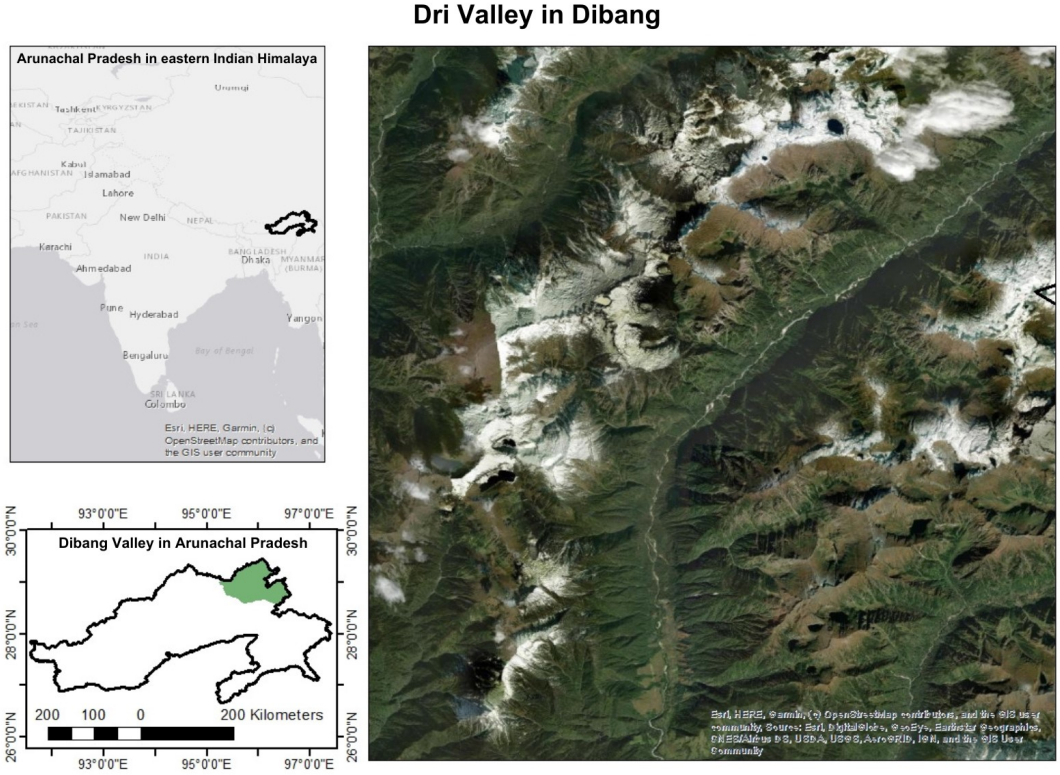

Figure 1: Dri Valley in Dibang Valley of Arunachal Pradesh

Dibang Valley, the largest district of Arunachal Pradesh state (Figure 1), is predominantly inhabited by the indigenous Idu-Mishmi community. Recent ecological research and expeditions have highlighted the ecological importance of the understudied Dibang Valley. Rusty-throated Wren-babbler *(Spelaeornis badeigularis)*, a vulnerable species endemic to Mishmi hills was rediscovered after almost 60 years in 2004 (King and Donahue,

2006). In 2012, tigers were recorded officially for the first time by the regional authorities from high elevations in Dibang Valley. Subsequently, detailed ethnographic studies have been conducted to investigate the relationships between tigers and the Idu-Mishmis that have been preserving the species for ages (Nijhawan, 2018; Beggiora and Exley, 2024).

A majority of land in Dibang Valley is managed by the Idu-Mishmi community through local customary laws, and is often utilised for agricultural activities, extracting timber and other bio-resources, and for various cultural purposes. Dibang Valley thus has a mosaic of several habitat types (Figure 2). The dominant habitat types in Dibang Valley comprise bamboo thickets, tropical evergreen, subtropical, temperate broad leaf, and temperate conifer forests, as well as high-altitude meadows (Champion and Seth, 1968).



Figure 2: A mosaic landscape with patches comprising of bamboo thickets in foothills, temperate broadleaf forests at peaks, slash-and-burn agricultural fields, and grazing lands in Dibang Valley in Arunachal Pradesh

Tropical montane habitat and its species of Dibang Valley face impending effects on both large scales such as climate change, landslides, and massive deforestation owing to hydroelectric dam development projects (Sheth et al., 2020), as well as small scale events such as hunting (Aiyadurai et al., 2010), and habitat degradation. While the species of Dibang Valley face several threats, community lands managed by the Idu-Mishmi people continue to protect mosaics of habitats in traditional ways which maintain biodiversity

and provide ecosystem services. The region is at a critical stage where not only continued documentation of species but also an intensive assessment of threats to them and their habitat is required.

Aims and outline of thesis

This thesis aims to examine how bird communities of tropical mountains of the eastern Indian Himalaya are affected by climate change and LULC changes at different spatial and temporal scales using a combination of primary and secondary datasets. I delve into understanding the role of species' abiotic niches, and ecological, and evolutionary traits in making communities resilient or vulnerable to climate change and LULC change. I ask, at a large scale, a) how are distributions governed by changing climate; at a small scale, b) how are community patterns related to microclimatic conditions in different LULC types of a mosaic landscape?, and c) how are forest-dependent bird communities impacted by short-term habitat disturbance?

In **Chapter 2**, I predict the impacts of climate change on the potential distributions of 60 species of flycatchers belonging to the Muscicapidae, one of the largest terrestrial bird families in the region, using Global Biodiversity Information Facility (GBIF) occurrence/ presence data. Given the scarcity of available data size for the eastern Indian Himalaya, I also geographically expand the assessment for the neighbouring parts of Indo-Burman hills for this chapter. It is largely expected that habitat specialists are climate specialists, that climate change will favour habitat generalists (Davey et al., 2012), and that closely related species with overlapping niches are likely to have similar responses to climate change (Losos, 2008). However, this hasn't been tested on montane birds of this region where habitat heterogeneity could lead to added complexities. Based on the emerging distribution patterns, I first explore if habitat generalists are less sensitive to climatic change as compared to habitat specialists of the Muscicapidae family. I then test the validity of the niche conservatism hypothesis to assess if closely related species within the family are expected to show similar sensitivity to climatic variables under different

scenarios.

The next two chapters are based on the primary data that I collected in Dibang Valley from 2021-2023. These are the first-ever ecological studies on bird communities of Dibang Valley. In **Chapter 3**, I examine multiple diversity and richness metrics, such as species richness, functional richness, and phylogenetic richness, and their relationships with microclimatic data in four different LULC types. Previous studies in the eastern Indian Himalayan region have largely explained the relationships between bird communities, temperature, and habitat changes, signifying the role of species' thermal niches in response to change (Srinivasan et al., 2019, 2018b; Chanda et al., 2023). However, species' hygric niches (characterised by humidity, rainfall, and precipitation) have largely been overlooked. I hypothesise, that in wet and humid environments of eastern Indian Himalaya, birds are also tracking their hygric niches. I highlight that humidity also plays a key role in determining community patterns due to LULC change in the mosaic landscape of Dibang Valley.

In **Chapter 4**, I investigate how short-term, small-scale disturbance shapes response in forest bird communities. It is observed that species richness declines in disturbed forests (Durães et al., 2013) since specialists are replaced by generalists (Tabarelli et al., 2012), and species belonging to specific guilds dominate the habitat (Gray et al., 2007), however, there could be nuances at the onset of the event. I assess how altering vegetation parameters in two stages of pre- and post-disturbances separated by a year, is affecting species diversity and the overall distribution of body mass for a transient period.

Lastly, in **Chapter 5** of General Discussion, I summarise my findings and discuss future directions.

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Chapter 2

Ecology and not phylogeny influences sensitivity to climate change in Muscicapidae Flycatchers in Eastern Himalayan and Indo-Burman hotspots

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ABSTRACT

Species' distributional responses to climate change can depend on ecology and phylogeny. The degree of habitat specialism is potentially important because habitat generalists with wider distributions are assumed to be less sensitive to environmental changes compared to narrowly distributed habitat specialists. We explore the effects of climate change on the potential distributions of 60 species of Muscicapidae Flycatchers in parts of the Eastern Himalayan Mountains and the Indo-Burman range. We used presences from the Global Biodiversity Information Facility to develop ecological niche models in Maxent under different climatic scenarios. We then extracted variables with high contributions to Maxent models to explore sensitivity to climate change based on habitat specialism while testing for phylogenetic signal using Phylogenetic Generalised Least Squares. We found that potential distributions of Muscicapidae Flycatchers were sensitive to temperature variable in the month of the highest precipitation and to the overall maximum temperature. Potential distributions of habitat generalists were particularly sensitive to these abiotic variables, and those of habitat specialists less so. Sensitivity to abiotic variables did not show a pattern of phylogenetic niche conservatism. We highlight that predicting which aspects of the changing climate impact species with different habitat associations may be particularly challenging in complex environments such as those of tropical mountains.

1. INTRODUCTION

Climate change has been implicated in biological responses in distributions, seasonal activities and migration patterns of approximately half of the species globally (IPCC, 2022), resulting in range shifts, adaptation, phenological tracking, or extinction in some species (Chen et al., 2011; Radchuk et al., 2019; Cleland et al., 2012; Maclean and Wilson, 2011, respectively). Out of these responses, latitudinal and altitudinal range shifts, and changes in species' local distributions remain most widely studied and predicted (reviewed

in Elith and Franklin, 2017). There are several factors such as dispersal ability, biotic interactions, phenology, available environmental space, and habitat specialisation which shape species' distributions, and thus their ability to respond to climate change (Urban et al., 2013; Ponti and Sannolo, 2022; Enriquez-Urzelai et al., 2019, respectively). Although data on a majority of such ecological factors remain unavailable, habitat specialisation can be often quantified and used to make predictions related to distribution patterns (e.g., Lira et al., 2020). It is expected that habitat specialists, including the uncommon and high-elevation endemics with narrow ecological requirements, are more likely to experience a decline in their distributions, whereas generalists capable of occupying several habitat types may not be severely impacted or could even be benefitting from climate change (review in Şekercioğlu et al., 2012).

Predicting responses to climate change may not be as straightforward for species occupying complex environments such as the tropical mountains. Tropical mountains are biodiversity hotspots (Myers et al., 2000) and are highly diverse ecosystems comprising complex topographies and habitats contributing to several ecological and evolutionary patterns and processes (reviewed in Rahbek et al., 2019), thereby mediating heterogeneous responses to climate change in species (Tovar et al., 2013). Even though tropical mountains have long provided stable refuge to species (Fjeldså et al., 1999), these systems are now fast changing which is expected to result in high rates of range shifts and biotic attrition (Colwell et al., 2008).

Expectedly, habitat specialists tend to be more sensitive to climate change but there are variations in predictions from different climatic components affecting species' distributions in tropical mountain systems. For example, forest specialist and insectivore bird species are more sensitive to increasing minimum temperatures than generalists with omnivore and herbivore guilds in tropical mountains of Africa (Dulle et al., 2016), whereas, in the mountains of Costa Rica, habitat specialist bird species are more sensitive to both temperature and precipitation changes (Gasner et al., 2010). The sensitivity to abiotic environments can aid in an informed understanding of species' niches and in identifying

areas of stable refugia for spatial conservation prioritisation in light of climate change (Keppel et al., 2012).

The patterns in predictions can be further explained by phylogenetically-explicit frameworks. Since closely related species are expected to have similar niches, commonly referred to as 'phylogenetic niche conservatism' (Losos, 2008), they may exhibit similar behavioural, ecological and life history traits (Kamilar and Cooper, 2013; but see Schuetz et al., 2019). Phylogenetic niche conservatism may explain various patterns in closely related species such as the divergence of foraging niches to avoid competition (Lovette and Hochachka, 2006), maintaining ancestral adaptation to certain environmental conditions (e.g., Morinière et al., 2016), and similarity in diversity-climate relationships (e.g., Wang et al., 2021).

Thus, phylogenetic relatedness needs to be accounted for to facilitate an improved understanding of species distributions, especially at regional scales (e.g., Pashirzad et al., 2018). Assessing phylogenetic relatedness can also have conservation implications as the climate-vulnerable traits, once identified in a species, can be extended to make assessments on its closely related species (Miller-Rushing et al., 2010). However, factors like high topographical variation and altitude may lead to distinct phylogenetic signal in closely related species such as those occupying highlands and lowlands of tropical mountains (e.g., Schwallier et al., 2016).

We explore the potentially complex responses to climate change in Muscicapidae Flycatcher birds occupying tropical mountain environments. We focused on the Muscicapidae family of passerines which includes flycatchers, thrushes, and chats having variations in habitat specialism, high phylogenetic diversity (Sangster et al., 2010), and recent well-resolved phylogeny (Zhao et al., 2023). This provides us with an opportunity to test for phylogenetic niche conservatism in closely related species at a large spatial scale in a complex tropical mountainous environment. We characterised species-specific potential distributions of 60 species by developing Ecological Niche Models (ENMs) under both present and future climatic conditions, in parts of two global biodiversity hotspots- the

Eastern Himalayan Mountains and the Indo-Burman Hills.

Parts of the Eastern Himalayan Mountain and Indo-Burman Hills- two global biodiversity hotspots (Mittermeier et al., 2011) encompass Bhutan and Northeast India which are located directly above the Tropic of Cancer at 21.94º - 29.46ºN and 97.41º - 88.01ºE (Figure 1). The Indo-Burma extends across southern parts of Northeast India, with plains of Brahmaputra in between- one of the largest rivers of Asia. The region provides highly heterogeneous environments with several altitudinal gradients (roughly from 10 metres to 7000 metres above sea level), varying climatic conditions and multiple habitat types, thereby facilitating high diversity in species such as birds (Acharya et al., 2011), plants (Saikia et al., 2017), mammals (Dhendup et al., 2019), and butterflies (Singh and Chib, 2014). Bhutan and Northeast India are also faced with severe effects of climate change resulting in faster melting of glaciers, increased frequency of floods, and decreased seasonal rainfall in some parts (Borah et al., 2022; Das, 2016; Choudhury et al., 2019, respectively), which is expected to have severe consequences on the biodiversity of the region.

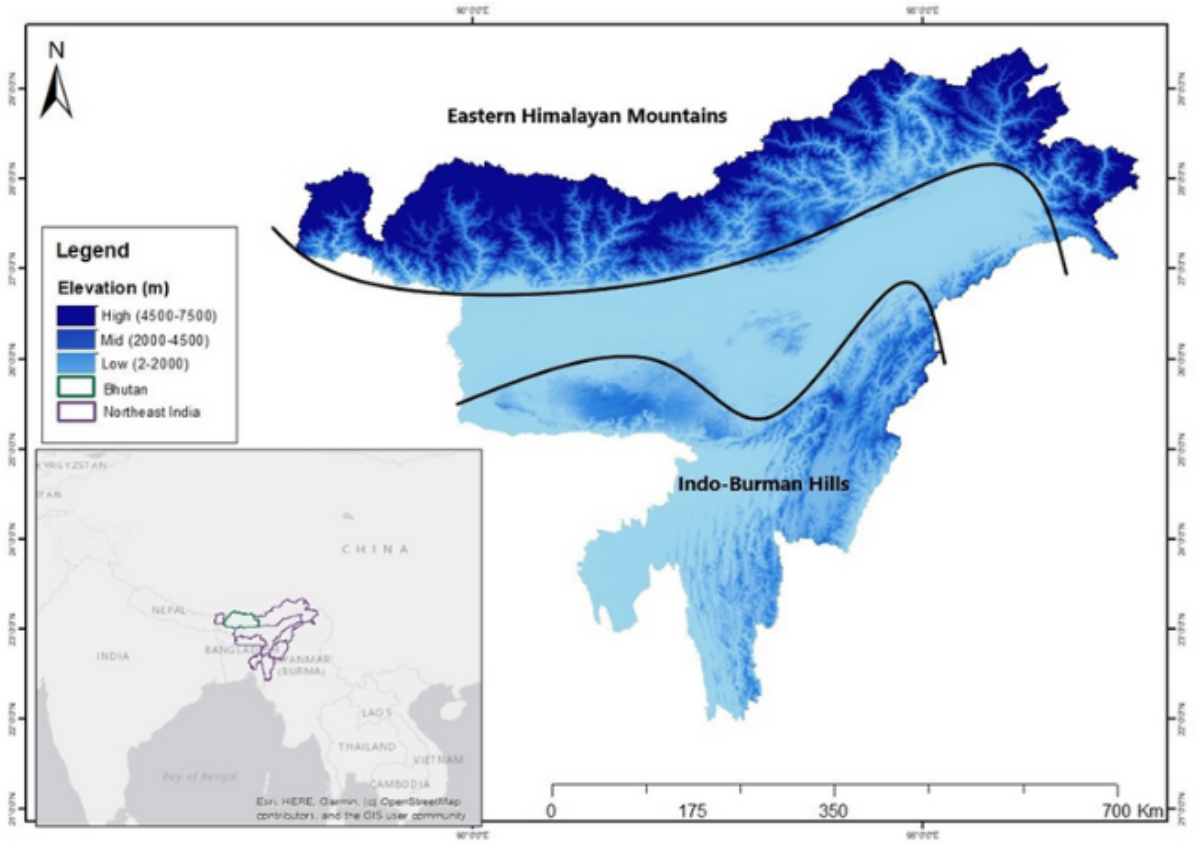

Figure 1: Bhutan and Northeast India with high-elevation Eastern Himalayan mountains in the north, low to mid-elevation Indo-Burman Hills in the south, and Brahmaputra river plains in the middle

Our first aim was to determine the potential distributions of the Muscicapidae Flycatchers in the region. Species' potential distribution or the fundamental niche reflects the abiotic conditions best suited for species (reviewed in Peterson and Soberón, 2012). We used Maxent, a widely used machine-learning program that predicts species' potential distributions based on presence points to develop ENMs representing habitat suitability (Phillips et al., 2006). We then extracted variables with the highest contributions to the ENMs which explained abiotic sensitivity for all species. We expected that the potential distributions of species will be most affected by not only temperature but by a combination of temperature and precipitation variables under both present and future climatic conditions since the region of Eastern Himalaya and Indo-Burma offers a complex suite of abiotic environments.

We then investigated the role of species' habitat specialism and evolutionary histories in explaining the patterns in potential distributions. We applied the Phylogenetic Generalised Least Squares method (PGLS) (Grafen and Hamilton, 1997) which explicitly incorporates phylogenetic non-independence between species with shared evolutionary histories (Symonds and Blomberg, 2014). We used the extracted abiotic variables with the highest contribution as a response variable and habitat specialism as the predictor variable while controlling for phylogeny in PGLS models. We then explored phylogenetic signal to assess if closely related species are likely to show similar sensitivity to abiotic variables under both present and future climatic scenarios in highly complex environments in parts of the Eastern Himalayan and the Indo-Burman hotspots. We expected that the habitat specialists would be more sensitive to these abiotic variables.

2. METHODS

2.1. Presence records

A list of Muscicapidae Flycatchers residents and migrants in our study region, excluding vagrant species found outside their home ranges, was collated from eBird (Sullivan, et al.,

2009), and Birds of the Indian Subcontinent: India, Pakistan, Sri Lanka, Nepal, Bhutan, Bangladesh and the Maldives (Grimmett et al., 2012) resulting in a list of 79 species from 26 genera. We collated presence records from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/), a biodiversity portal offering free and open-access geo-tagged species records (Telenius, 2011). Three categories of 'basis of records' from the GBIF database were extracted: human observation, observation, and living sample, as these represent direct field observation records. Species with less than 10 presence records and those with taxonomic uncertainties were eliminated at this stage. We thus proceeded with 60 species for developing ENMs and performing subsequent PGLS analysis.

2.2. Bioclimatic variables

Gridded 19 bioclimatic variables for historical or near-current climatic conditions were downloaded from WorldClim (https://worldclim.org/) at a spatial resolution of 2.5 minutes (Fick and Hijmans, 2017). To check for, and remove bioclimatic variables with high collinearity, we performed a Variance Inflation Factor (VIF) analysis (Thompson et al., 2017) using usdm package (Naimi, 2017). Variables with VIF values greater than 10 were removed (Yoo et al., 2014), yielding seven variables: bio2, bio3, bio8, bio14, bio15, bio18 and bio19 (Table 1).

Table 1: Seven Bioclimatic predictor variables for current climate scenario retained after performing Variance Inflation Factor (VIF) test of collinearity.

Codes	**Description**	**VIF values**
bio2	Mean diurnal range (mean of monthly (max temp- min temp))	3.466
bio3	Isothermality x 100	1.711
bio8	Mean temperature of the wettest quarter	2.160
bio14	Precipitation of the driest month	6.290
bio15	Precipitation seasonality (coefficient of variance)	1.738
bio18	Precipitation of the warmest quarter	3.077
bio19	Precipitation of the coldest quarter	7.509

ASTER Global Digital Elevation Model was obtained for the study area from the United States Geological Survey AppEEARS website (https://lpdaacsvc.cr.usgs.gov/appeears/) at a spatial resolution of 30 metres and resampled in ArcGIS Desktop 10.6.1 Advanced (ESRI, 2018). Elevation was used as the eighth predictor variable in addition to those in

Table 1.

Future climatic gridded data for the next two decades (2021-2040) was obtained from WorldClim at a spatial resolution of 2.5 minutes for which we chose Beijing Climate Center Climate System Model BCC-CSM2-HR, a global circulation model downscaled from CMIP6 and widely used for Asia (Eyring et al., 2016). Four climate change scenarios described by Shared Socio-economic pathways (SSPs) representing different possible future greenhouse gas emissions were SSP1-2.6 (low emission scenario), SSP2-4.5 (intermediate emission scenario), SSP4-6.0 (medium emission scenario), and SSP5-8.5 (high emission scenario) (van Vuuren et al., 2011; Thomson et al., 2011; Masui et al., 2011; Riahi et al., 2011, respectively) in which the global mean temperature is projected to increase by 0.9℃, 1.1℃, 1.0℃ and 1.3℃ for 2021-2041, respectively (IPCC, 2019). We used four variables for each of the four SSPs - maximum temperature (tmax), minimum temperature (tmin), and precipitation (prec), also obtained from WorldClim, along with elevation from ASTER.

2.3. Maxent settings for ENMs

Maxent is one of the best-performing models for presence-only data (Elith et al., 2006) and is frequently used to predict species distribution changes due to climate change (Zhang et al., 2018). Maxent compares environmental conditions where a species has been recorded to those of the auto-generated random 'background points' following the principle of maximum entropy using a set of restraints provided as 'settings' by the modeler (Phillips et al., 2017). We used Maxent.jar software to produce potential distribution maps for each species (https://www.cs.princeton.edu/). Maxent.jar tends to develop complex maps under default settings which can be avoided by manually selecting settings to furnish simpler maps (Halvorsen et al., 2016). Thus, we selected quadratic features to reflect the species' physiological response curve which generally represents a Gaussian-shaped unimodal curve (Austin, 2007), along with linear features to ensure Maxent does not choose background points for species from areas they are not likely to inhabit, such as those in freezing temperatures (Merow et al., 2013). This particularly applies to tropical

species as they can have truncated niches and do not occupy the full range of available climatic conditions (Smith et al., 2020).

We used 10 model replicates and set bootstrapping as the replicated run type since it assesses the likelihood of the predictor variable being independent and also generates parsimonious predictive models (Austin and Tu, 2004). The random test percentage was set to 25% for model validation (Xu and Goodacre, 2018). We then explored the effect of varying the maximum number of background points using 2,000, 5,000 and 10,000 points as suggested by Merow et al. (2013), but found no differences in present climate models. Hence, we proceeded with 10,000 background points for all present and future climate change models to maintain consistency.

Raw output was selected for all models which correspond to relative occurrence rate (ROR) in Maxent (Merow et al., 2013) since presence-only data can at best estimate ROR and not absolute occurrence rates (Fithian and Hastie, 2013; Guillera-Arroita et al., 2014). The maximum number of iterations was set to 500 and the jackknife method was used to assess the variable importance of all ENMs. Receiver operating characteristics analysis or area under the curve (AUC) was used to estimate the accuracy of the models, which is considered a relatively better measure of predictive accuracy in comparison to other criteria such as Naive Bayes Classifier and Decision Trees for evaluating and comparing machine learning algorithms (Huang et al., 2003). We selected a mean model of ten replicated models to compute AUC scores. AUC scores range from 0 to 1 to describe how well a model has performed by discriminating between sensitivity (presence correctly predicted as presence) and specificity (absence correctly predicted as absence) such that a score above 0.5 is considered well-performing and those below 0.5 are poor-performing (Jiménez-Valverde, 2012). Furthermore, previous studies have highlighted a strong relationship between AUC scores and species rarity, indicating species with fewer presence points are likely to have a high AUC score and thus have better-performing models (Connor et al., 2018; Veloz, 2009). We explored if such a relationship exists between AUC scores and the total number of presence points in our focal species by fitting

a generalised linear model.

2.4. Phylogenetic analysis

Data wrangling and analyses were performed in R base software version 4.0.4 (R Core Team, 2020) using RStudio Desktop version 2023.03.0+386. Data files including PCVs, model AUCs, and R script are available at https://github.com/aavikad/muscicapidae-flycatchers-v1.0 .

2.4.1. Percentage Contribution of Variables- response variable

We used the Percentage Contribution of Variables (PCVs) from ENMs of each species as a proxy for sensitivity to climate change under both present and future climatic scenarios. PCVs are continuous percentage measures of variable importance. We extracted means of PCVs of 10 bootstrapped models for each of the species from the Maxent output file called 'maxentresults'. Out of the eight variables used under present climate, i.e., bio2, bio3, bio8, bio14, bio15, bio18, bio19 (refer to Methods Table 1), and elevation; bio8 (mean temperature of wettest quarter) and elevation had the highest percentage contribution for most species. From the variables used for four future climate scenarios, i.e., tmax, tmin, prec, and elevation, the variables tmin and tmax had the highest percentage contribution in ENMs of most species under each of the four scenarios. Thus, the percentage contribution of bio8 and elevation under the present climate, and tmax and tmin under future climate scenarios were selected for subsequent PGLS modelling.

2.4.2. Species Specialisation Index - explanatory variable

There are several habitat specialisation metrics used for birds, however, most are based on abundances, such as the Rank occupancy-abundance Profile (Collins et al., 2009) or Marsh Specialisation Index (Correll et al., 2016), and on expert opinion (e.g., Gardali et al., 2012a); all frequently limited for the understudied systems. We used the Species

Specialisation Index (SSI) which orders species from specialists to generalists based on the variances of average densities of species in the total number of habitats without having to rely on expert knowledge (Julliard et al., 2006). To score each species according to its habitat preferences, we extracted information from Birds of the World (2023) and categorised all the habitat types into 10 broad classes that the Muscicapidae Flycatchers in the study region are found in forests, secondary forest, bamboo, scrub, reeds, riverain forests, rivers and streams, alpine, rocky slopes, and open. We then calculated SSI for 60 species across 10 habitats, where h represents the number of habitat classes a species is found in, and H represents the total habitat classes (1).

$$SSI = \left(\frac{H}{h} - 1\right)^{\frac{1}{2}} \tag{1}$$

The index was then normalised on the scale of 0 to 1, and termed *S'*, with 0.5 selected as a central value such that species with $S' < 0.5$ were categorised as habitat generalists while those with $S' > 0.5$ were categorised as habitat specialists. For instance, *Copsychus saularis* (Oriental Magpie-Robin) (found in 6 out of 10 habitats) with $S' = 0$ was termed as an extreme habitat specialist, whereas *Niltava grandis* (Large Niltava) (found in 1 out of 10 habitats) with S'= 1 was called an extreme habitat generalist.

2.4.3. Phylogenetic modelling

We obtained complete phylogeny of 60 species for Muscicapidae Flycatchers family built using mitochondrial and nuclear data from Zhao et al. (2023). We used the ape package to read, plot and manipulate the phylogenetic tree (Paradis and Schliep, 2019), and gls function in nlme package (Pinheiro et al., 2017) to fit multiple PGLS models. First, linear model residuals using PCVs and *S'* were tested for normality. Model residuals of bio8, elevation, and tmax under low, intermediate, medium, and high emission scenarios were normal. The remaining variable, i.e., tmin was log-transformed but did not conform to normality under any future emission scenario, hence was not used in the PGLS models.

To investigate the role of species habitat specialism in explaining the highest percentage contribution of abiotic variables in ENMs, we fit two PGLS models for present climatic conditions; one, using the percentage contribution of bio8, and another using the percentage contribution of elevation as response variable, and *S'* as a predictor variable in both the models. We repeated the same procedure with tmax for future climatic conditions. We used phylogeny as a fixed effect and the fixed variances in distances from the root to the tip of each tree as weights. The PGLS analysis was performed based on the Brownian motion model (Felsenstein, 1985).

We measured the phylogenetic signal in contributions from abiotic variables based on the significant PGLS models using phylosignal package (Keck et al., 2016). Blomberg's K was used to estimate the strength of phylogenetic signal such that $K<1.0$ represents less phylogenetic signal than expected and $K>1.0$ represents greater phylogenetic signal than expected under Brownian motion (Blomberg et al., 2003). We then estimated local Moran's I score to detect for phylogenetic autocorrelation, where the values of I denote degree of autocorrelation between closely related species (Gittleman and Kot, 1990). Phylogenetic trees with annotations of PCVs resulting in significant PGLS models constructed using ggtree package (Yu et al., 2017).

3. RESULTS

3.1. Model performance and variable contributions

Model AUC scores ranged from 0.66 to 0.98 for present climatic conditions, and from 0.63 to 0.97 under four future climate change scenarios. These values (all above 0.5) denote that the models performed well and were either sufficient, good or very good at discriminating between sensitivity and specificity (Šimundić, 2009). While all models performed well, generalised linear models predicted a significant negative relationship between AUC scores and the total number of presence points under present climatic conditions ($P < 0.001$), and all future climatic conditions - SSP 1-2.6 ($P < 0.001$), SSP

2-4.5 ($P < 0.001$), SSP 4-6.0 ($P < 0.001$), SSP 5-8.5 ($P < 0.001$). This relationship could be attributed to Maxent's tendency to better discriminate between specificity and sensitivity for species with fewer presences as compared to those with several presence points (Stokland et al., 2011), since species with more presence points and thus wider distributions can make it challenging for Maxent to distinguish between suitable and unsuitable areas (Franklin et al., 2009).

The percentage contributions of bio8 and elevation varied amongst the species. Bio8 contributed the most to potential distribution of *Copsychus saularis*, and the least to *Ficedula parva*, while elevation contributed the most to *Phoenicurus hodgsoni* and the least to *Copsychus saularis*- all of which are habitat generalists (Figure 2). Under the four future climate scenarios, tmax consistently retained the most information in potential distributions of *Copsychus saularis*, a habitat generalist, and *Niltava grandis*, a habitat specialist (Supplementary Figure S59 to S62).

3.2. Potential distribution maps

The predicted potential distribution maps of an extreme generalist and an extreme specialist species, *Copsychus saularis* and *Niltava grandis*, respectively, are presented as exemplars. Under the present climate, *C. saularis* has high suitability along the plains and the Indo-Burman Hills, and low suitability in parts of Eastern Himalayan Mountains (Figure 3). *N. grandis* has low suitability in the plains, but medium to high suitability in parts of Eastern Himalaya (Figure 4). Under future climatic scenarios, the potential distribution of *C. saularis* remains largely unaffected, while that of *N. grandis* further decreases in parts of Indo-Burman Hills but remains roughly the same in the Eastern Himalaya.

For the other 58 species (Supplementary Figures S1 to S58), Maxent predicted restricted potential distributions for *Phoenicurus erythrogastrus* (White-winged Redstart) (Figure S43), *Brachypteryx hyperythra* (Rusty-bellied Shortwing) (Figure S3), *Monticola cinclorhyncha* (Blue-capped Rock Thrush) (Figure S31), and *P. schisticeps* (White-throated

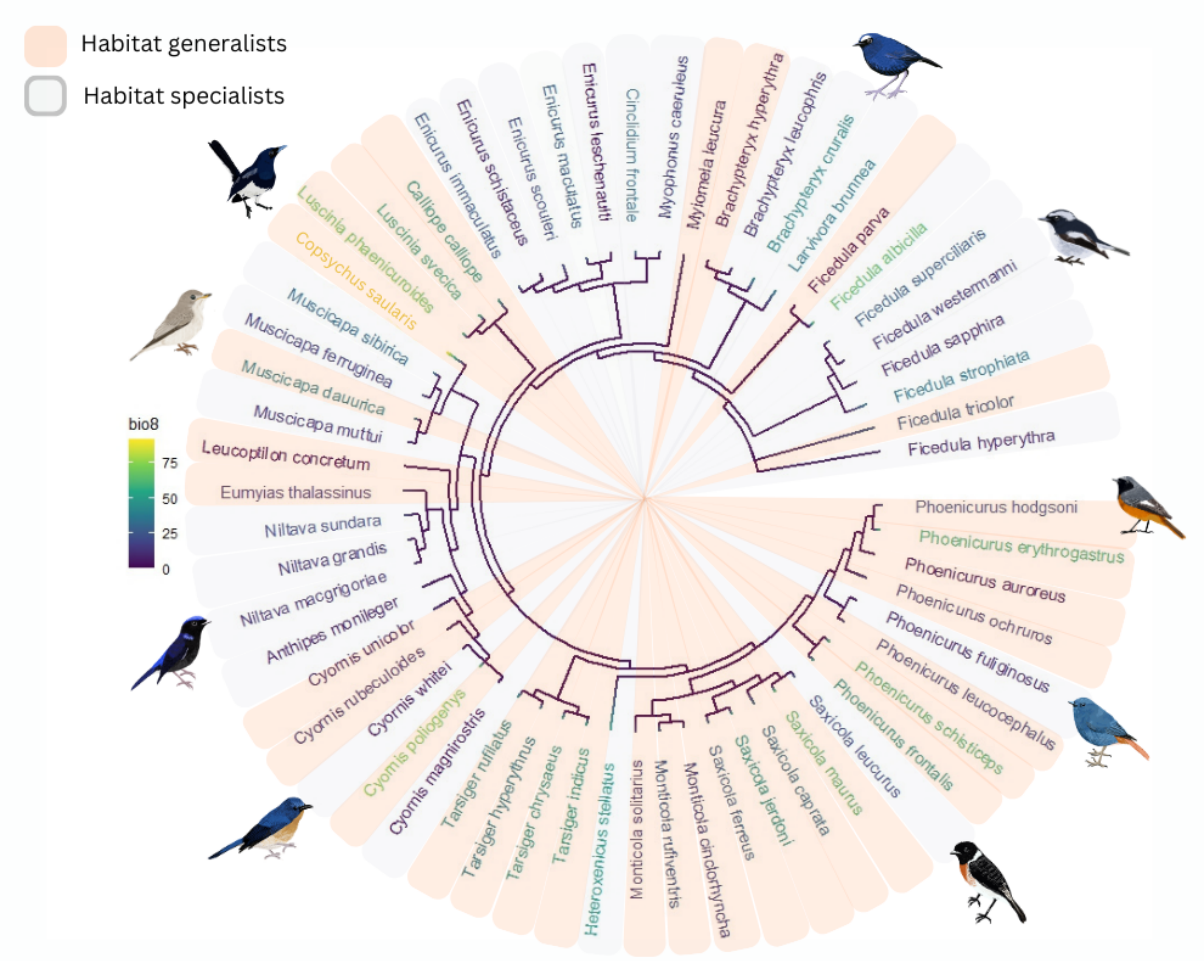

Figure 2: Percentage contribution of bio8 (Mean temperature of wettest quarter) of the under the present climate in Ecological Niche Models of Muscicapidae Flycatcher species categorised as habitat generalists ($S' < 0.5$) or habitat specialists ($S' > 0.5$) using Species Specialisation Index (SSI).

Redstart) (Figure S49), and wider potential distributions for *Saxicola maurus* (Siberian Stonechat) (Figure S54), *P. auroreus* (Daurian Redstart) (Figure S42), *Ficedula parva* (Red-breasted Flycatcher) (Figure S20), and *Muscicapa muttui* (Brown-breasted Flycatcher) (Figure S36).

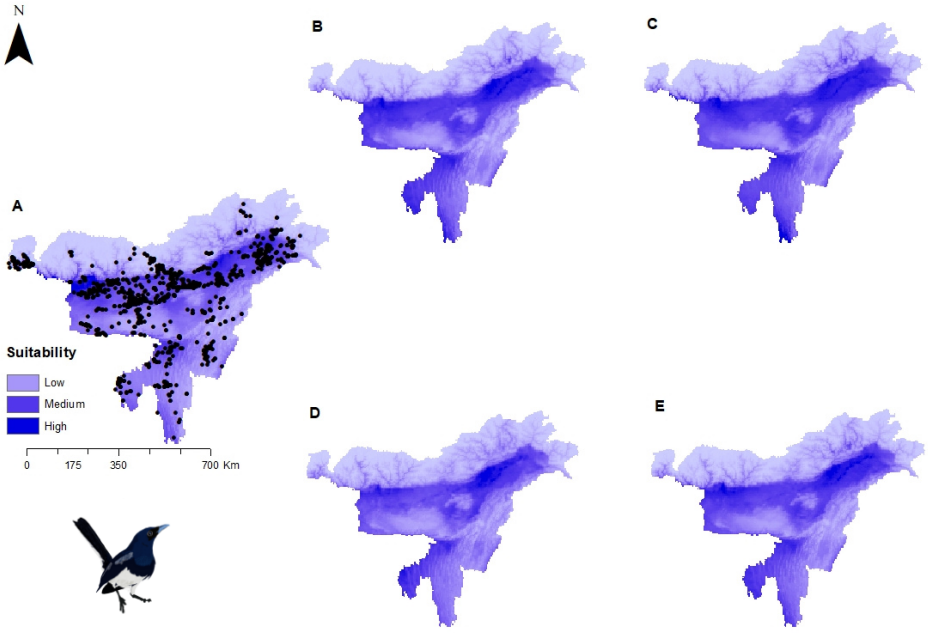

Figure 3: Potential distributions of *Copsychus saularis* (Oriental Magpie-Robin), a habitat generalist, under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

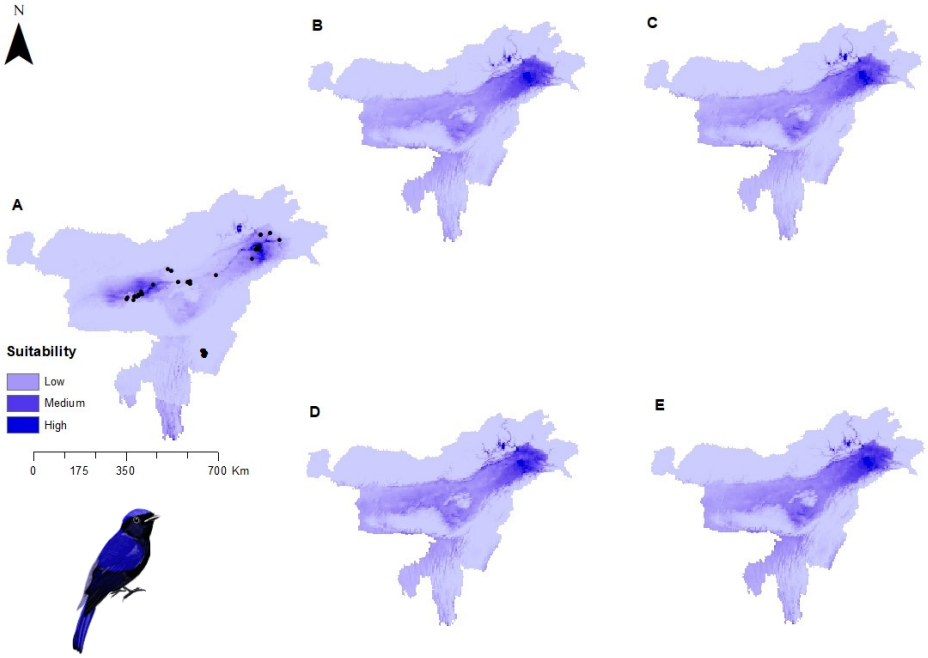

Figure 4: Potential distributions of *Niltava grandis* (Large Niltava), a habitat specialist, under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

3.3. Phylogenetic analysis

S', a measure of habitat specialism, was negatively correlated with percentage contribution of bio8 under the present climate, and with the percentage contribution of tmax under low, intermediate, medium, and high emission scenarios (Table 2). However, there was no correlation between *S'* and elevation under present climate.

Table 2: Results from Phylogenetic Generalised Least Squares (PGLS) models using Percentage Contribution of Variables (PCVs) for present and future climatic conditions (significant results (P-value<0.05) are highlighted in **bold**)

	Value	**Standard error**	**t-value**	**P-value**
Present climate				
bio8	-27.36	13.52	-2.02	**<0.05***
elevation	10.15	8.49	1.19	0.23
Future climate				
tmax (SSP1-2.6)	-37.26	13.62	-2.73	**<0.01***
tmax (SSP2-4.5)	-32.22	12.44	-2.58	**<0.05***
tmax (SSP4-6.0)	-41.57	12.52	-3.31	**<0.01***
tmax (SSP5-8.5)	-2.05	0.57	-3.55	**<0.001***

Moran's *I* dot plot demonstrated the presence of autocorrelation amongst variables with the highest percentage contributions and tips of the phylogenetic tree representing species. Although there was positive correlation in contribution of bio8 amongst *Niltava macgrigoriae*, *N. grandis*, *Myophonus caeruleus*, *Myiomela leucura*, *Muscicapa sibirica*, and amongst *Muscicapa dauurica*, *Monticola solitarius*, *Monticol rufiventris* (Figure 5), the phylogenetic signal had overall low strength (K= 0.40) generally implying that closely related species of Muscicapidae Flycatchers did not have an overlap in contributions of bio8 to their niche models.

Under future climatic conditions, positive correlation continues in contribution of tmax amongst species such as *N. sundara*, *N. macgrigoriae*, *M. caeruleus*, and amongst *M. dauurica*, *M. rufiventris*, *M. solitaries* (see Supplementary Figure S63). However, there was low strength in phylogenetic signal in response to tmax under low emission scenario (K=0.41), intermediate emission scenario (K=0.46), medium emission scenario (K=0.41), and high emission scenario (K=0.34).

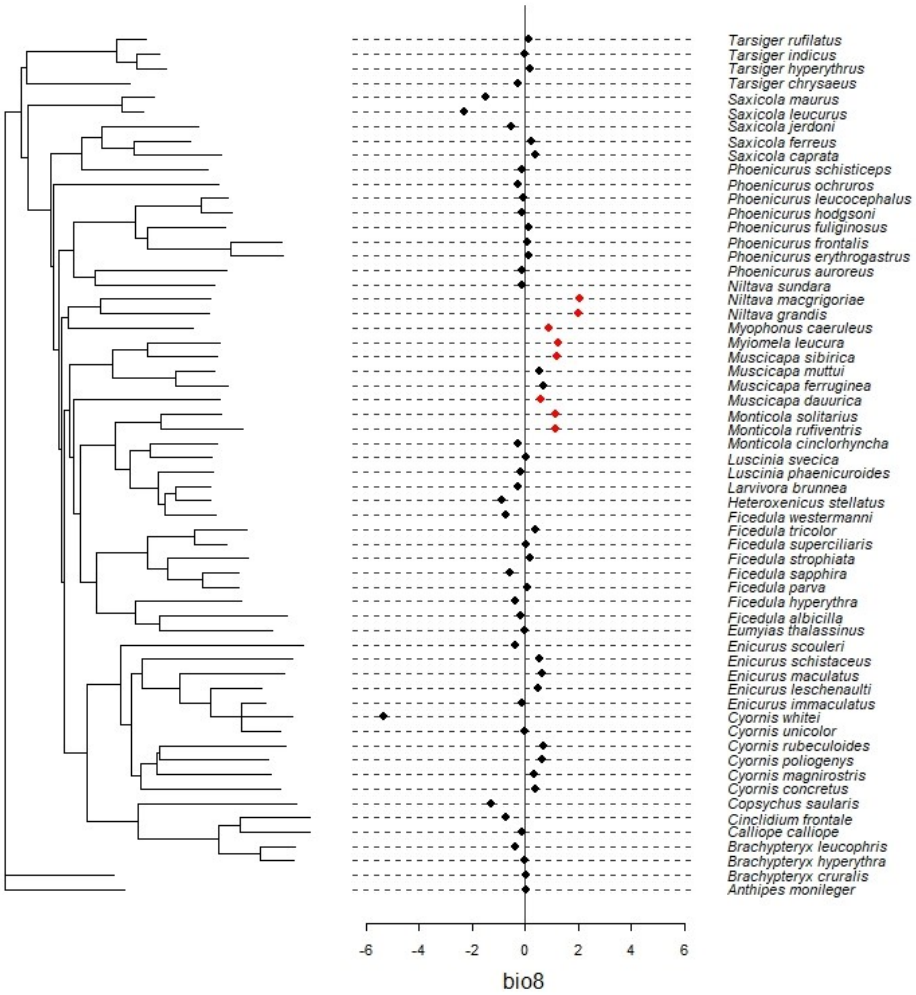

Figure 5: Local Moran's I plot of phylogenetic signal in percentage contribution of bio8. The red dots falling on and side of zero line correspond to significant relationships indicating positive correlation

4. DISCUSSION

The region of Northeast India and Bhutan is highly susceptible to climate change (Bajracharya et al., 2007; Ravindranath et al., 2011), but its effects on species inhabiting the region are largely understudied. The predicted distribution effects of climate change on the Muscicapidae Flycatchers, one of the largest terrestrial bird families in this region, showed varied responses across the family with little evidence of phylogenetic niche conservatism in species' sensitivity to abiotic variables under all climate scenarios. Rather, habitat specialism explained sensitivity to bioclimatic variables under both present and future climate scenarios. However, in contrast to expectations, we found evidence that the distributions of habitat generalists rather than specialists, were most responsive to bioclimatic variables.

First, the variable contribution to potential distributions followed our general expectations under present climatic conditions. Most birds had high contributions from the mean temperature of the wettest quarter (bio8), implying that the potential distributions, and thus the abiotic niches of our species, are impacted by a combination of temperature and precipitation conditions. Bio8 has previously shown high contributions to potential distributions of many Himalayan and Indo-Burman species such as the medicinal plants of Liliaceae family (Rana et al., 2017), the native pheasant- Himalayan Monal Lophophorus impejanus (Rai et al., 2020), the invasive *Lantana camara L.* (Bushi et al., 2022), the threatened orchid *Satyrium nepalense* (Kumar and Rawat, 2022), the Crayfish *Cherax quadricarinatus* and *Procambarus virginalis* (Zeng and Yeo, 2018), and the falcon *Falco jugger* (Sutton et al., 2020). Thus, several species of this region may be expected to track their thermal as well as hygric niches, which may lead to complex patterns of directions of range shifts or distribution changes in the future. We expected the trend to continue, i.e. high contributions from temperature and precipitation variables to the ENMs under future climatic scenarios as well, but we found the maximum temperature (tmax) had the highest contribution while precipitation (prec) had the lowest. The lower importance of

precipitation to potential distributions of species under future climate scenario models is plausibly due to the large uncertainties in precipitation projections in the CMIP6 General Circulation Models (John et al., 2022), causing in an underestimation of contributions of the precipitation variable.

The second important finding is that the sensitivity to abiotic components bio8 under present climate, and tmax under future climate was explained by species specialisation index in PGLS models, and contrary to our expectation, we found that as habitat specialism increased, species' sensitivity to abiotic variable declined. However, highly habitat specialist species such as *Brachypteryx cruralis* (Himalayan Shortwing), *E. leschenaulti* (White-crowned Forktail), and *Muscicapa muttui* (Brown-breasted Flycatcher) had sparse presence points in fewer grids to begin with which might have been insufficient in predicting precise degrees of sensitivity to abiotic variables across a large spatial scale. We expect such patterns could be because of uncertainties associated with gridded climatic data over the region, extrapolations from which may lead to added challenges for conservation planning and management under climate change.

Third, we did not find evidence of phylogenetic niche conservatism in the contributions of abiotic variables to potential distributions under climate change. Closely-related species are expected to have overlapping ecological niches (Losos, 2008) and therefore may have similar responses to climate change. A global assessment of thermal traits reported a strong signal of phylogenetic niche conservatism in pantropical birds and mammal species at a large geographical scale (Khaliq et al., 2015). Phylogenetic niche conservatism in closely-related species has also been reported in responses to climate change in regional examples such as diversity-climate relationships in Rosaceae species in China (Wang et al., 2021), and overlapping prediction ranges for some of the western *Plethodon* species in the Pacific Northwest (Nottingham and Pelletier, 2021). However, there are also empirical examples to the contrary- at regional and local scales, for instance, *Prionailurus* species show disparate spatial overlap resulting in heterogeneous responses to environmental responses in the Indian subcontinent (Silva et al., 2020), and closely-related Atlantic corals

exhibiting random patterns of associations between functional traits and distributional shifts (Rodriguez et al., 2019). As more empirical examples accrue, we will gain a better understanding of when phylogenetic niche conservatism in response to climate change may be important, however we should not assume that phylogeny is predictive along all axes of responses.

Caveats

While all our Maxent models performed well, it is important to highlight the role of spatial scales and data acquired to develop ecological niche models. We expect the results could vary for the Muscicapidae Flycatchers if undertaken over a larger scale or smaller scale which will lead to an increase or decrease in the number of habitat types available for species to occupy. Since most of the tropical regions are largely data deficient (Butchart and Bird, 2010), we were limited by data availability for these species in our region and hence proceeded with the presence-only models. It is likely that the availability of information on dispersal ability and biotic interactions will improve findings (e.g., Heikkinen et al., 2007). However, it is also likely that even with additional data on biotic interactions, the predictions may continue to remain the same as these effects are difficult to capture at macro-scales (Araújo and Luoto, 2007). Lastly, the niche models we used are static and do not take into consideration the mechanisms of evolutionary adaptations which cannot be ruled out for complex mountainous environments offering opportunities for high speciation.

Author contributions

AD and SC conceptualized the idea. AD designed the methodology, performed modeling and data analysis, and prepared the original draft. MTJ co-performed modeling. SC and TC contributed to model interpretation. All authors contributed to giving critical feedback to drafts.

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Supplementary

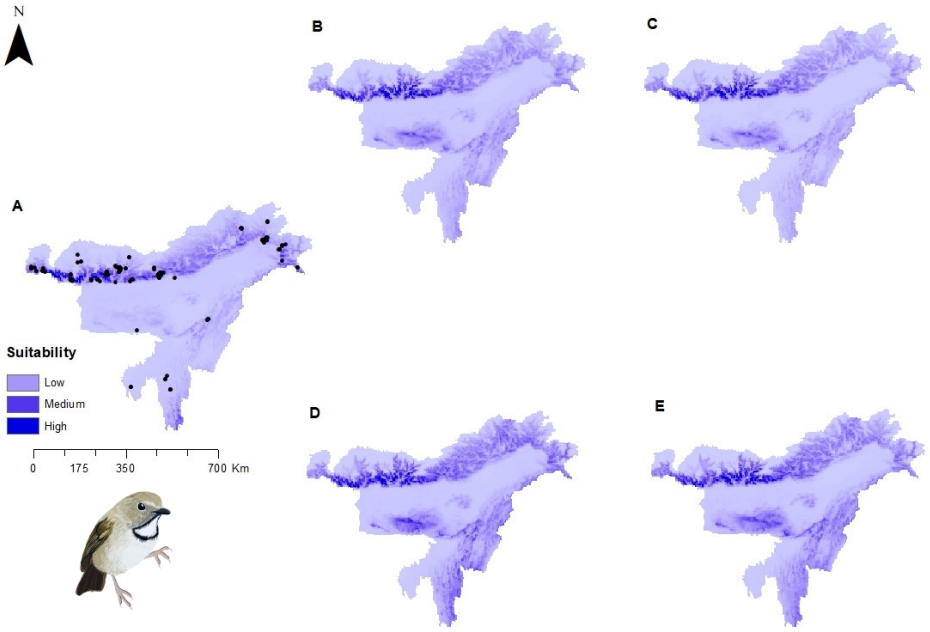

Figure S1: Potential distributions of *Anthipes monileger* (White-gorgeted Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

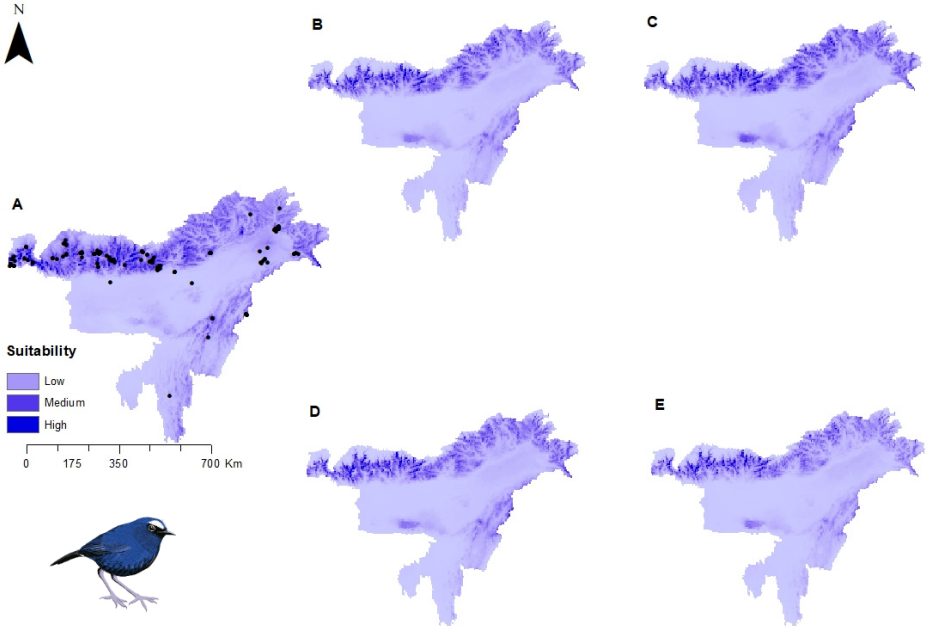

Figure S2: Potential distributions of *Brachypteryx cruralis* (Himalayan Shortwing) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

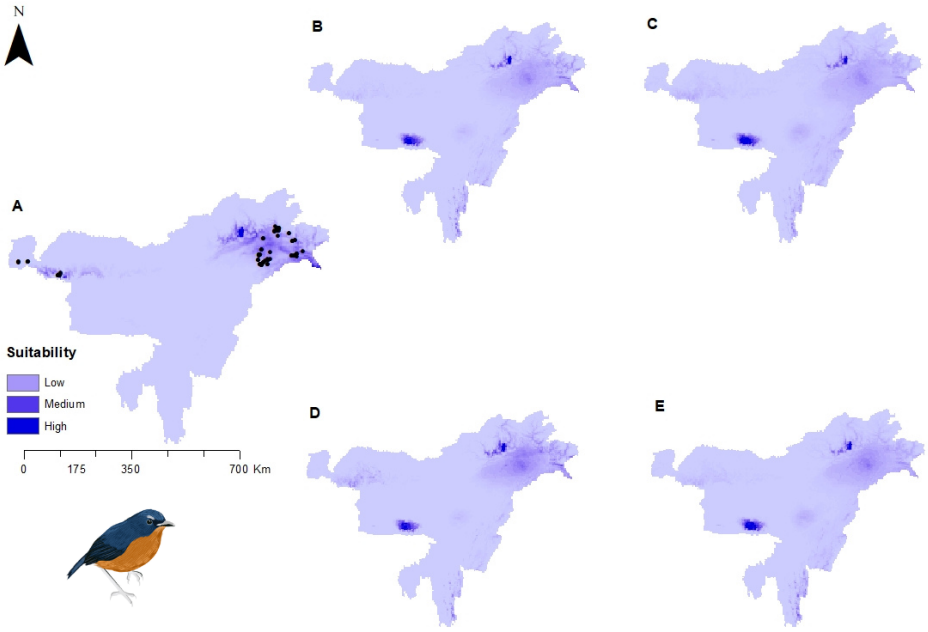

Figure S3: Potential distributions of *Brachypteryx hyperythra* (Rusty-bellied Shortwing) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

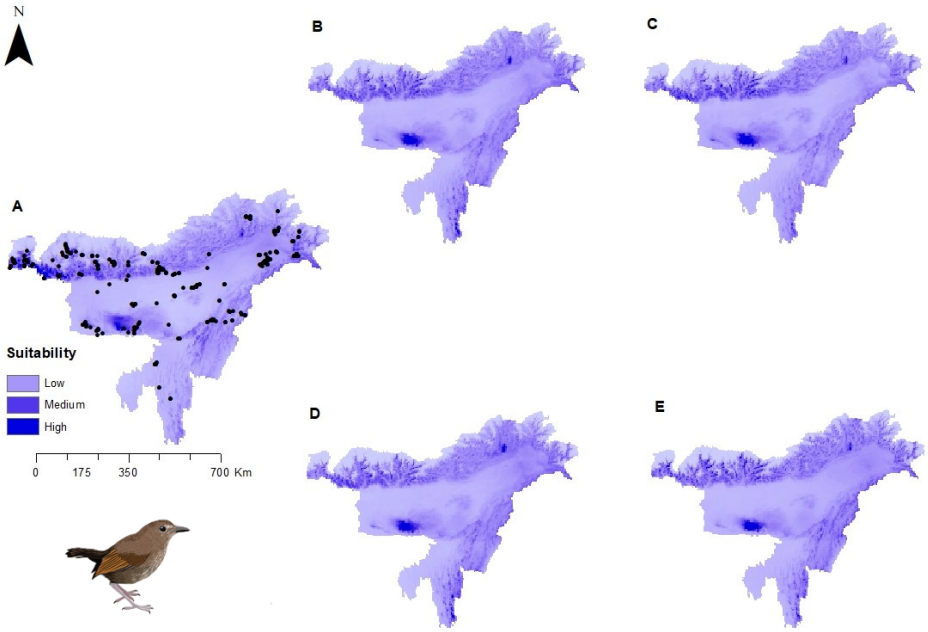

Figure S4: Potential distributions of *Brachypteryx leucophris* (Lesser Shortwing) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

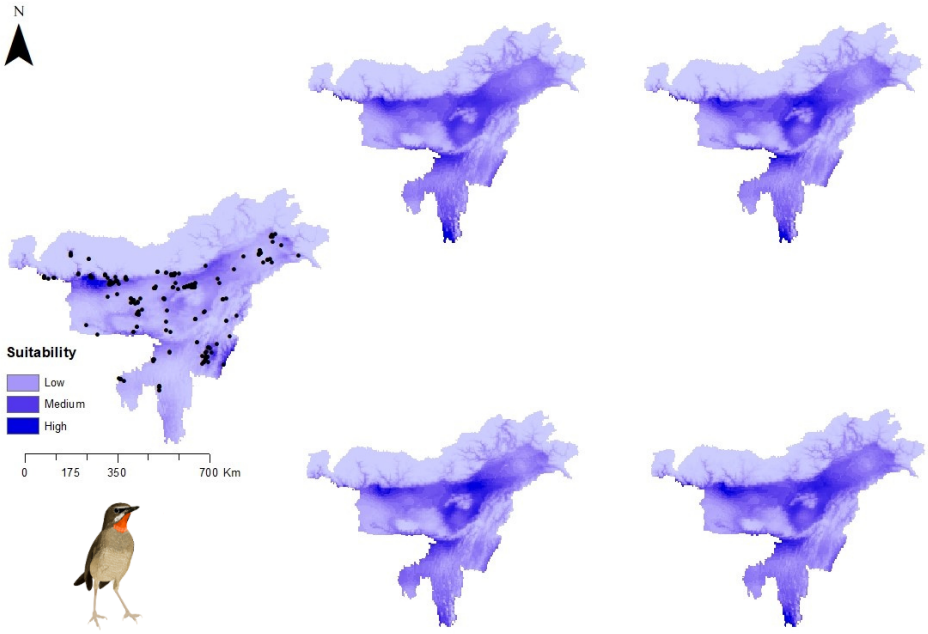

Figure S5: Potential distributions of *Calliope calliope* (Siberian Rubythroat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

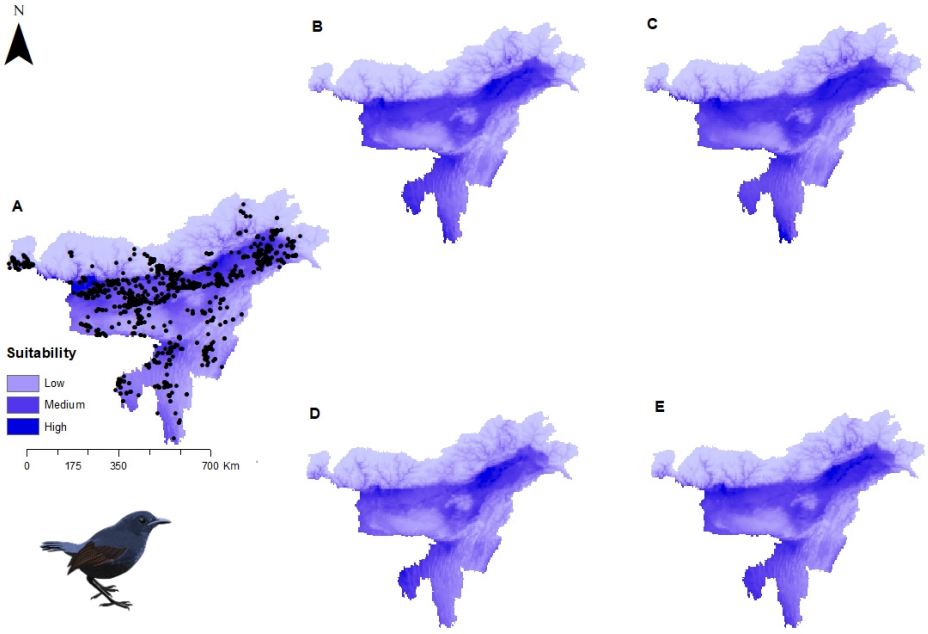

Figure S6: Potential distributions of *Cinclidium frontale* (Blue-fronted Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

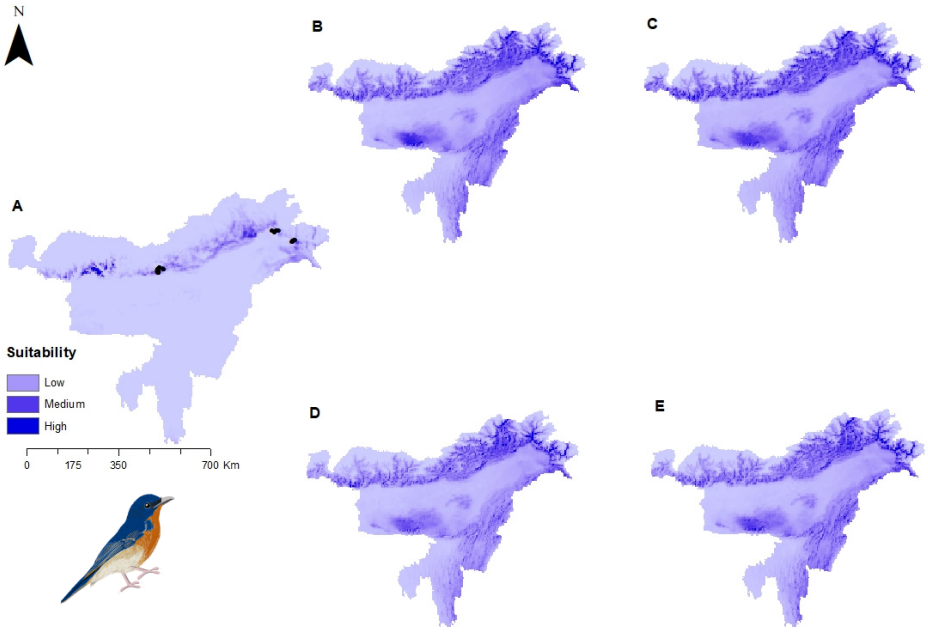

Figure S7: Potential distributions of *Cyornis magnirostris* (Large Blue Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

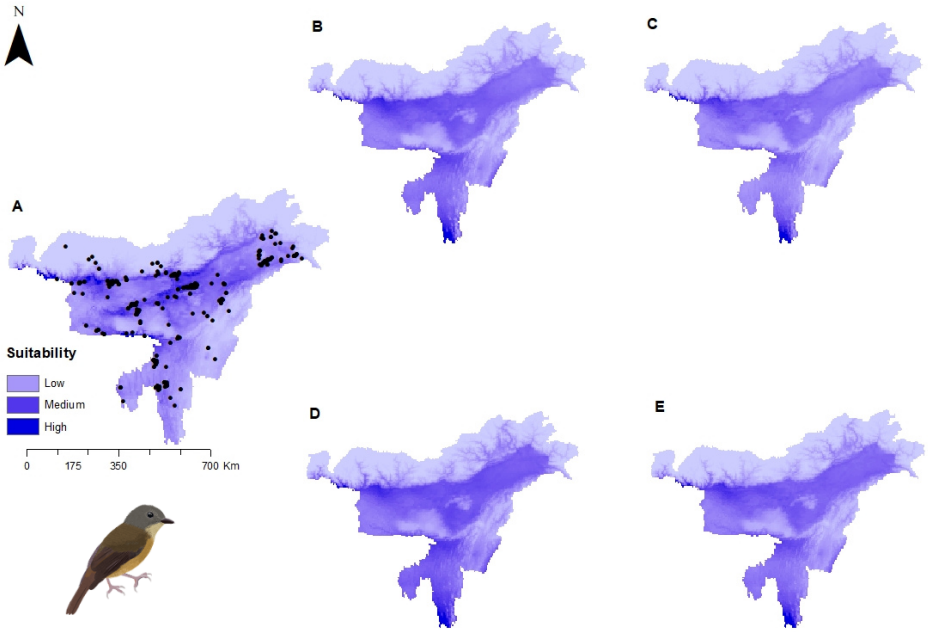

Figure S8: Potential distributions of *Cyornis poliogenys* (Pale-chinned Blue Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

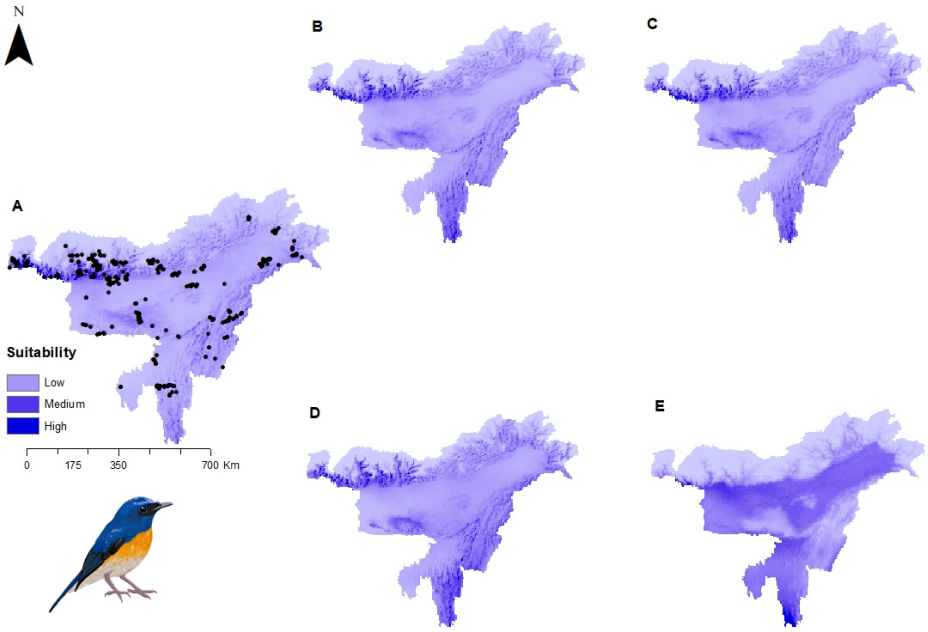

Figure S9: Potential distributions of *Cyornis rubeculoides* (Blue-throated Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

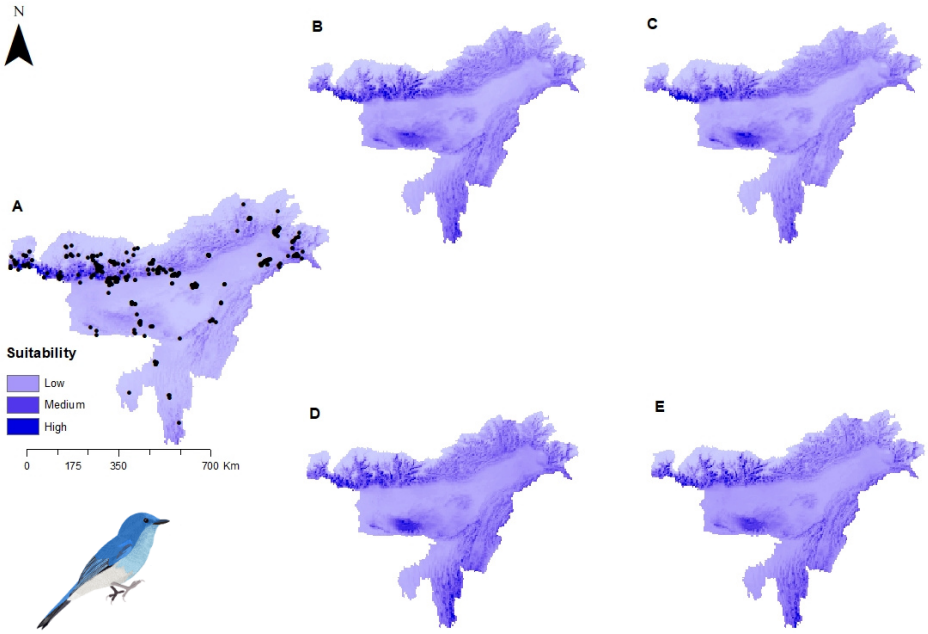

Figure S10: Potential distributions of *Cyornis poliogenys* (Pale-chinned Blue Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

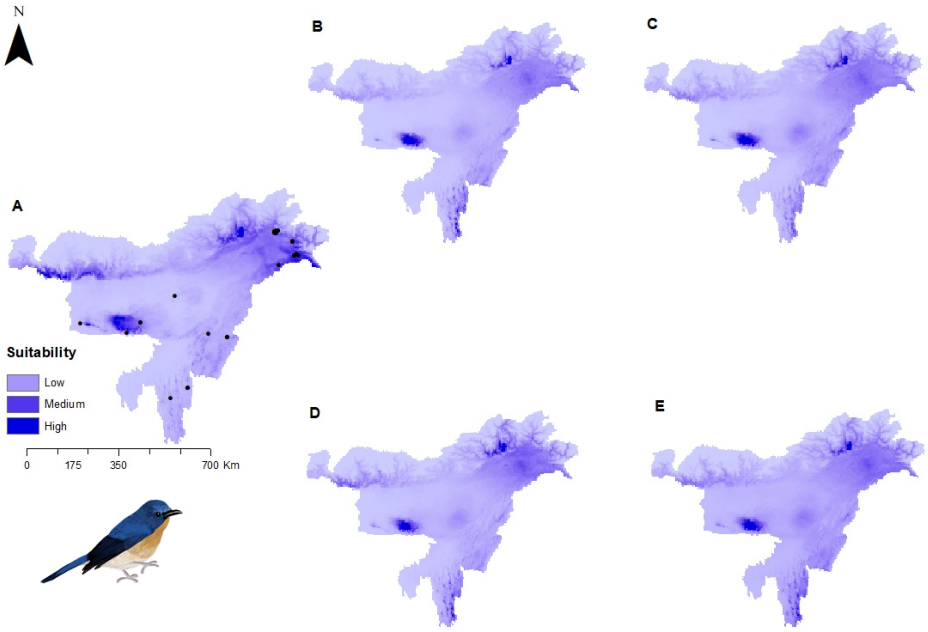

Figure S11: Potential distributions of *Cyornis whitei* (Hill Blue Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

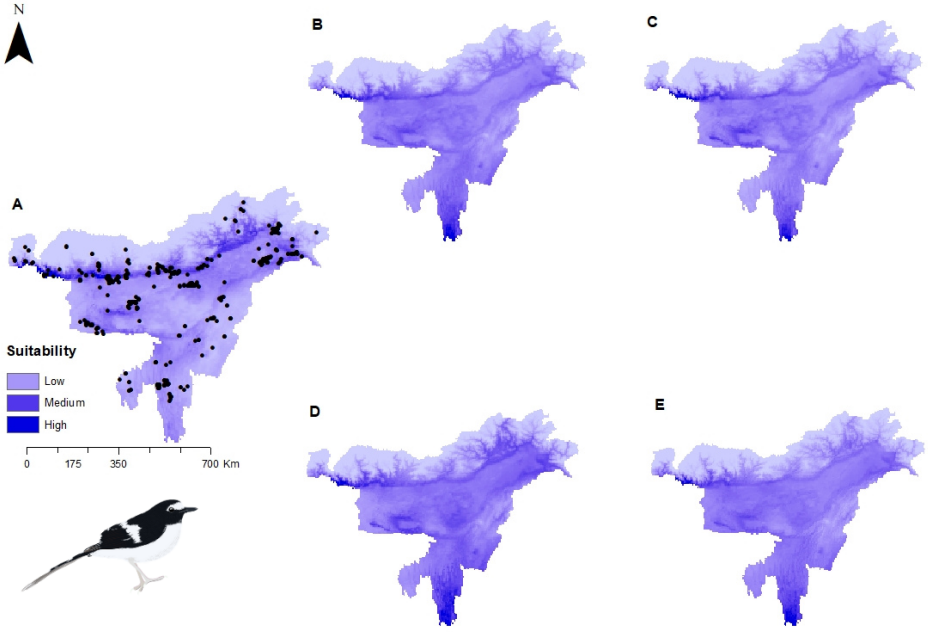

Figure S12: Potential distributions of *Enicurus immaculatus* (Black-backed Forktail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

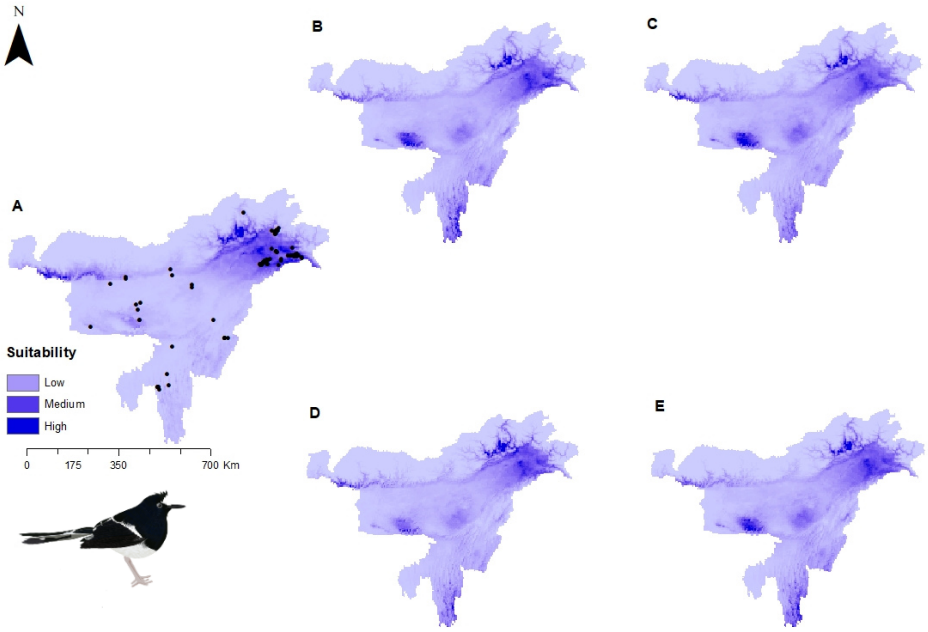

Figure S13: Potential distributions of *Enicurus leschenaulti* (White-crowned Forktail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

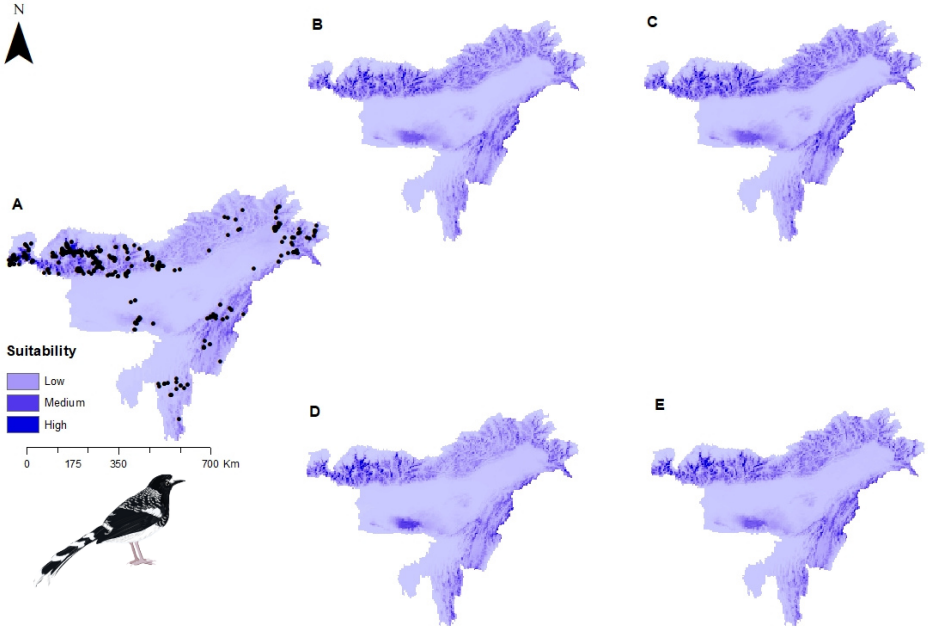

Figure S14: Potential distributions of *Enicurus maculatus* (Spotted Forktail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

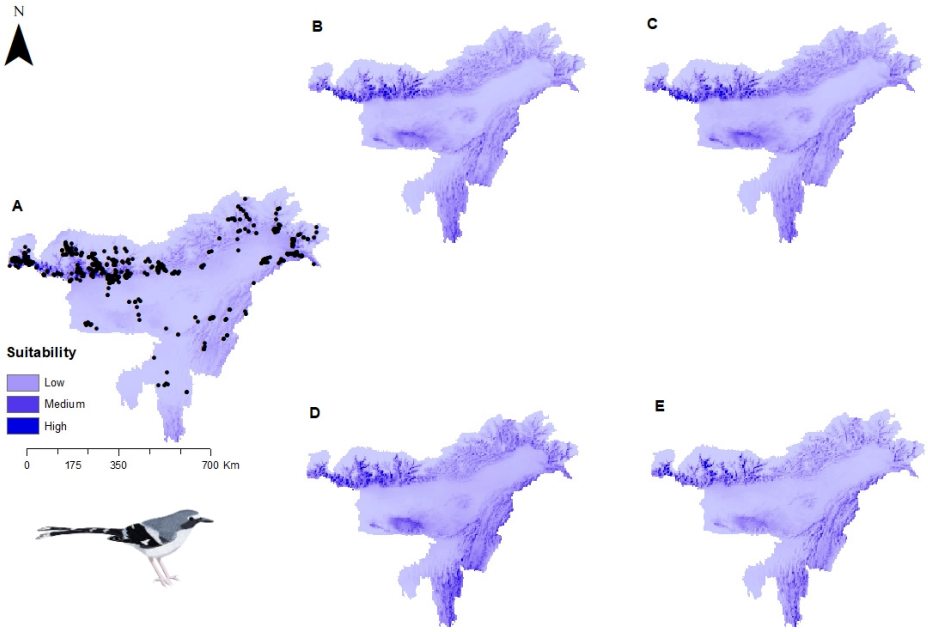

Figure S15: Potential distributions of *Enicurus schistaceus* (Slaty-backed Forktail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

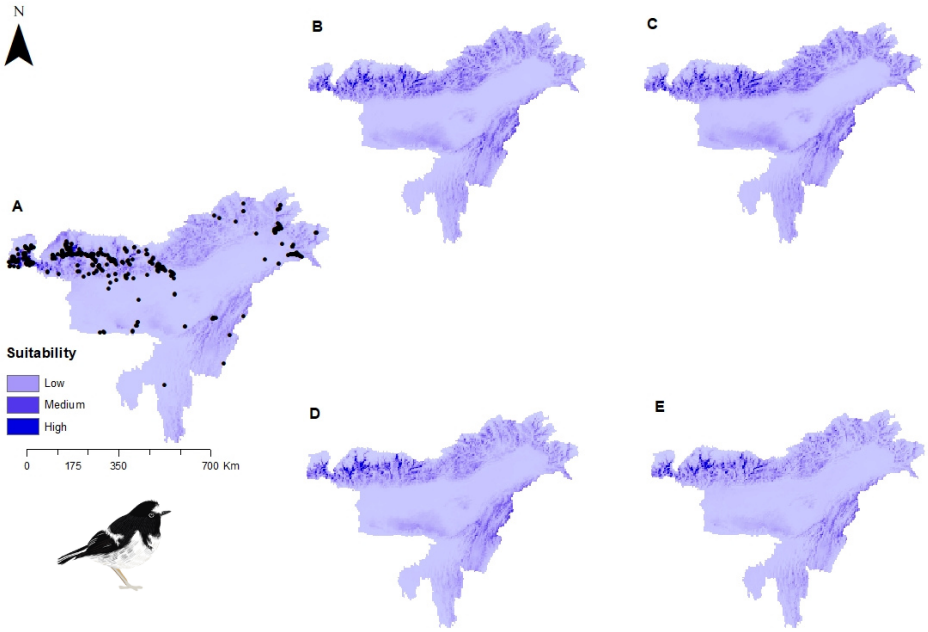

Figure S16: Potential distributions of *Enicurus scouleri* (Little Forktail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

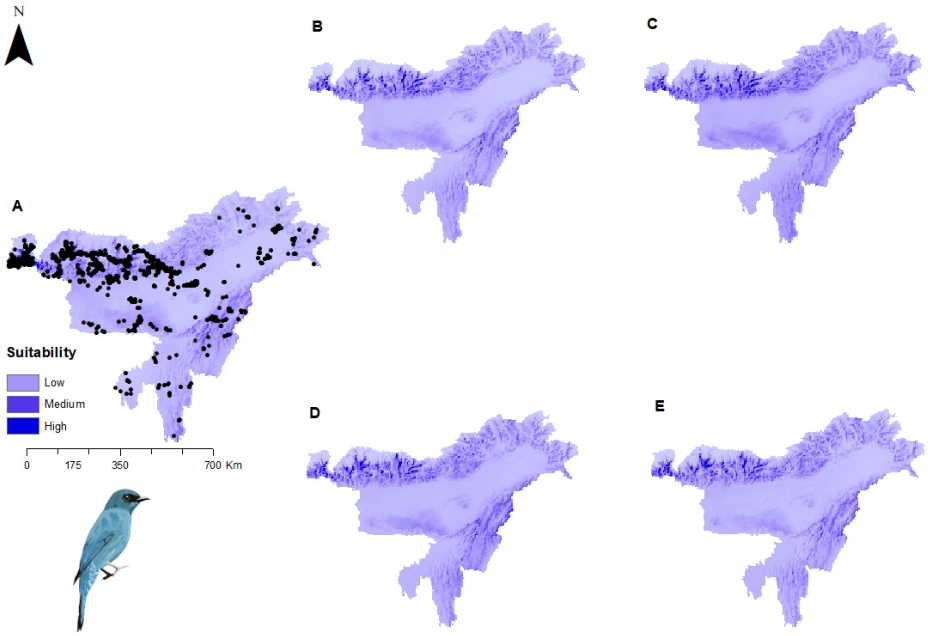

Figure S17: Potential distributions of *Eumyias thalassinus* (Verditer Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

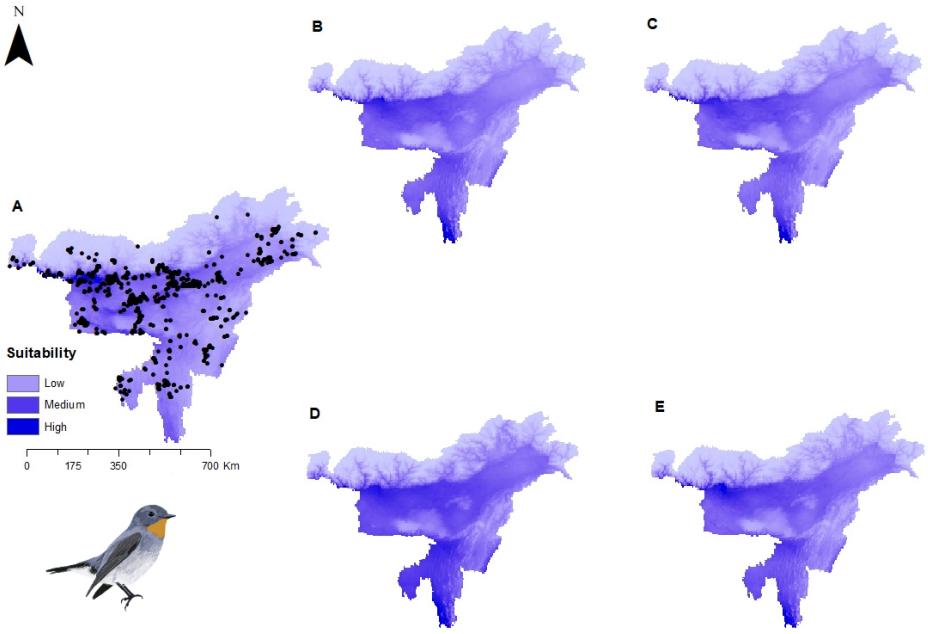

Figure S18: Potential distributions of *Ficedula albicilla* (Taiga Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

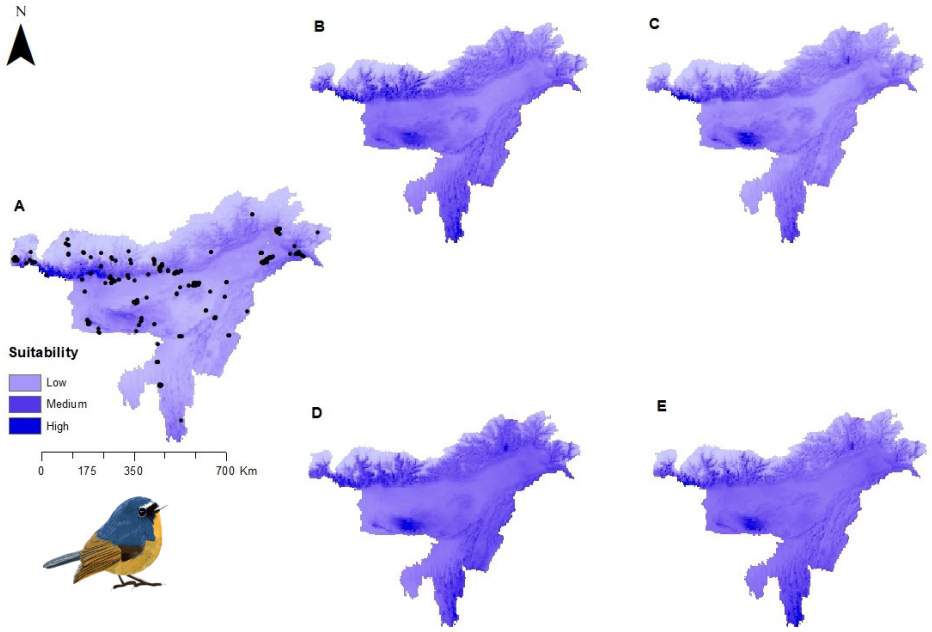

Figure S19: Potential distributions of *Ficedula hyperythra* (Snowy-browed Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

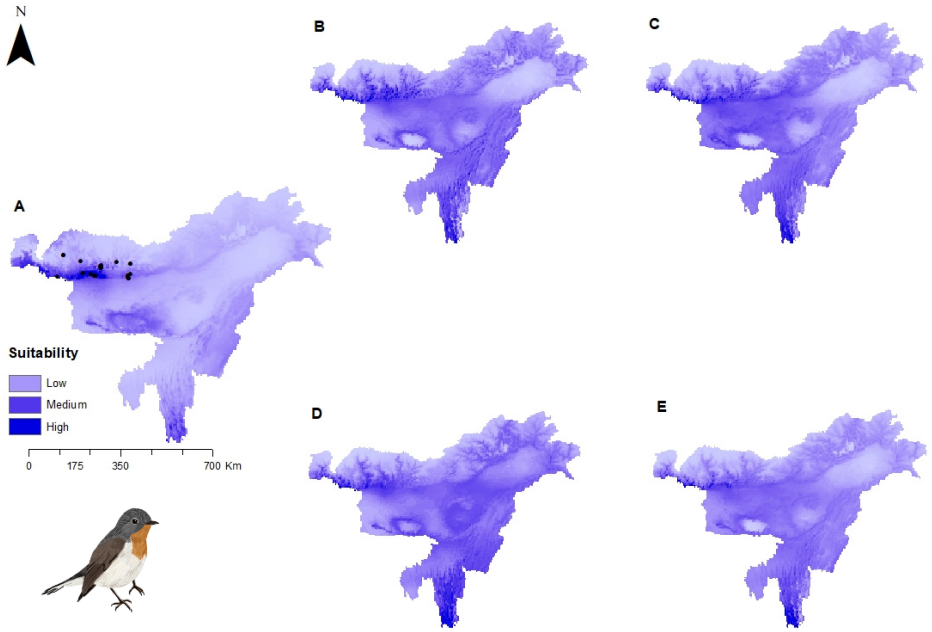

Figure S20: Potential distributions of *Ficedula parva* (Red-breasted Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

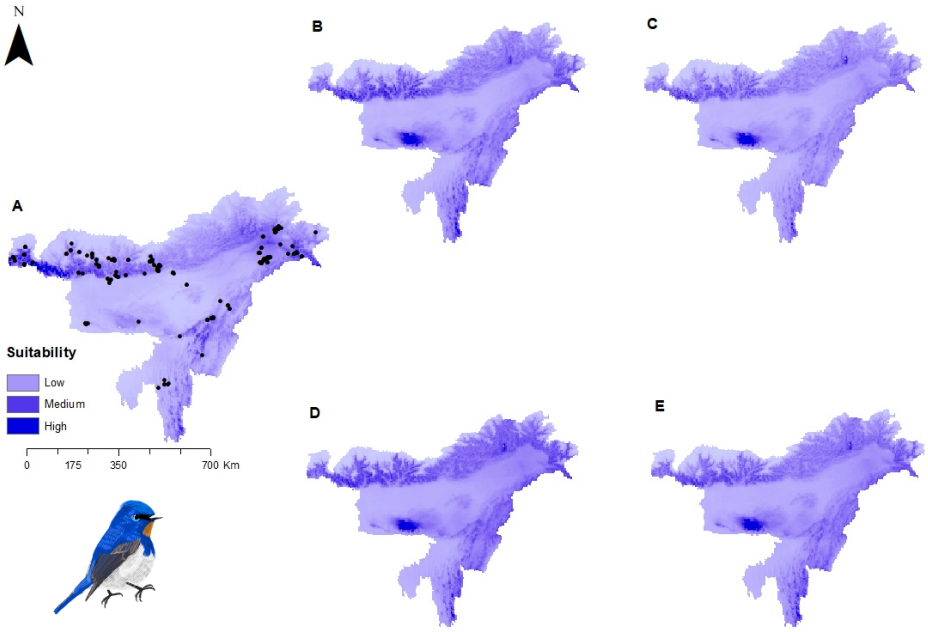

Figure S21: Potential distributions of *Ficedula sapphira* (Sapphire Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

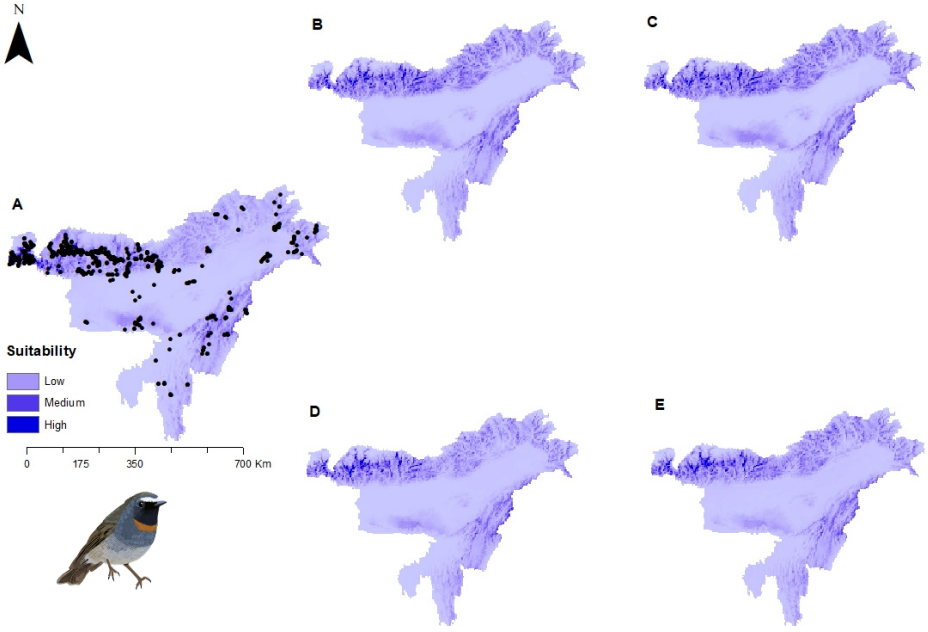

Figure S22: Potential distributions of *Ficedula strophiata* (Rufous-gorgeted Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

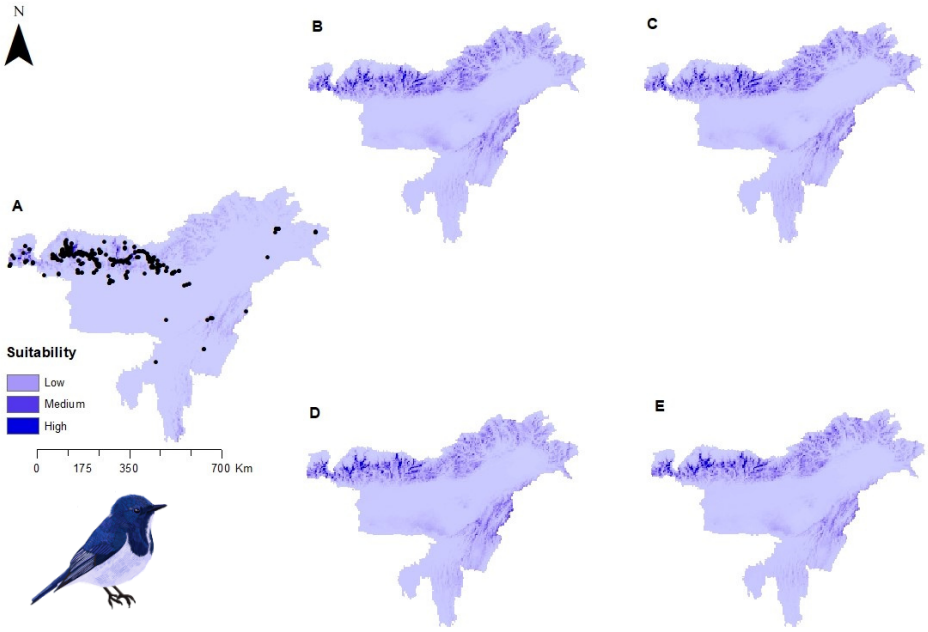

Figure S23: Potential distributions of *Ficedula superciliaris* (Ultramarine Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

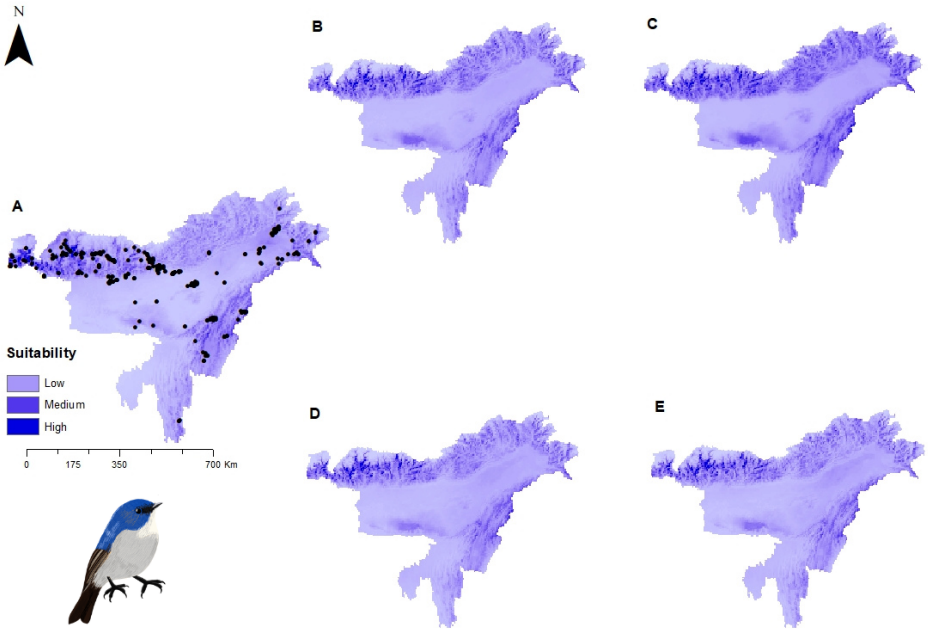

Figure S24: Potential distributions of *Ficedula tricolor* (Slaty-blue Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

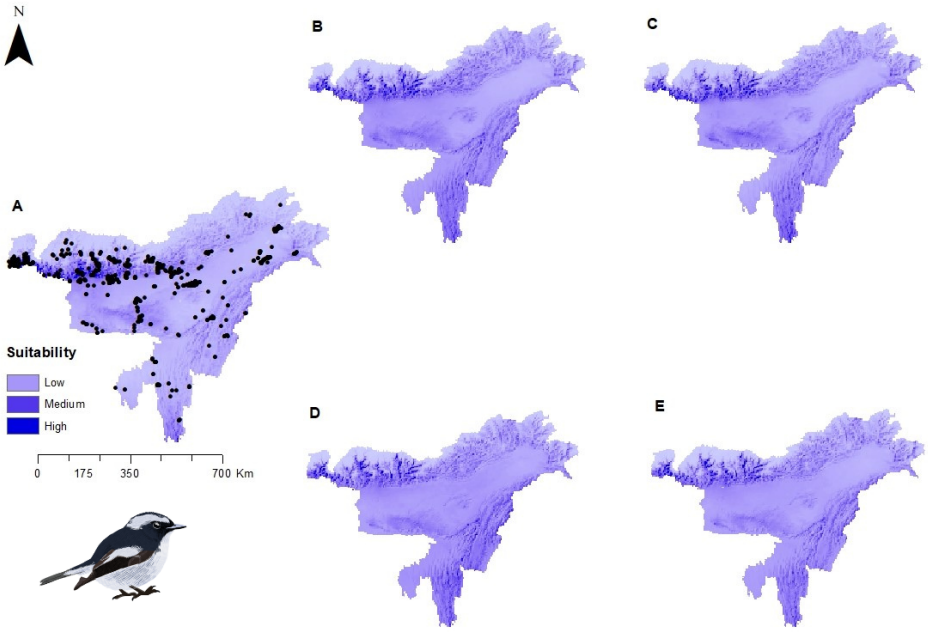

Figure S25: Potential distributions of *Ficedula westermanni* (Little Pied Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

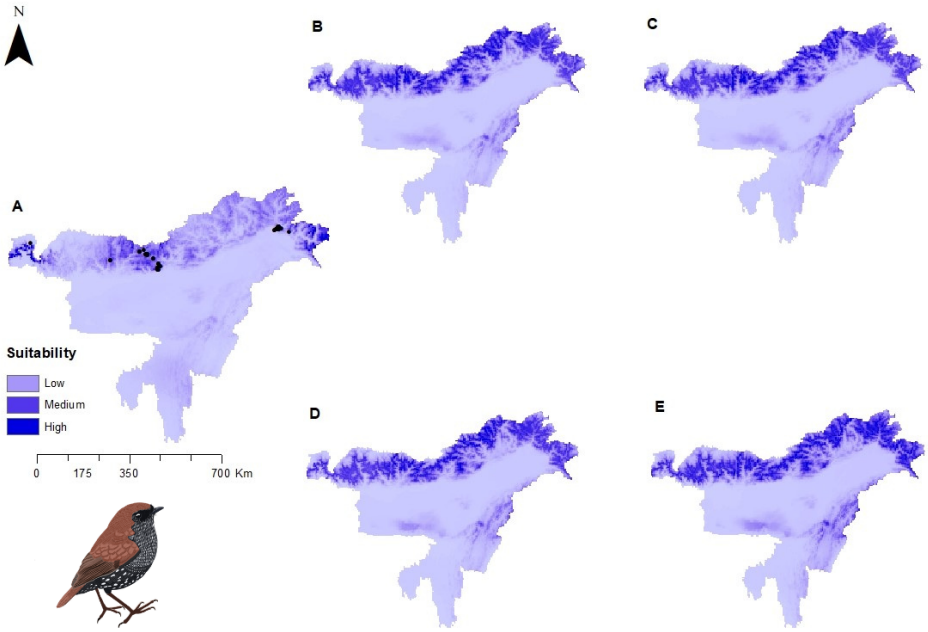

Figure S26: Potential distributions of *Heteroxenicus stellatus* (Gould's Shortwing) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

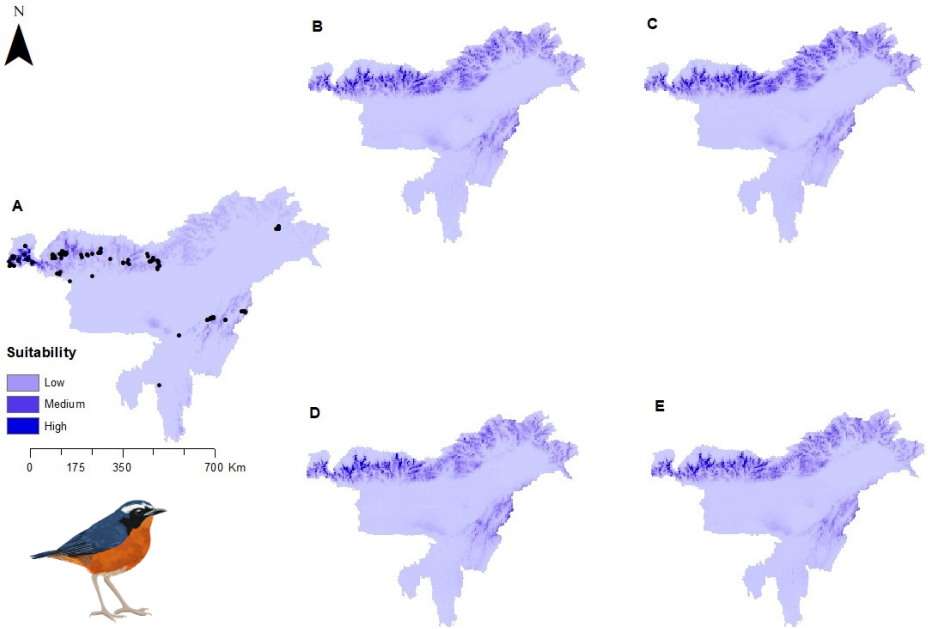

Figure S27: Potential distributions of *Larvivora brunnea* (Indian Blue Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

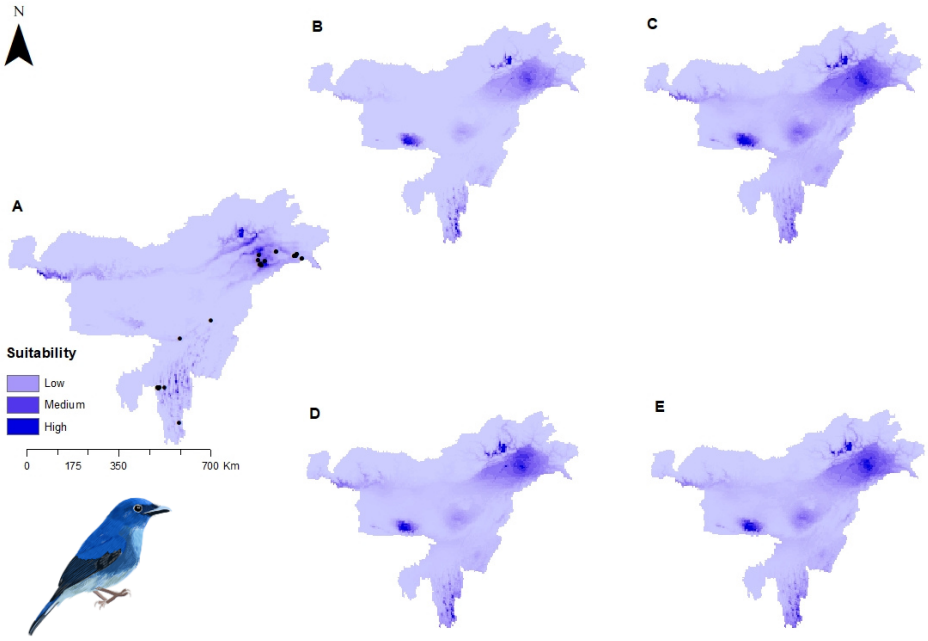

Figure S28: Potential distributions of *Leucoptilon concretum* (White-tailed Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

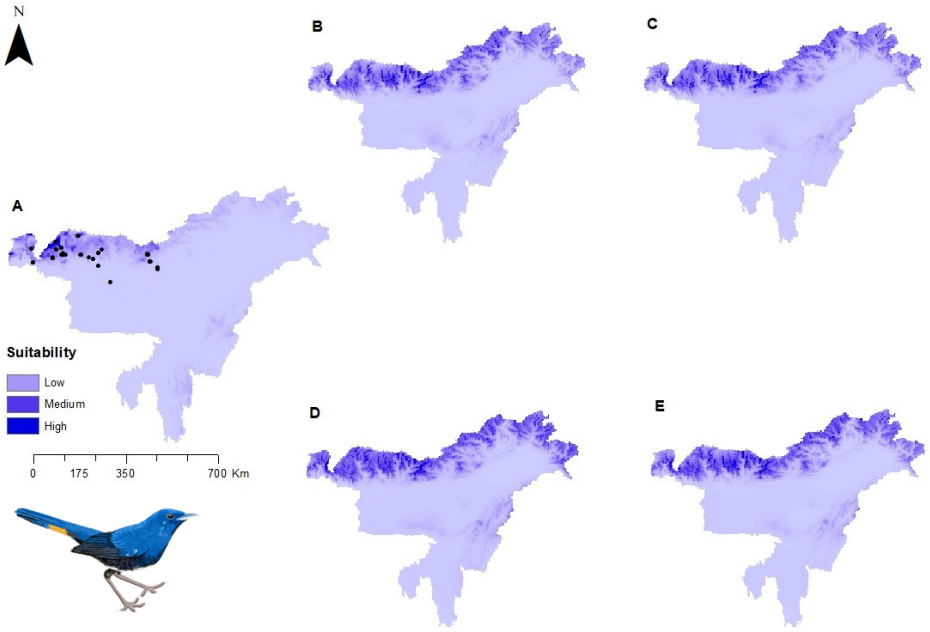

Figure S29: Potential distributions of *Luscinia phaenicuroides* (White-bellied Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

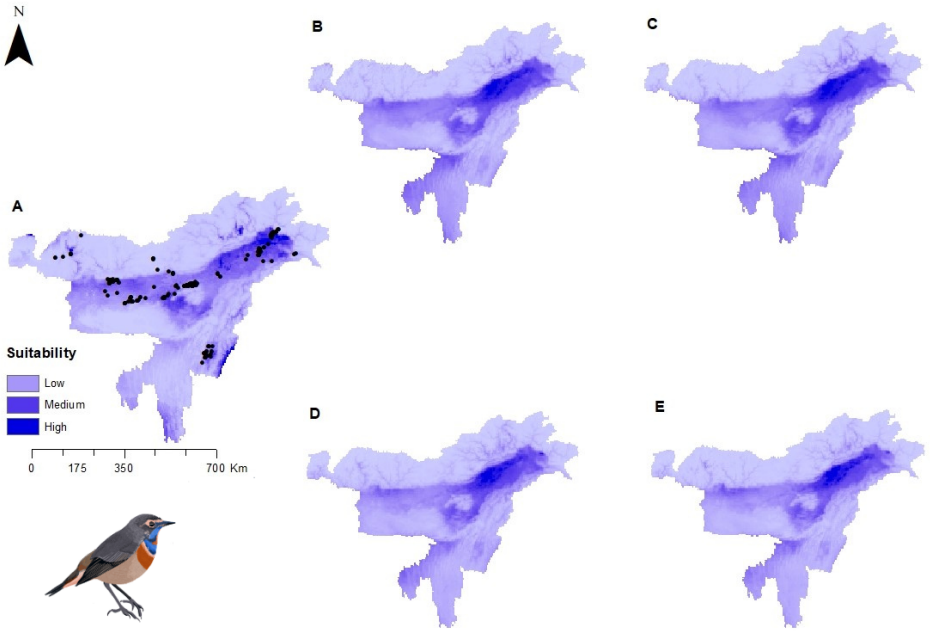

Figure S30: Potential distributions of *Luscinia svecica* (Bluethroat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

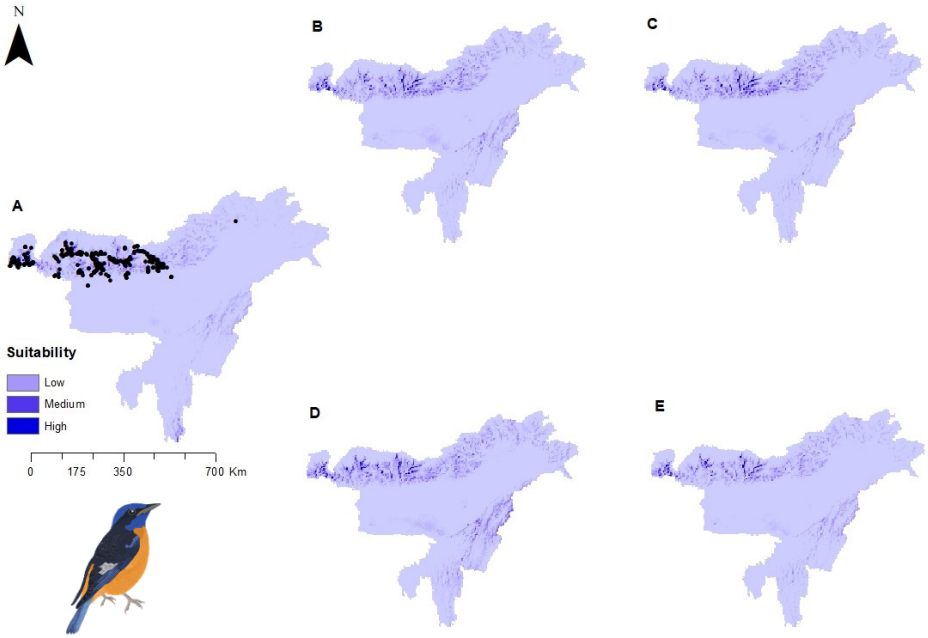

Figure S31: Potential distributions of *Monticola cinclorhyncha* (Blue-capped Rock Thrush) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

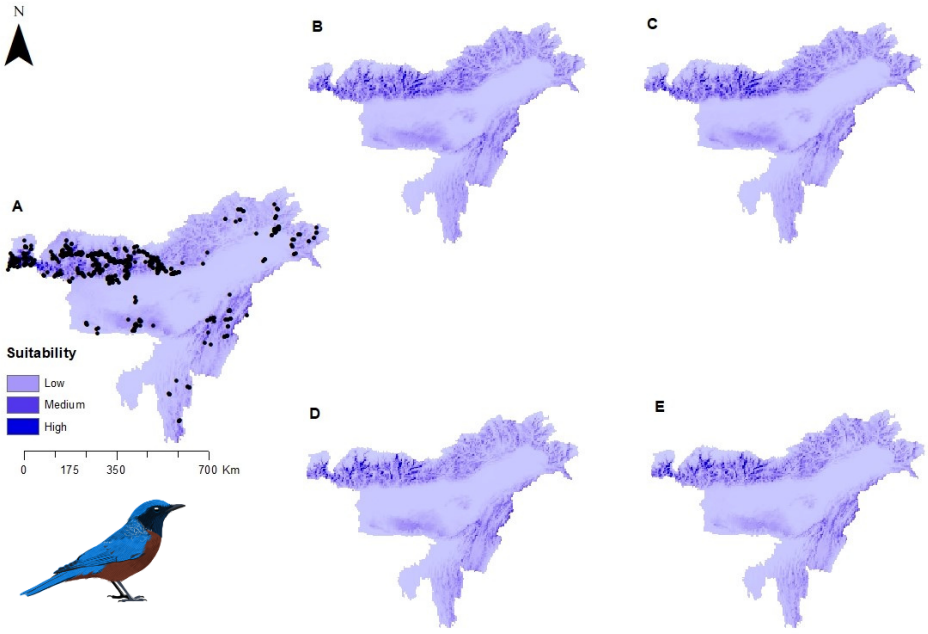

Figure S32: Potential distributions of *Monticola rufiventris* (Chestnut-bellied Rock Thrush) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

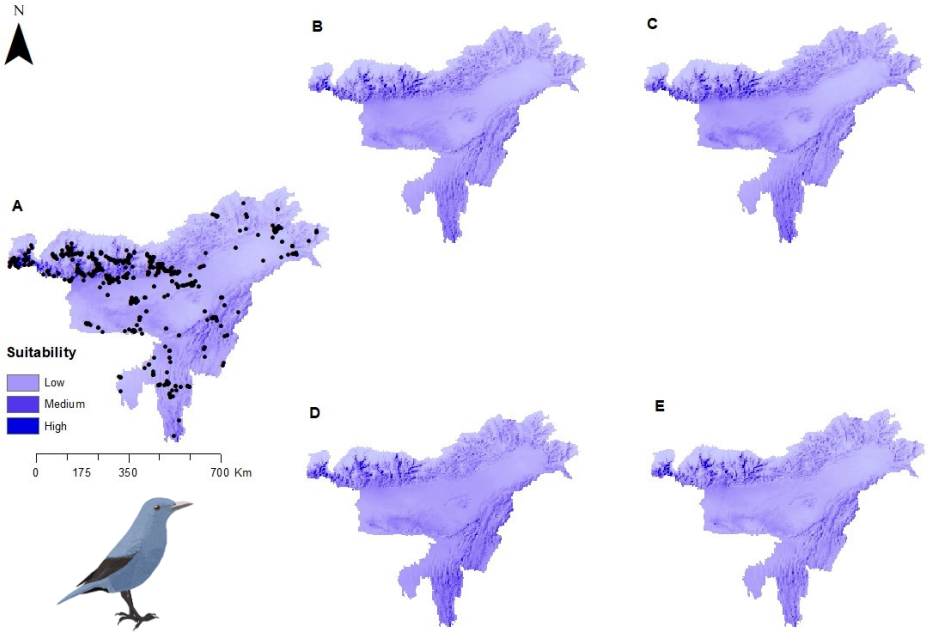

Figure S33: Potential distributions of *Monticola solitarius* (Blue Rock-Thrush) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

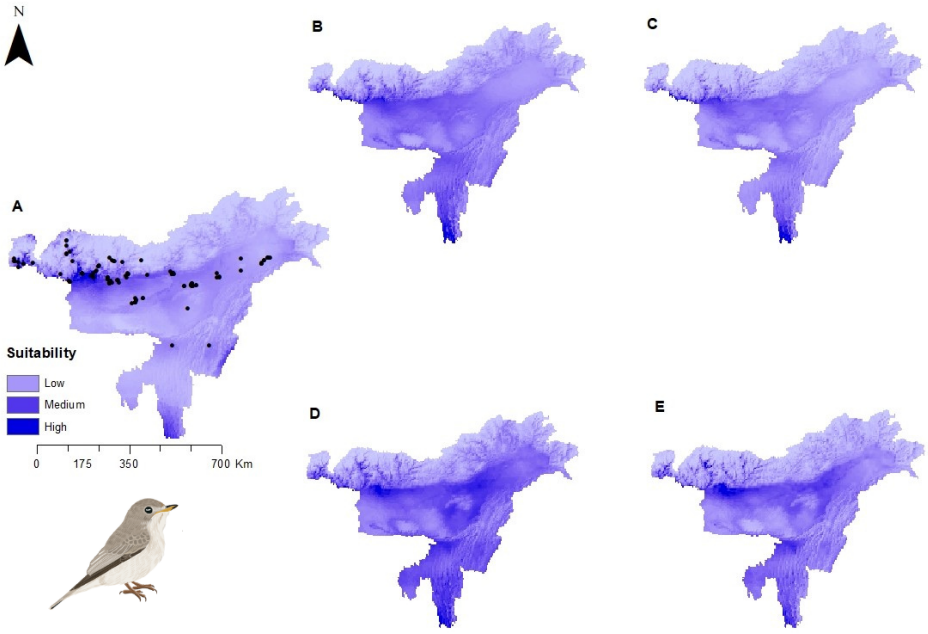

Figure S34: Potential distributions of *Muscicapa dauurica* (Asian Brown Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

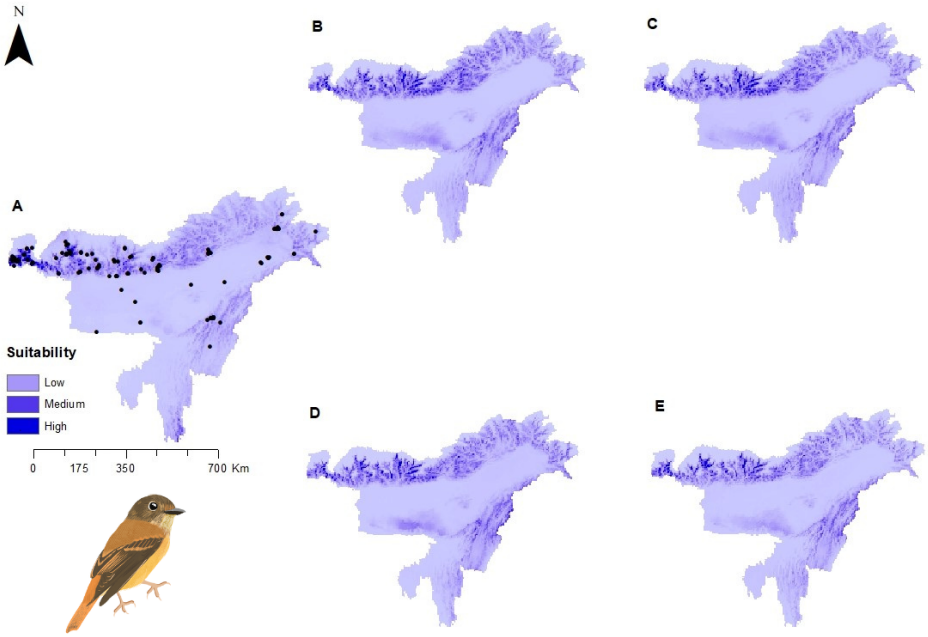

Figure S35: Potential distributions of *Muscicapa ferruginea* (Ferruginous Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

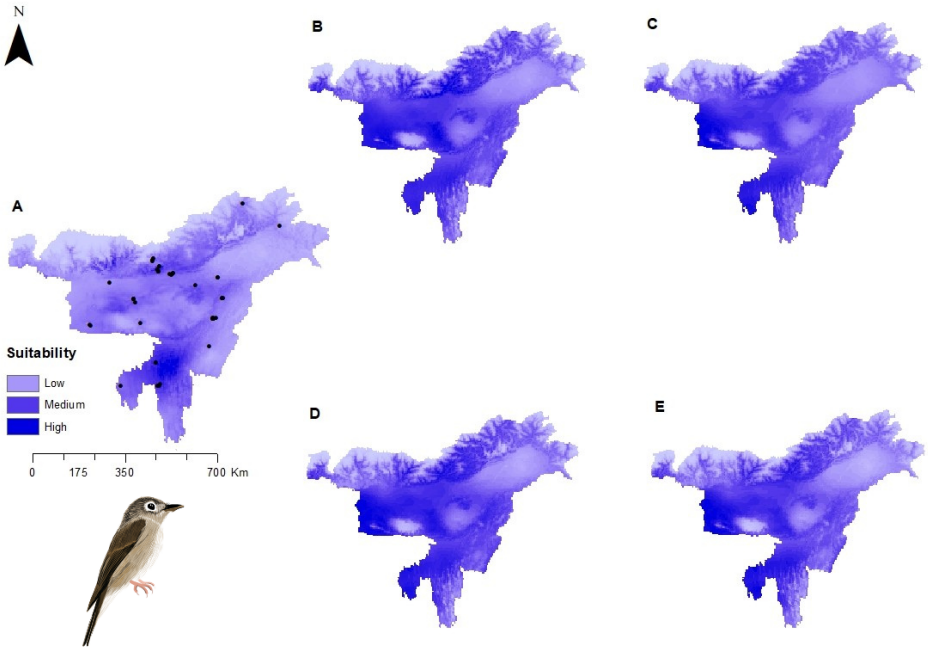

Figure S36: Potential distributions of *Muscicapa muttui* (Brown-breasted Flycatcher) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

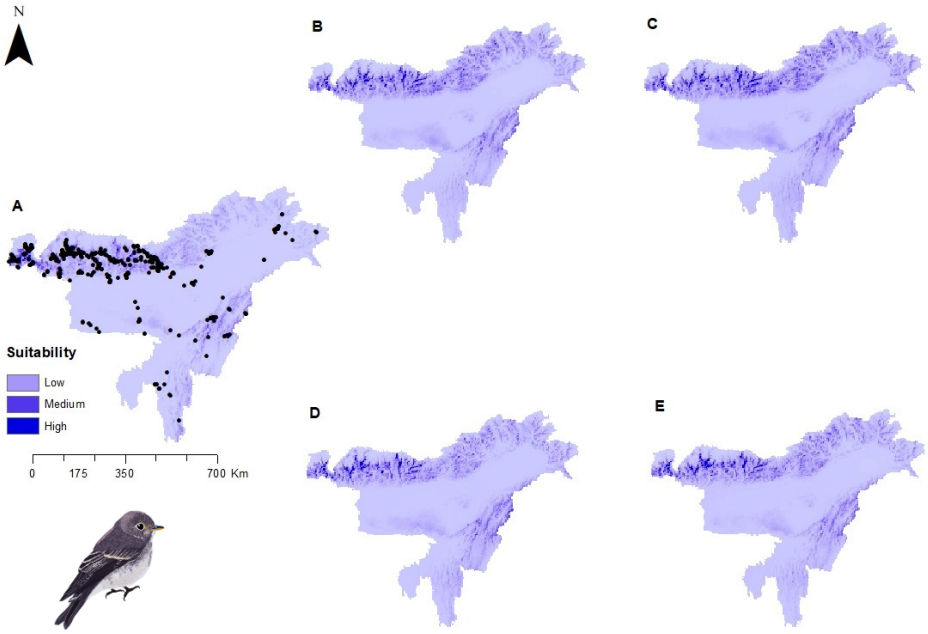

Figure S37: Potential distributions of *Muscicapa sibirica* (Dark-sided FlycatcheR) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

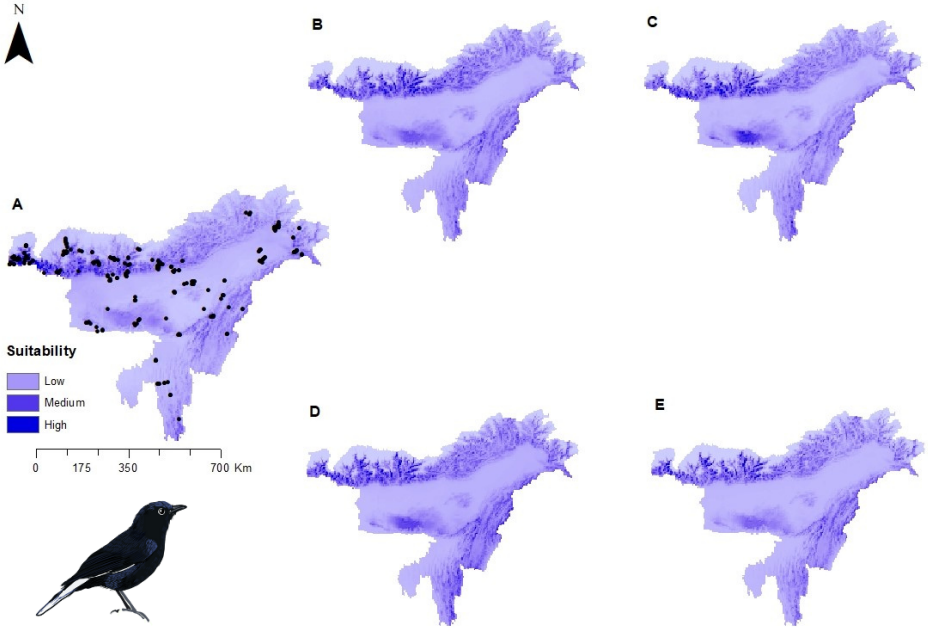

Figure S38: Potential distributions of *Myiomela leucura* (White-tailed Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

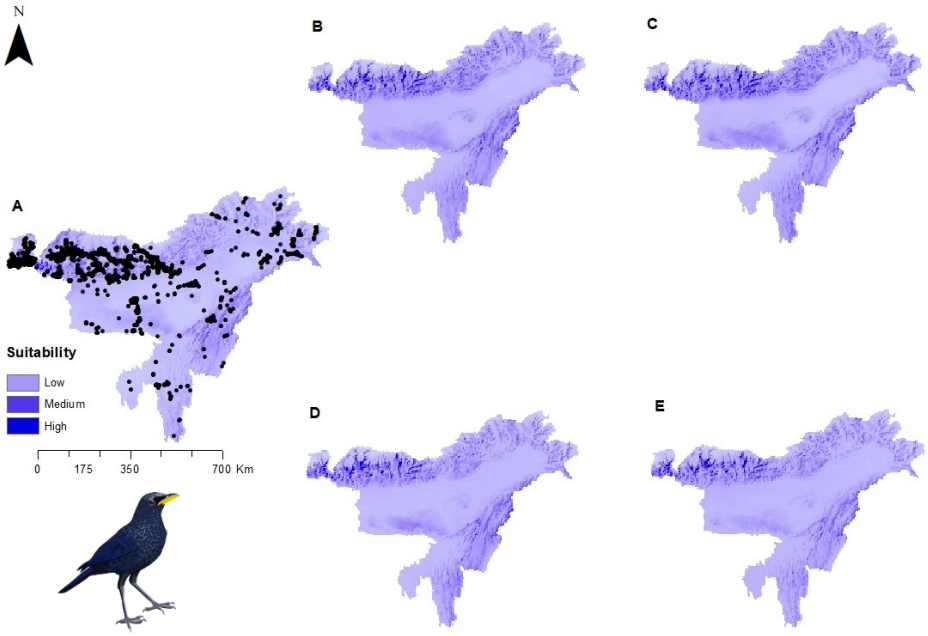

Figure S39: Potential distributions of *Myophonus caeruleus* (Blue Whistling-Thrush) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

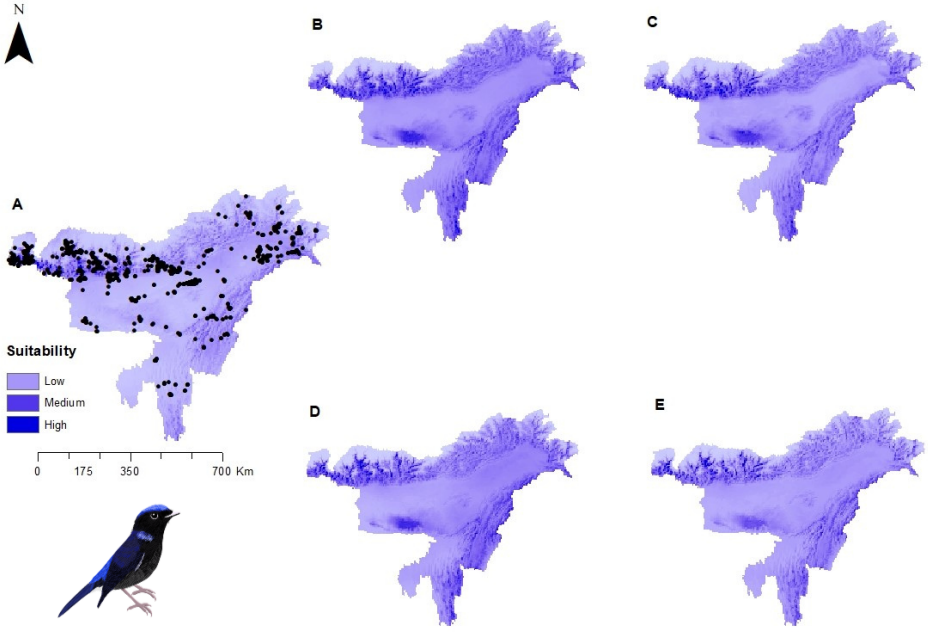

Figure S40: Potential distributions of *Niltava macgrigoriae* (Small Niltava) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

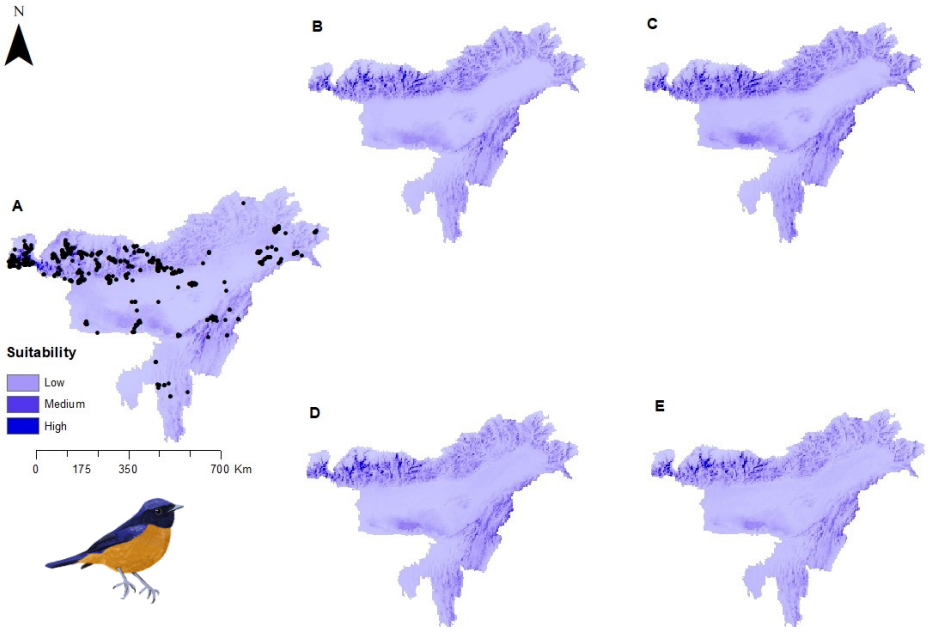

Figure S41: Potential distributions of *Niltava sundara* (Rufous-bellied Niltava) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

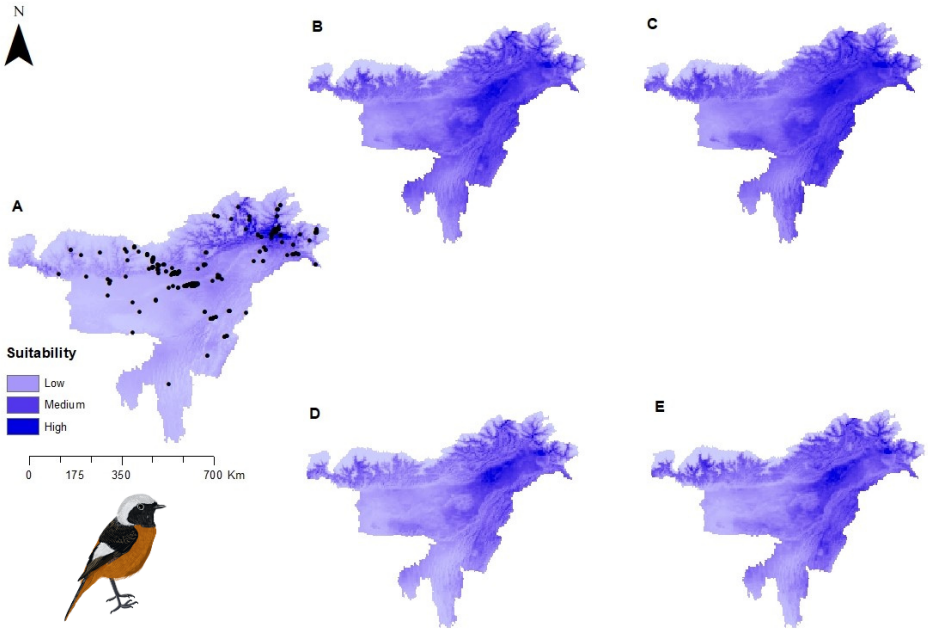

Figure S42: Potential distributions of *Phoenicurus auroreus* (Daurian Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

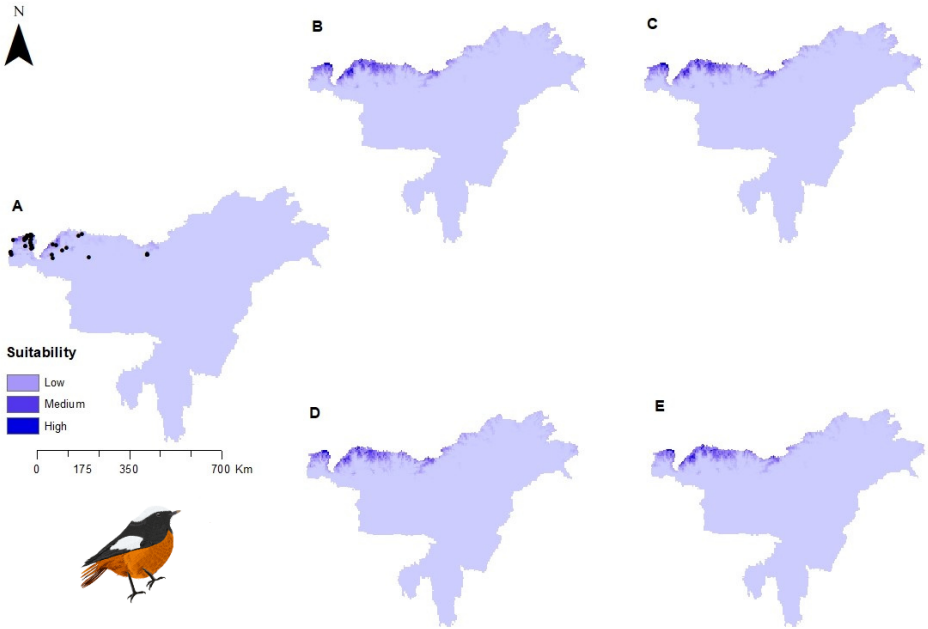

Figure S43: Potential distributions of *Phoenicurus erythrogastrus* (White-winged Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

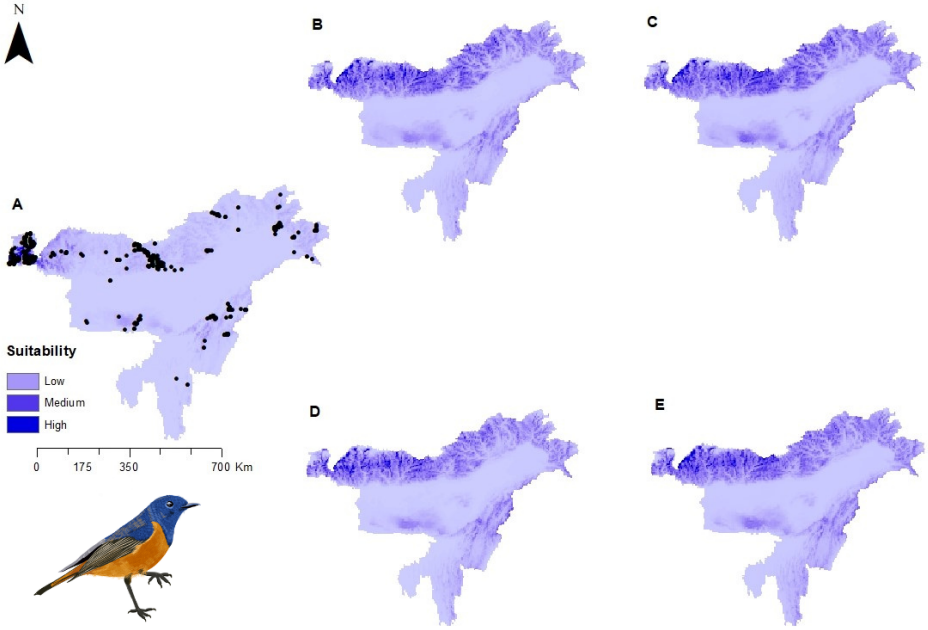

Figure S44: Potential distributions of *Phoenicurus frontalis* (Blue-fronted Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

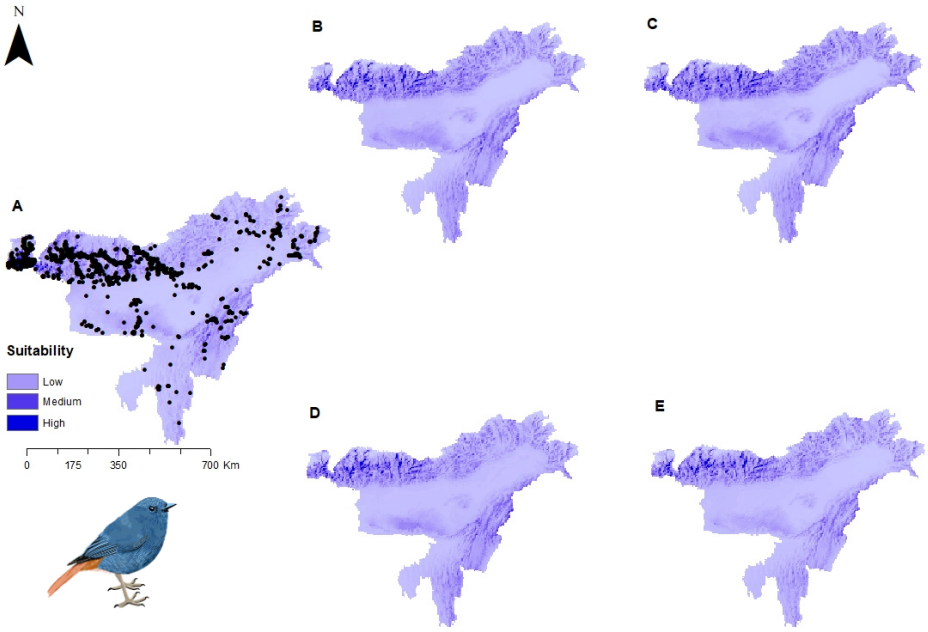

Figure S45: Potential distributions of *Phoenicurus fuliginosus* (Plumbeous Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

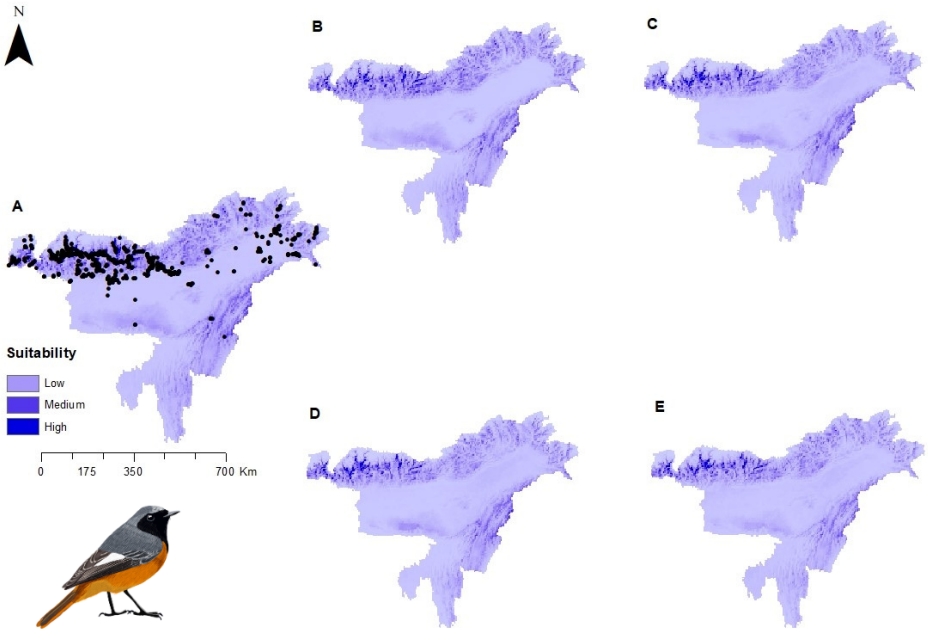

Figure S46: Potential distributions of *Phoenicurus hodgsoni* (Hodgson's Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

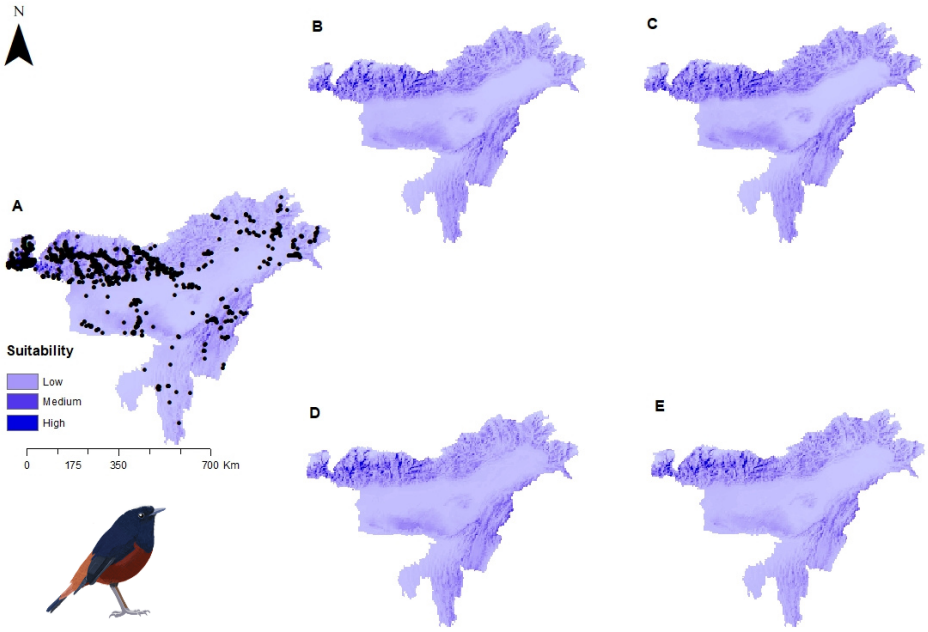

Figure S47: Potential distributions of *Phoenicurus leucocephalus* (White-capped Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

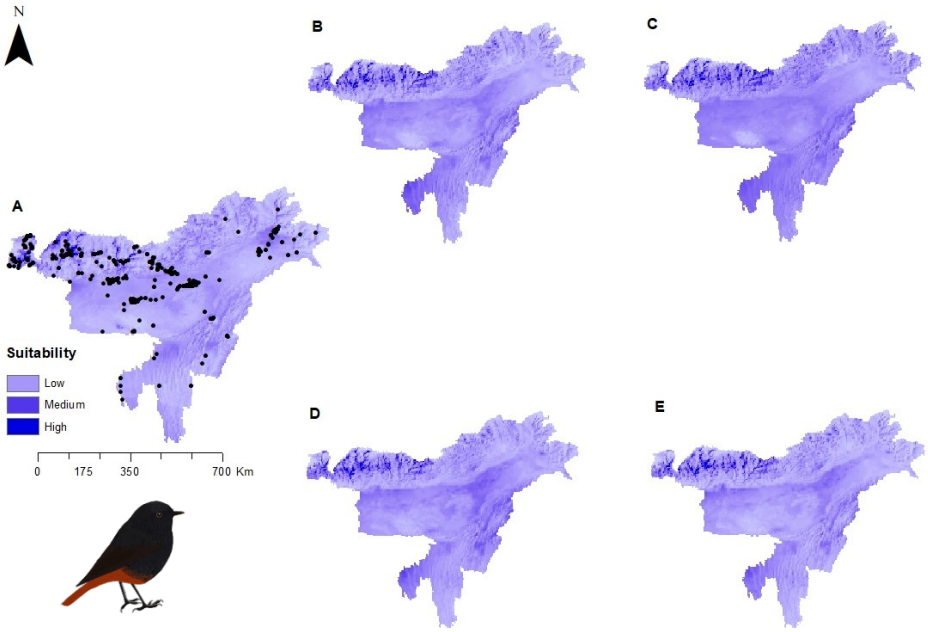

Figure S48: Potential distributions of *Phoenicurus ochruros* (Black Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

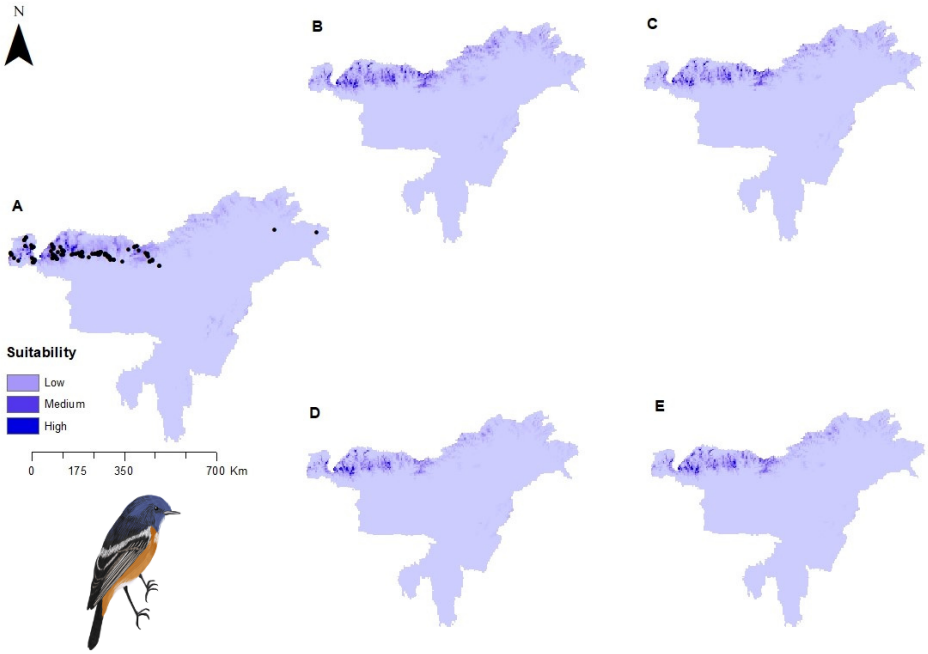

Figure S49: Potential distributions of *Phoenicurus schisticeps* (White-throated Redstart) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

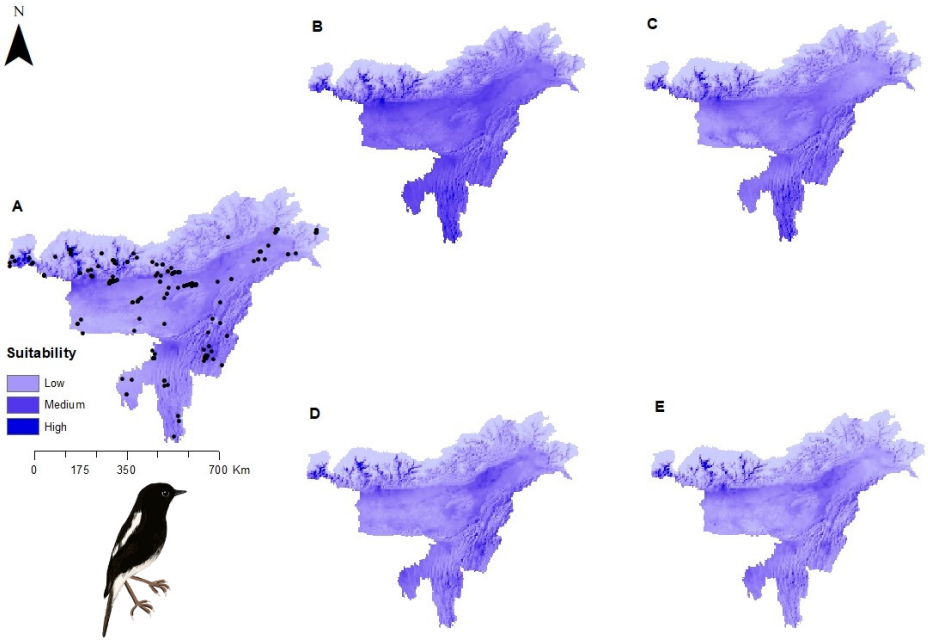

Figure S50: Potential distributions of *Saxicola caprata* (Pied Bushchat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

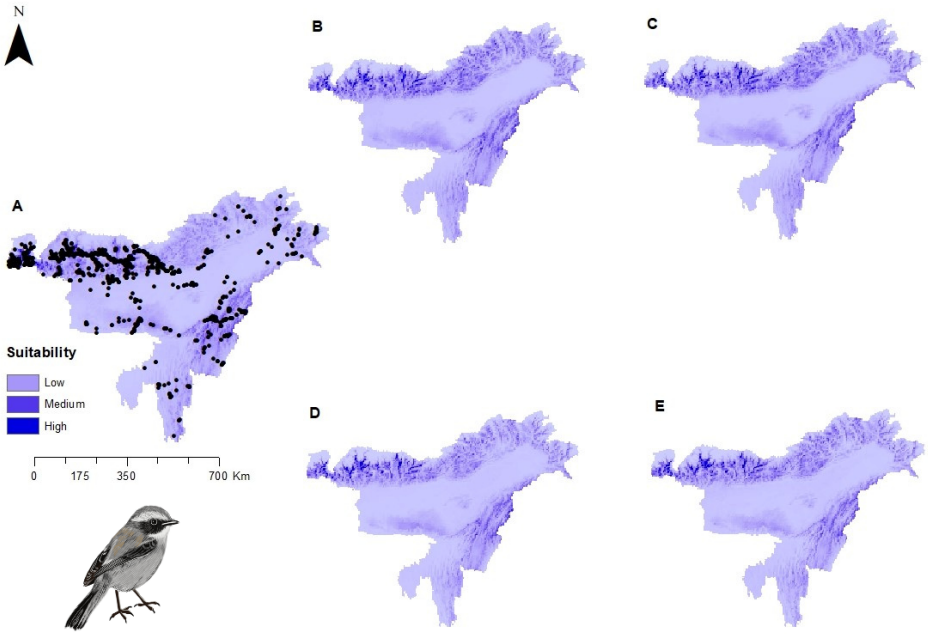

Figure S51: Potential distributions of *Saxicola ferreus* (Grey Bushchat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

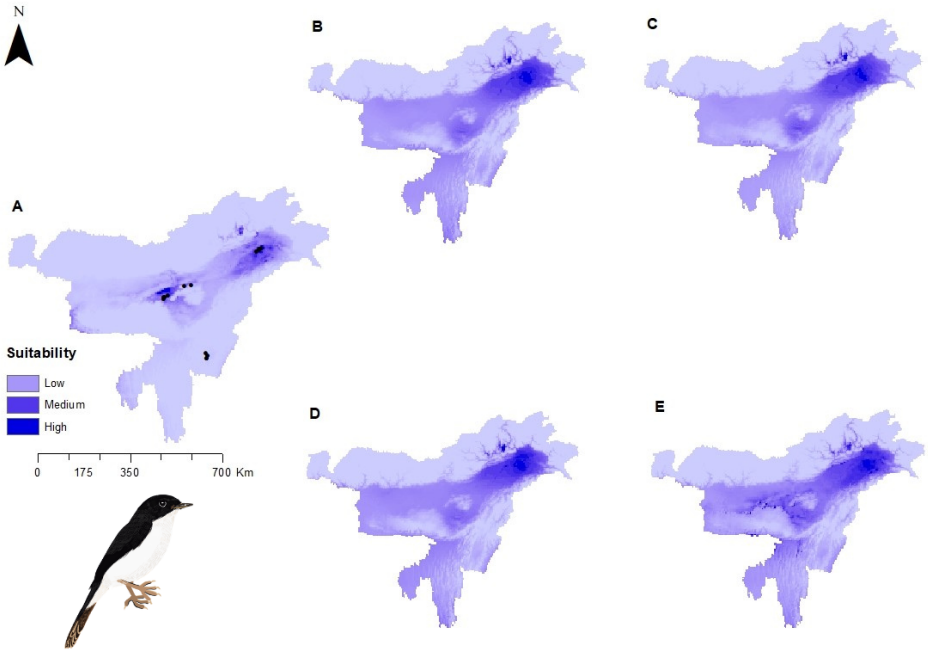

Figure S52: Potential distributions of *Saxicola jerdoni* (Jerdon's Bushchat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

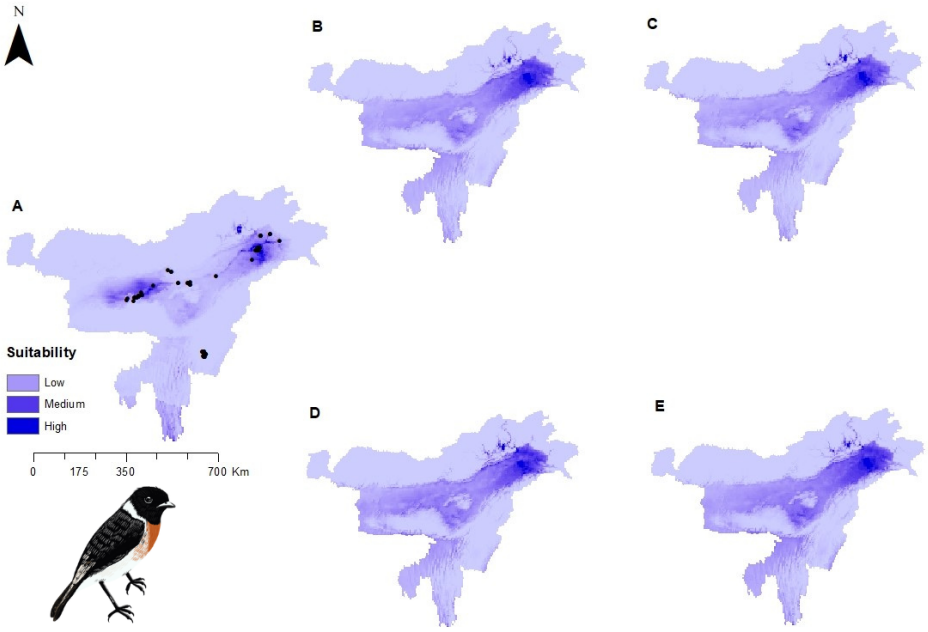

Figure S53: Potential distributions of *Saxicola leucurus* (White-tailed Stonechat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

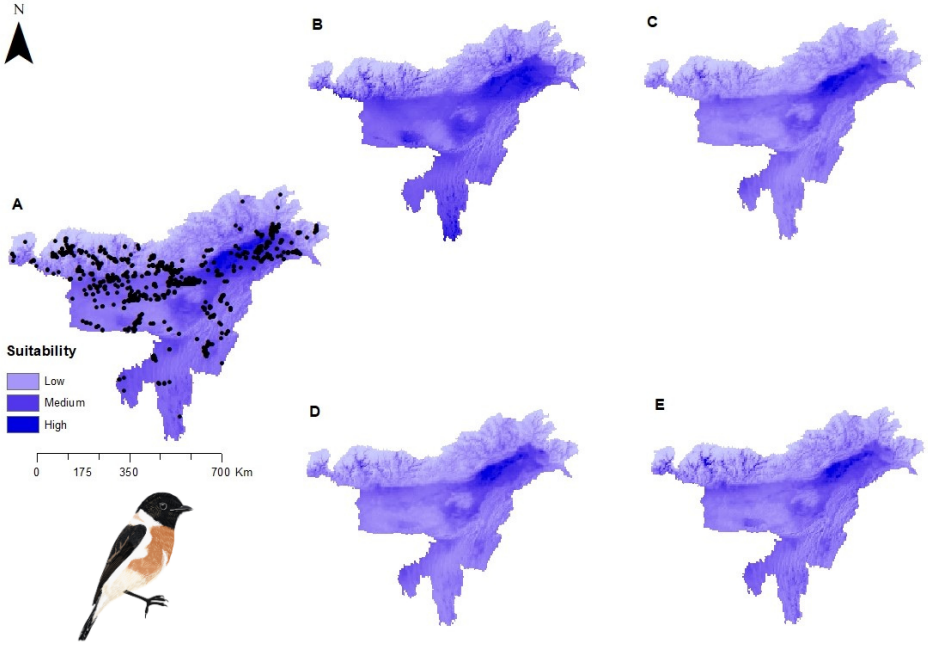

Figure S54: Potential distributions of *Saxicola maurus* (Siberian Stonechat) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

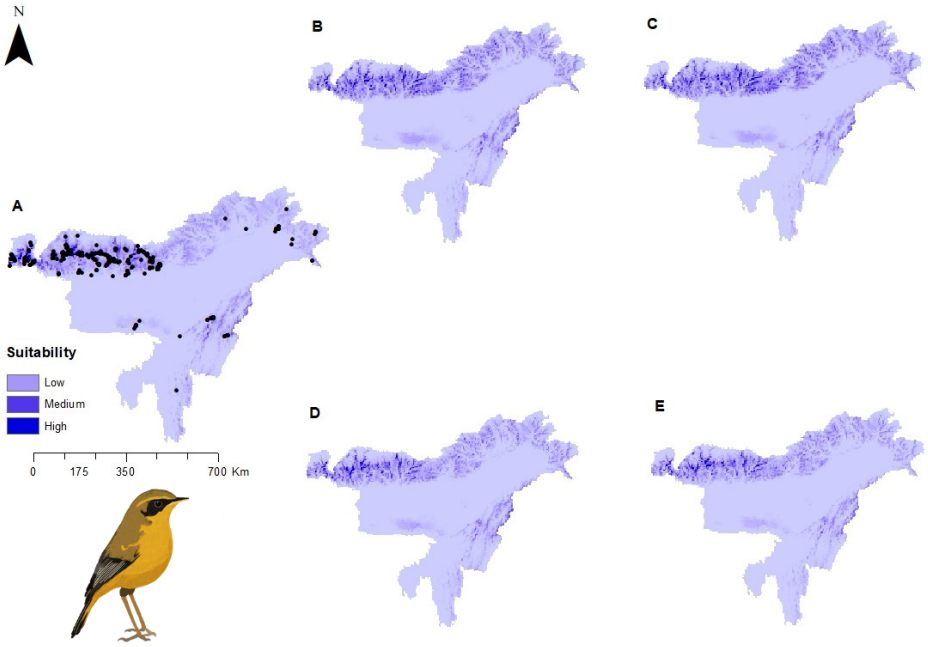

Figure S55: Potential distributions of *Tarsiger chrysaeus* (Golden Bush-Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

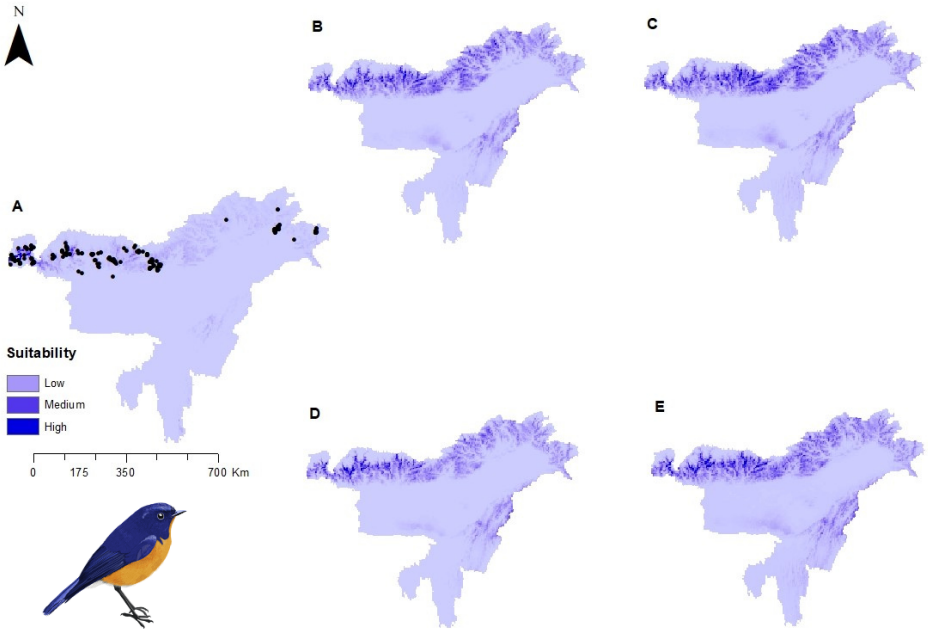

Figure S56: Potential distributions of *Tarsiger hyperythrus* (Rufous-breasted Bush-Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

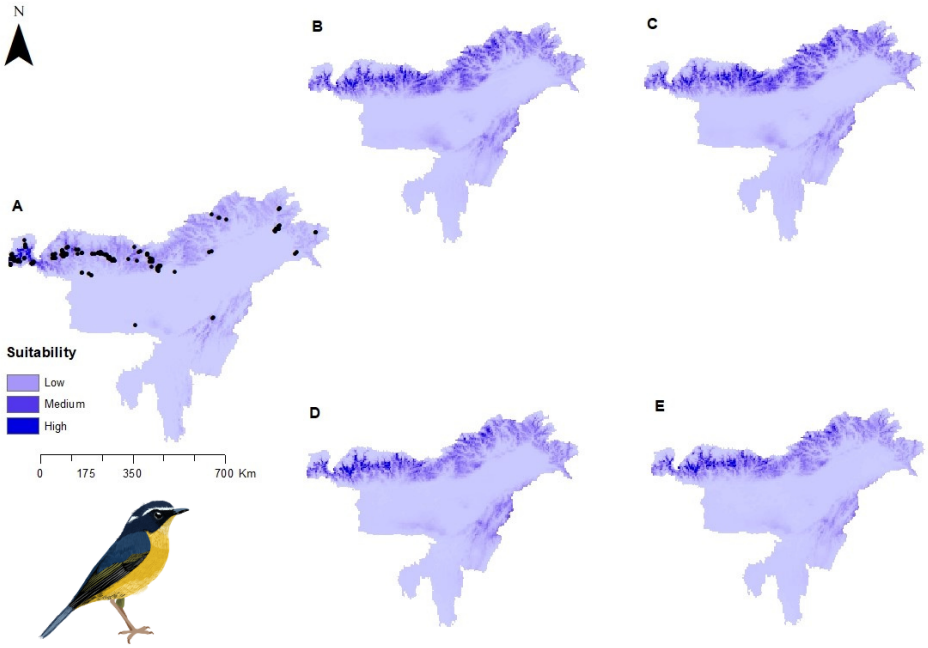

Figure S57: Potential distributions of *Tarsiger indicus* (White-browed Bush-Robin) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

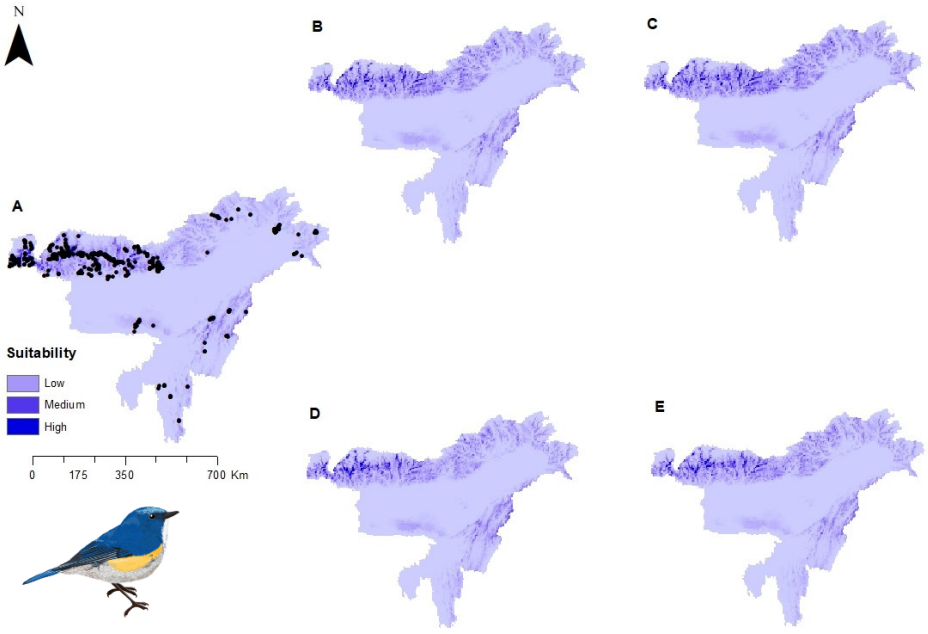

Figure S58: Potential distributions of *Tarsiger rufilatus* (Himalayan Bluetail) under present climate with presence points (A) and under four future climatic scenarios- (B) SSP1-2.6 (low), (C) SSP2-4.5 (intermediate), (D) SSP 4-6.0 (medium) and (E) SSP5-8.5 (high)

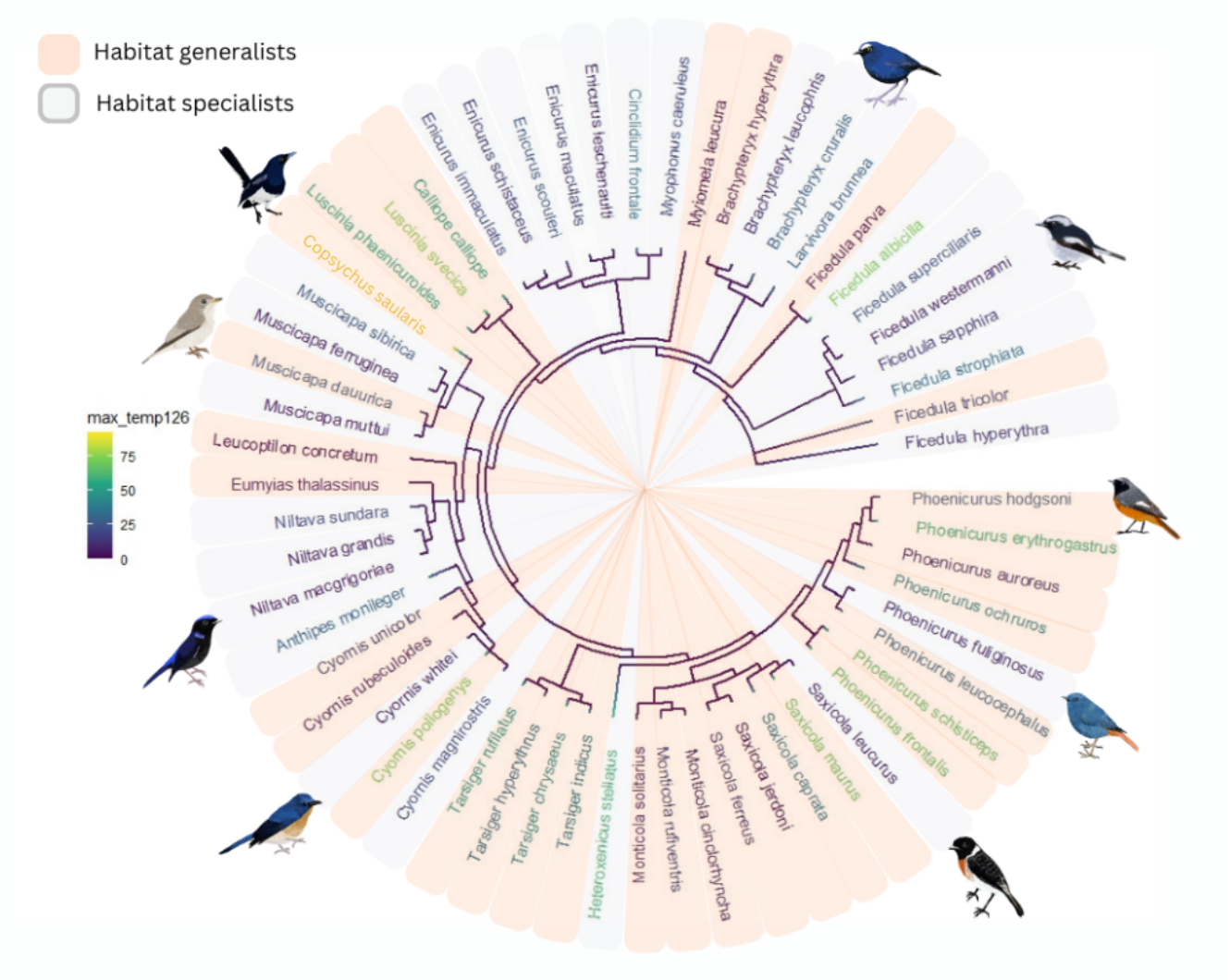

Figure S59: Percentage contribution of tmax (maximum temperature) under future climate scenario-SSP1-2.6 (low) to Ecological Niche Models of Muscicapidae (Flycatchers) species categorised as habitat generalists ($S' < 0.5$) or habitat specialists ($S' > 0.5$) using Species Specialisation Index (SSI)

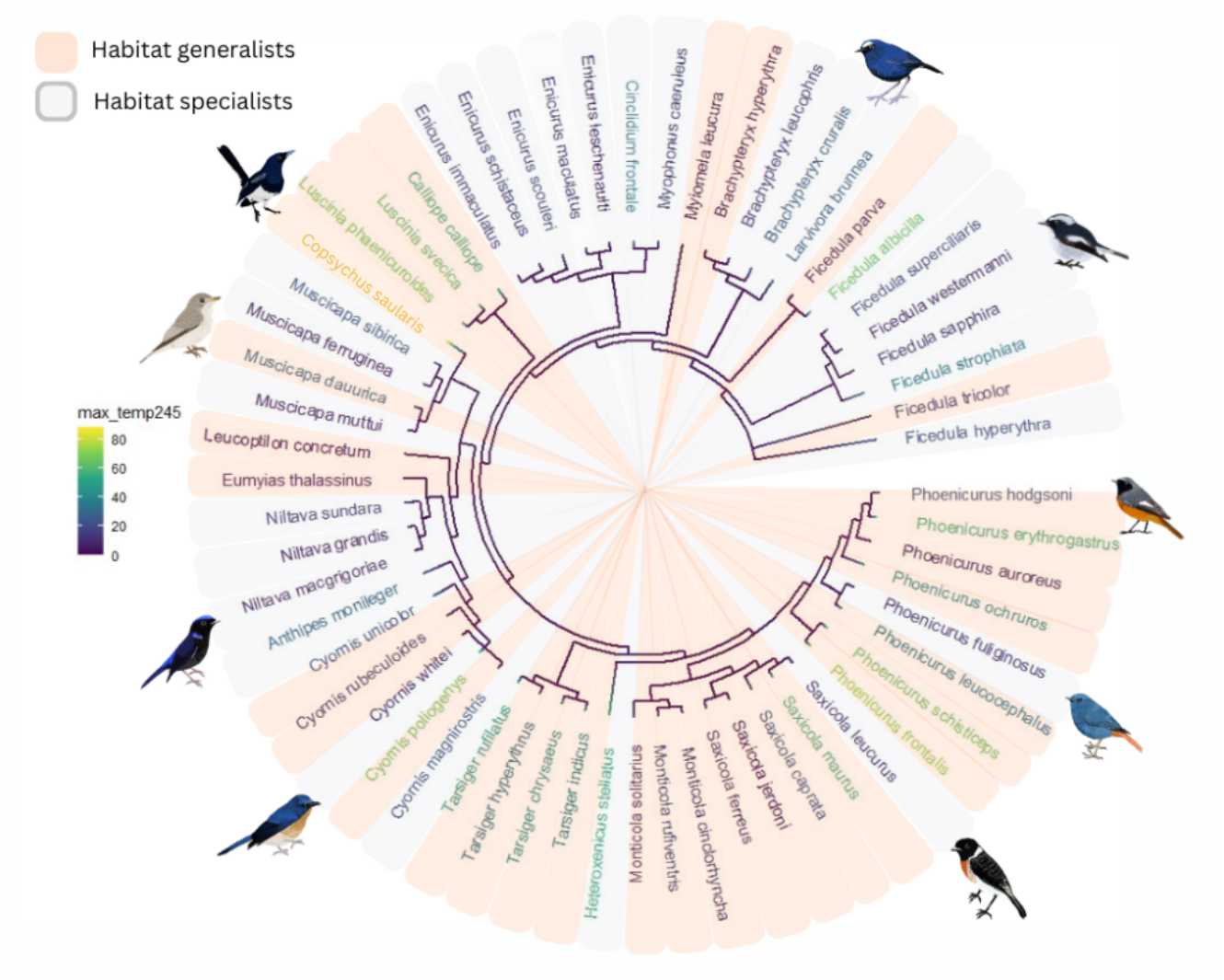

Figure S60: Percentage contribution of tmax (maximum temperature) under future climate scenario-SSP2-4.5 (intermediate) in Ecological Niche Models of Muscicapidae (Flycatchers) species categorised as habitat generalists ($S' < 0.5$) or habitat specialists ($S' > 0.5$) using Species Specialisation Index (SSI)

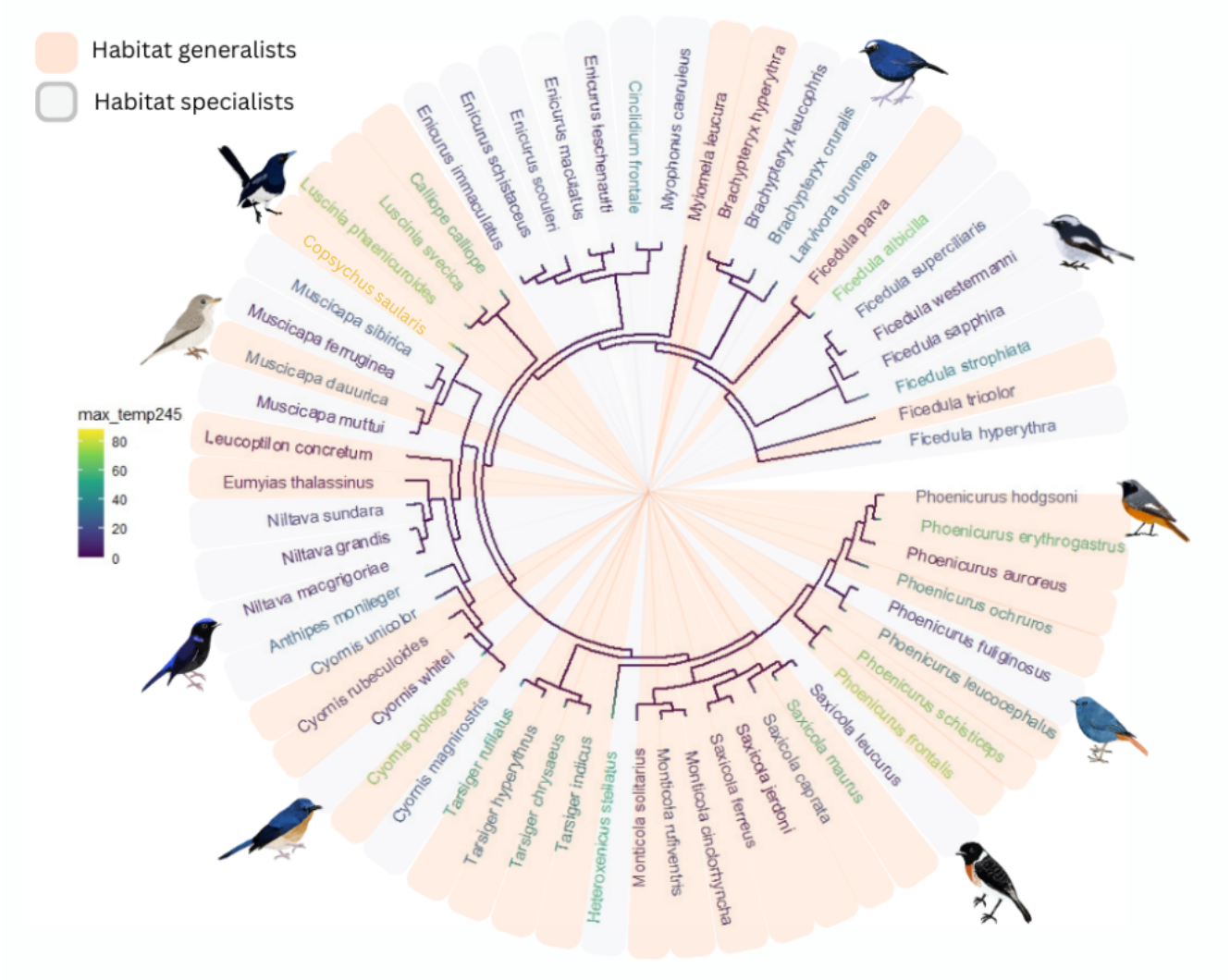

Figure S61: Percentage contribution of tmax (maximum temperature) under future climate scenario- SSP 4-6.0 (medium) in Ecological Niche Models of Muscicapidae (Flycatchers) species categorised as habitat generalists ($S' < 0.5$) or habitat specialists ($S' > 0.5$) using Species Specialisation Index (SSI)

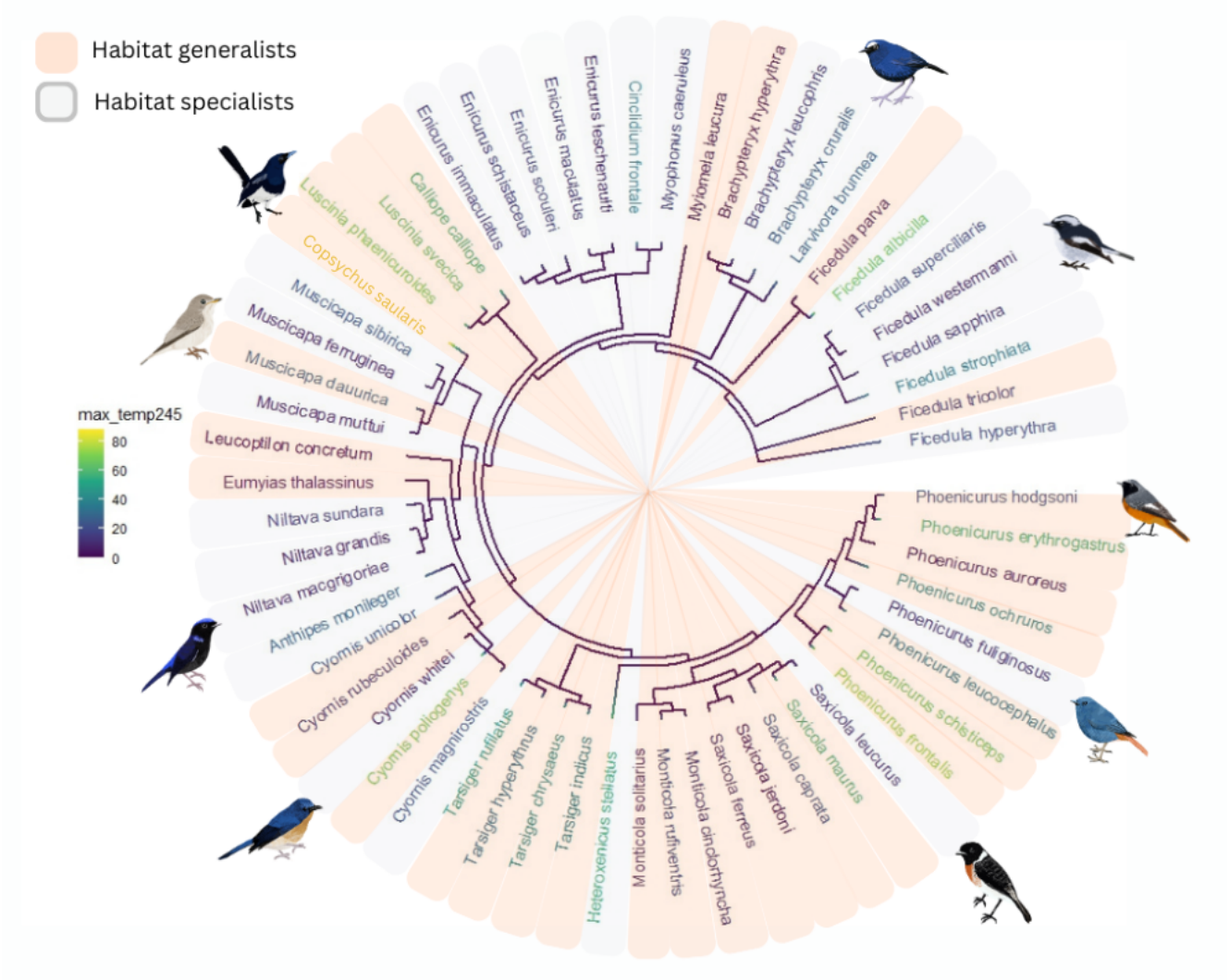

Figure S62: Percentage contribution of tmax (maximum temperature) under future climate scenario-SSP5-8.5 (high) in Ecological Niche Models of Muscicapidae (Flycatchers) species categorised as habitat generalists ($S' < 0.5$) or habitat specialists ($S' > 0.5$) using Species Specialisation Index (SSI)

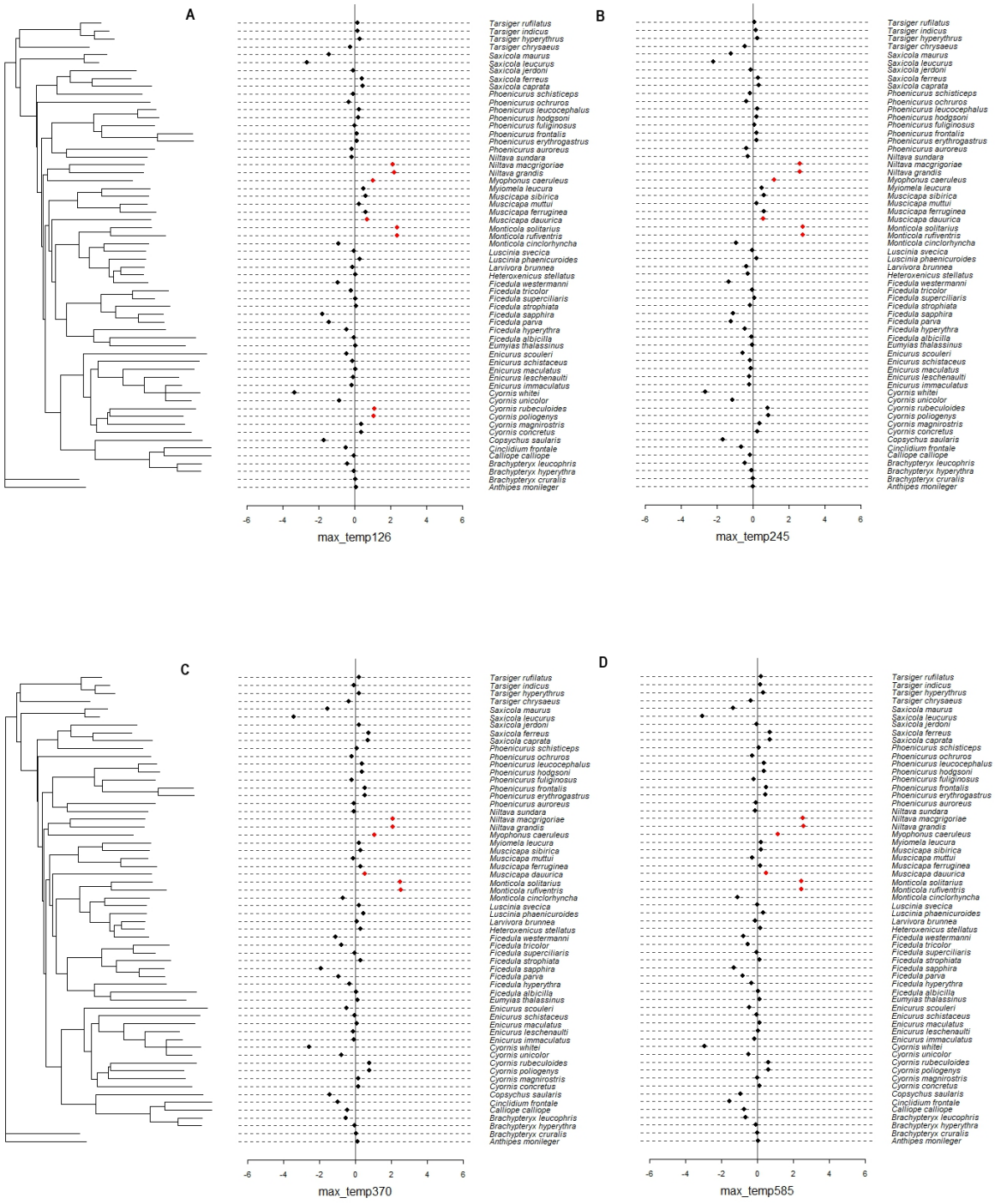

Figure S63: Local Moran's I plot of phylogenetic signal in percentage contribution of maximum temperature (tmax) under different emission scenarios- (A) SSP1-2.6 (low), (B) SSP2-4.5 (intermediate), (C) SSP 4-6.0 (medium) and (D) SSP5-8.5 (high). The red dots falling on and side of zero line correspond to significant relationships indicating positive correlation

Chapter 3

Linking patterns of alpha, functional, and phylogenetic diversity to microclimatic variation in a mosaic landscape of eastern Indian Himalaya

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ABSTRACT

Tropical mountains offer complex environmental conditions that shape patterns of regional biodiversity. However, tropical mountains also face myriad alterations due to human-mediated activities, resulting in non-contiguous and isolated habitat patches with varying microclimatic conditions. Using seasonal field data across two years, we investigate how temperature and relative humidity explain diversity patterns of bird communities in four habitat types in indigenous lands of Dibang Valley, eastern Indian Himalaya. We found that varying microclimatic conditions in heterogeneous patches of indigenous landscape maintain diversity and shape niches of birds in the eastern Indian Himalaya. We demonstrated that α-, and phylogenetic diversity were higher in primary forest, followed by bamboo thickets, and were lower in both active and abandoned slash-and-burnt agricultural lands. Generalised linear models explained that the bird communities of the forest were found to have affinities for cool and wet conditions, whereas that of bamboo exists in warm and wet conditions. In the active and abandoned slash-and-burnt agricultural lands, bird communities existed in cool and dry or warm and dry conditions. We detected uniform patterns of functional hotspots across the four habitats, although functional richness was greater in agricultural lands and abandoned agricultural lands, these patterns were not explained by site-specific microclimatic conditions. Generally, the bird communities were detected to be tracking their thermal as well as hygric niches.

1. INTRODUCTION

Local land-use changes in rural areas of tropical mountains are dynamic in nature and arise from ancient traditional management systems. These multifunctional landscapes are integral to the survival of rural communities and their management is underpinned by socioeconomic, cultural, and political factors and are centuries old, for example, in Mexico (Ribeiro Palacios et al., 2013), Ethiopia (Simane et al., 2013), and Andes (Kintz

et al., 2006). The result is a complex "mosaic" of habitats that may comprise patches of agricultural fields, forests, grazing lands, degraded areas, fragmented habitats, and settlements within the same landscape, as seen in Mt Kilimanjaro, Tanzania (Soini, 2005). Roughly 10% of the natural habitats and primary forests across the tropics are fragmented and patchy (Taubert et al., 2018), and are assumed to have little ecological value in the global context (Wintle et al., 2019). However, these mosaic landscapes in rural areas of tropical mountains can support biodiverse environments with high provisions for the ecosystem (Atangana et al., 2014).

Patches of forests, edge habitats, and open areas in a mosaic landscape have complex microclimatic configurations. Once a forest is fragmented, the resultant isolated patches experience altered microclimatic conditions (Ewers and Banks-Leite, 2013). Fire-induced open edge areas have increased air temperatures and high evaporative drying rates compared to closed edges that are dominated by regenerating vegetation (Didham and Lawton, 1999). Additionally, larger forest areas ensure microclimatic buffering to surrounding open areas by constantly providing heat and moisture exchanges (Pinto et al., 2010), which may not be efficiently maintained by smaller forest remnants (Moreno et al., 2014). These varying microclimatic conditions are likely to affect species' behaviour, and physiology, (Jucker et al., 2020) with severe implications for the relative abundance, richness, functional diversity, and phylogenetic diversity of the communities (Rajpar and Zakaria, 2015; Díaz-García et al., 2017a; Shen et al., 2022, respectively). Community patterns can be highly disparate owing to locally-specific conditions. For instance, in Southern Ethiopia, forest patches neighboured by agricultural lands can harbour a high diversity of species (Baudron et al., 2019). In the cloud forests of Kenya, fragment size does not explain functional diversity (Ulrich et al., 2016), while in Brazil, phylogenetic richness in forest-dependent species is positively related to forest cover (Morante-Filho et al., 2018). Species of the same community can thus respond differently depending on their relative sensitivity to patch sizes and inter-patch distances (Garmendia et al., 2013), habitat type (Gray et al., 2007), as well as to altering microenvironments in the interior versus at the edge (Carvajal-Cogollo and Urbina-Cardona, 2015).

Microclimate plays a crucial role in determining sensitivity to habitat changes in tropical montane birds. Tropical forest birds are physiologically sensitive to changes following forest fragmentation (Sekercioglu et al., 2002), particularly, the understory insectivores accustomed to low light exposure and relatively stable microclimates (Stratford and Robinson, 2005). Moreover, the heterogeneous environments of tropical mountains can affect the seasonal selection of sites in birds (Frey et al., 2016). While it is widely presumed that tropical birds generally have narrow thermal tolerances which affect their habitat selection (Polato et al., 2018; Pollock et al., 2021), they could be limited by precipitation and humidity regimes, thus shaping their hygric niches (Boyle et al., 2020). Given that tropical mountain birds often have restricted ranges, low dispersal abilities, and high site fidelity (Janzen, 1967; Freeman et al., 2022; Habel et al., 2016, respectively), likely, the temperature and humidity changes in patches following local land-use land-cover (henceforth LULC) changes will also affect their community assemblages and diversity patterns.

The tropical mountain forests of the eastern Indian Himalaya, a global biodiversity hotspot, provide a suite of ecosystem services, and harbour highly diverse and distinctive biodiversity, but are a highly threatened landscape (Mittermeier et al., 2011). The eastern Indian Himalayan forests are subjected to various natural and human-induced disturbances operating at large and small spatial scales. Climate change, massive deforestation due to hydropower developmental projects, and land degradation due to landslides have exceptionally severe effects on regional biodiversity across large spatial scales (Banerjee et al., 2022; Pandit et al., 2007; Mishra et al., 2022, respectively). At smaller spatial scales, LULC changes due to cash-cropping, monoculture plantations, and slash-and-burn agriculture have substantial impacts on the local biodiversity (Kurmi et al., 2024; Raman, 2001).

Dibang Valley, situated in the eastern Indian Himalayan State of Arunachal Pradesh, has diverse habitat types across varying elevation ranges and is also part of the Dihang-Dibang Biosphere Reserve. Dibang Valley is inhabited mainly by the indigenous Idu-Mishmi

community who are the stewards of a majority of "community lands" that they manage through local and ancient traditional practices. Idu-Mishmi people depend on these lands for subsistence farming, consumption of natural resources, livestock grazing, and many important cultural activities. The traditional land-use and management system in Dibang Valley results in a mosaic landscape comprises of multiple habitat types in both contiguous and non-contiguous spatial arrangements, thereby providing opportunities to explore the relationships between microclimate and avian community assemblages. Using field data collected over two seasons in two years, we compare different diversity measures across four dominant LULC types in the region to ask: 1) how do α- and β-diversity vary; 2) how do functional trait space and functional diversity differ; 3) how does phylogenetic diversity vary; and 4) how are the variations in α- , functional, and phylogenetic diversity related to microclimatic conditions?

2. METHODS

2.1. Study area and land-use land-cover (LULC) types

Dri Valley situated in the Basin of Dri River, a glacial-fed river in Dibang Valley, comprises sub-tropical, temperate, and coniferous forests, bamboo thickets, alpine meadows, agricultural, and fallow lands. However, four of the most pronounced land-use/ land-cover (henceforth LULC) types in a mid-elevation range of roughly 1220 to 1620 meters above sea level in Dri Valley are both the natural types- temperate broadleaved forests, and bamboo thickets, and the modified types- slash-and-burnt agricultural lands (locally called jhum or *paku*), and abandoned jhum lands.

Temperate broadleaved forests are used and managed for several purposes such as foraging for food resources, timber harvesting, taboo-based hunting of wild meat (Nijhawan and Mihu, 2020), and burial purposes (Chaudhari, 2008), hence making them crucial for the existence of the Idu-Mishmi community. The second LULC type, bamboo thickets (individual stands of clumps), often naturally interspersed with the temperate broadleaved

forests, are a highly utilized natural resource for making houses, and in day-to-day activities (Ray, 2020). The third type, traditional jhum, involves selecting a patch of bamboo thickets and clearing and burning it after the winter season for subsistence farming. These jhums, distantly or closely neighboured by bamboo patches, are utilised for growing seasonal vegetables and grains and are abandoned after two to three years. The fourth type, four to eight-year-old abandoned jhums, are fallow jhums and are first naturally succeeded by wild grass, which is grazed upon by Mithun or gayal *(Bos frontalis)*- a free-ranging, semi-domesticated cattle, followed by succession of bamboo. The complete process of natural succession of bamboo in abandoned jhum may take anywhere between five to twelve years.

2.2 Sampling design and bird surveys

We studied bird communities in the four dominant LULC types (forest, bamboo, jhum, abandoned) of Dri Valley intermittently from October 2021 to March 2023. We selected 8 sites for each LULC type based on local community knowledge, accessibility, and a minimum distance of 50-100 meters from roads and water bodies, resulting in a total of 32 sites (Figure 1). In terms of spatial arrangement, all the forest sites were homogenously surrounded by forested areas forming a contiguous habitat. Similarly, all bamboo sites exhibited a contiguous spatial arrangement. However, jhum and abandoned jhum sites were either distantly or closely by bamboo, forest, or burnt patches of habitats, resulting in non-contiguous arrangement.

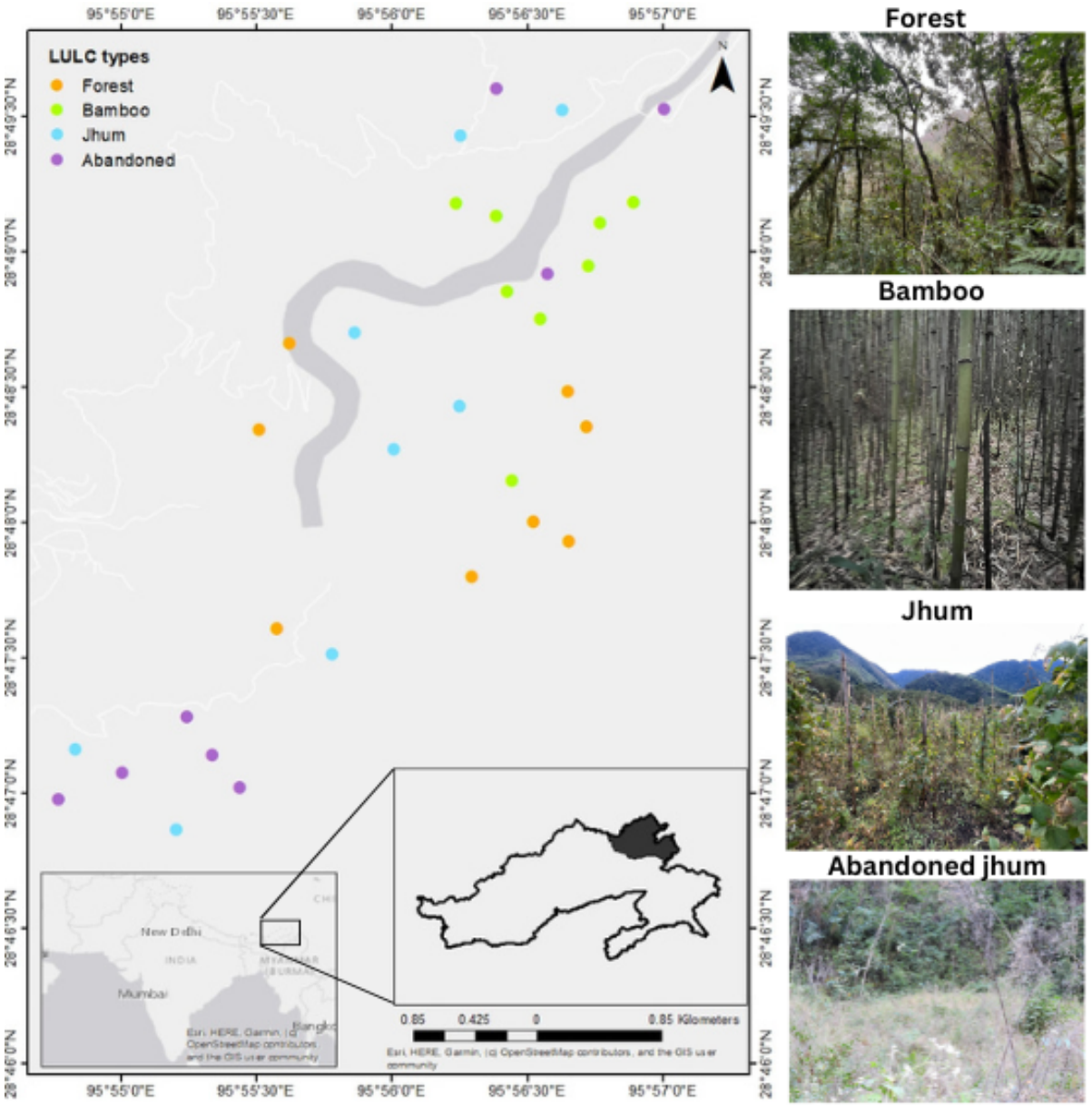

Figure 1: Sampled sites representing four dominant LULC types of Dri Valley

Avian surveys were performed in phases during two seasons across two years: 1st pre-winter from October to December 2021 (year 1), 1st post-winter from February to March 2022 (year 1), 2nd pre-winter from October to November 2022 (year 2), and 2nd post-winter from February to March 2023 (year 2). Pre-winter seasons in the region are generally cooler and drier, whereas post-winter season is warmer but also wetter owing to pre-monsoon showers in March.

Avian surveys consisted of standardised point counts which are preferred over line transects in a mosaic and patchy landscape (Buckland et al., 2005) and were logistically

more feasible in this region due to rugged terrain and the absence of trails in many sites of forest and bamboo. We followed standard point count recommendations for tropical environments: surveying for the duration of 15 minutes (Robinson et al., 2018) within a 30-meter fixed radius (Hutto et al., 1986) and at a minimum distance of 250 meters from each other (Ralph et al., 1995). All point counts were conducted between 0600 to 0930 hours, and birds were detected both visually and aurally (Lee and Marsden, 2008). Birds seen flying overhead and those at the edges of the habitat were not included in point count surveys. All point count surveys were conducted only on clear weather days in the absence of mist or fog. Repeat visits to every site were temporally spaced by at least seven to 12 days as different-day repeat sampling has proven to be effective for estimating richness (Field et al., 2002). Each site was visited twice in each season over two years resulting in eight visits per site and thus 256 point counts amounting to an effort of 3,840 minutes in total.

Previous studies have highlighted the limitations of conventional timed point counts in estimating species richness in tropical forests due to identification issues and leaving rare species unnoticed (Karr, 1981; Mao and Colwell, 2005; Robinson et al., 2018). One way to fill this sampling gap is by employing acoustic recorders in conjunction with point counts to improve richness estimations and enhance the chances of species detection (Haselmayer and Quinn, 2000; Leach et al., 2016). An audioMoth recorder (Open Acoustic Devices, United Kingdom), a passive acoustic monitoring device, was installed in a waterproof case for one hour after each point count in forest and bamboo, where species detection is challenging owing to poorer visibility in dense vegetation compared to open areas of jhum and abandoned jhum sites. Recordings of 64 hours each were generated from forest and bamboo. All recordings were manually annotated in Raven Pro 1.6 software (Cornell Lab of Ornithology, NY, USA) based on a subsampling approach which involves extracting and identifying recordings in different periods and thereby reducing false detections (Metcalf et al., 2022). Hourly recordings were split into four equivalent quarters and annotations were performed for the first and third quarters, resulting in 32 hours of annotations for forest and bamboo each. All point counts and annotations were conducted by AD to

maintain consistency and avoid observer bias. AD identified calls and songs primarily based on field observations and later by comparing them with those available on xeno-canto (www.xeno-canto.org/) and Birds of the World (www.birdsoftheworld.org/). A few recordings were also identified with the help of villagers and ornithologists with experience in birds of Arunachal Pradesh.

An ibutton logger was installed securely in a case at each site at roughly 1.7 metres above the ground immediately after undertaking the first point count and re-collected after the repeat point count was completed. The loggers recorded temperature and relative humidity (quantity of water vapour held in the air) between the two point counts at a sampling rate of one reading per 60 minutes to achieve a comprehensive calibrated measure of the microclimatic conditions of each site. Data from ibutton loggers for each season and year were used to calculate annual and seasonal means of temperature and relative humidity.

2.3 Statistical analyses

All analyses were performed in R base software version 4.2.3 (R Core Team, 2020) using RStudio Desktop version 2023.03.0+386. Bird checklist and data files along with the R script are provided at https://github.com/aavikad/microclimate-dibang-v1.0. In total, there were 1,656 detections combined from point counts and subsampled audio recordings comprising 119 species. Across the four seasons of sampling, 86 species were recorded in primary forests, 51 species in bamboo, 40 species in jhum, and 36 species in abandoned jhum. We compared means of temperature and relative humidity amongst the four habitats using ANOVA followed by Tukey's post-hoc test.

2.3.1 Species richness (α- and β-diversity)

Forest bird species in the tropics are expected to have smaller population sizes, and are therefore not encountered in point counts (Gillespie, 2000), which may result in biased

species richness estimates (Lennon et al., 2004). To give equal consideration to rare and common species, we converted all records to presence-absence (detection- non-detection) for calculating two main components of diversity, alpha (α-) and beta (β-) diversity at both seasonal and overall scales.

We estimated α-diversity at the site-specific level by performing coverage-based rarefaction/ -extrapolation (R/E) analysis using iNEXT package with 'incidence_raw' datatype for Hill numbers order q=0 (species richness) (Hsieh et al., 2016). Coverage-based R/E measures species richness based on equal completeness and not by the traditional method of equal sample size, allowing relevant comparisons across different communities while accounting for varying accuracies in detection for each habitat (Chao and Jost, 2012). We extracted α-diversity for each site (n=32) in each season (n=4) resulting in 128 estimates which were later used as response variables in generalised linear mixed effects models (Methods section 2.3.4).

We measured the extent of community dissimilarities among sites within each habitat, a component of β-diversity. We used the vegan package to create a Jaccard distance matrix among sites and then calculated mean dissimilarities within each habitat (Oksanen et al., 2009). The mean dissimilarities were scaled from 0 to 1 such that habitats with a score closer to 0 have lower variation in community composition, whereas those closer to 1 have higher variation. We visualised dissimilarities within the communities of each habitat using non-metric multidimensional scaling (NMDS).

2.3.2 Statistical analyses

Species' ecological traits mediate habitat selection and as a result response to LULC changes (Newbold et al., 2013). In particular, dietary and morphological traits can aid in predicting the sensitivity and persistence of species in a landscape matrix (Kennedy et al., 2010; Coetzee and Chown, 2016). We collated species' trait data from the AVONET database (Tobias et al., 2022). Traits were divided into three groups (modified from Chapman et al., 2018)- a) "foraging traits" that are directly associated with foraging

strategy (bill length, bill depth, and bill width); b) "locomotory traits" that are directly responsible for movement (wing length, Kipp's distance, tarsus length, and tail length); and c) "dietary traits" explaining primary diets comprising of the trophic niche (aquatic predator, frugivore, granivore, invertivore, nectarivore, omnivore, vertivore), and primary lifestyle (aerial, generalist, insessorial, terrestrial). Body mass was treated separately since it likely has an overlapping role in almost all ecological functions of foraging, locomotion, and diet. All continuous traits were log-transformed and sub-groups of dietary traits and primary lifestyle were converted to binary. We conducted a principal component analysis (PCA) using the princomp function for foraging and locomotory traits separately. For PCs of both foraging and locomotory traits, PC1 was interpreted as a size variable, having similar magnitude of loadings for each univariate trait, while PC2 was interpreted as a shape variable, with contrasting signs of loadings for univariate traits (PCA loadings in Supplementary, Table S1). PC1 explained over 80% of the variation in both cases. PC scores for each species describing bill shape and size, and body size and shape, were extracted and used along with body mass, trophic niche, and primary lifestyle for mapping functional trait space and analysing functional diversity (proportion of trophic niche in Figure S1, and proportion of primary lifestyle in Figure S2 in Supplementary).

We mapped functional trait space, a hypervolume niche space of multidimensional trait space, based on an ordination technique for all the data considered together, and for seasonal considered separately. We first created a dissimilarity matrix with function vegdist in the vegan package (Oksanen et al., 2009) using the Gower method which is suited for a combination of continuous and categorical data types (Gower, 1971). We then performed non-metric multidimensional scaling (NMDS) on the dissimilarity matrix. We used the funspace package to build and analyse functional space (Carmona et al., 2024a) on the dissimilarity matrix. The funspace package allows the efficient generation of functional spaces using a kernel density-based method wherein darker-coloured areas represent high probabilistic distribution of multi-dimensional traits while lighter-coloured areas represent low probabilistic distribution of traits in a community (Carmona et al., 2024b). The areas with darker colours or high concentrations of functional traits in spaces

are also denoted as functional hotspots (Cox et al., 2021).

We extracted functional richness (FRich) and functional divergence (FDiv) estimates for each season and each year for every LULC type using the funspace package. FRich and FDiv are two of the major components of functional diversity indicating niche differentiation. FRich is a measure of niche space occupied by species, and FDiv is a measure of the distribution of divergence in traits (Mason et al., 2005). In a multidimensional space, higher FRich signifies a wide range of traits within a community, whereas higher FDiv indicates the presence of varying functional traits amongst species that are the most abundant (Villéger et al., 2008). The FRich and FDiv estimates were later used as response variables in generalised linear mixed effects models (Methods section 2.3.4).

2.3.3 Phylogenetic diversity analysis

We downloaded a set of 1000 Hackett All Species phylogenetic trees with each 9993 OTUs from the Vertlife database (www.vertlife.org) (Jetz et al., 2012). Out of a total of 119 species, phylogenetic data was not available for 35 species that had recently undergone taxonomic revisions (some examples in Pittie et al., 2020). We thus proceeded with 84 species for phylogenetic diversity analysis (58 species in forest, 34 species in bamboo, 30 species in jhum, and 25 species in abandoned jhum).

We used the picante package for phylogenetic diversity analysis (Kembel et al., 2020). We estimated Faith's Phylogenetic Diversity (PD) and Phylogenetic Species Richness (PSR), the two of the most commonly used measures of phylogenetic α-diversity and evolutionary relatedness within an ecological community, for each season, each year, and for every LULC type. PD is calculated by the summation of lengths of all branches in a phylogenetic tree of a community (Faith, 1992), while PSR calculates the number of species with unique branches and compares phylogenetic diversity by standardizing sampling efforts across different habitats (Helmus et al., 2007; Gotelli and Colwell, 2001). Higher PD indicates higher phylogenetic niche differentiation (Srivastava et al., 2012), and higher PSR signifies the presence of phylogenetically distinct species within a community

(Helmus et al., 2007). PD and PSR were calculated and averaged across 1000 trees and were later used as response variables in generalised linear mixed effects models (Methods section 2.3.4). We used the ape package for reading and plotting an extracted ultrametric phylogenetic tree for each of the LULC types (Paradis et al., 2023).

2.3.4 Relationships between diversity and microclimatic variation

Previous studies have emphasised the direct role of temperature, but not of precipitation or humidity in explaining community composition and species richness patterns in eastern Indian Himalayan taxa (e.g., plants (Acharya et al., 2011a); reptiles (Chettri et al., 2010); ants (Marathe et al., 2020); birds (Schumm et al., 2020)). However, the majority of studies rely on satellite data which is coarser in resolution and likely to underestimate water-related trends in the region (Jain et al., 2022). Since we used point-sourced and well-calibrated microclimatic data recorded over multiple days at each site, we expect patterns in community diversity could be influenced by both temperature and humidity. We first investigated the correlation between mean temperature and mean relative humidity using a Pearson correlation test (Thompson et al., 2017) and then explored the relationship between α-diversity, FRich, FDiv, PD, and PSR with microclimatic conditions in individual GLMMs. We used pre-winter as a reference season and forest as a reference LULC type.

In the first set of GLMMs, we specified site-specific α-diversity as the response variable with mean temperature, season, and LULC type as predictor variables using the lmer function in the lmerTest package with Gaussian log link family (Kuznetsova et al., 2020). We used site as a random intercept since the sites for each type were visited repeatedly and hence were not independent. A second GLMM was substituted with relative humidity for mean temperature as both the variables were highly correlated and could not be included in the same model (refer to Results section 3.5).

In the next set of GLMMs, we used FRich, FDiv, PD, and PSR as response variables with mean temperature and mean relative humidity in turn, with predictor variables using

the glmmTMB package (Brooks et al., 2023) (PD and FDiv were log-transformed for an improved model fit). Functional and phylogenetic metrics were calculated for each season (n=4) and each habitat (n=4) resulting in 16 estimates each, thereby limiting the number of predictor variables that could be included to ensure model convergence, Hence, we included the main effect of microclimatic variable, LULC, and season, in separate models. Since these estimates were not site-specific, we used year as an intercept to account for non-independence at an annual level. We used the Gaussian log link family for FRich, FDiv, and PD, and the Poisson family for PSR.

We checked model performance for all GLMMs by fitting a null (intercept-only) model and compared the AIC of the null model to all GLMMs to select the best-performing model. Akaike Information Criteria (AIC) is a frequently employed criterion that assesses the goodness-of-fit such that the model with the lowest AIC score is reliable (McDonald, 1989). We then assessed the normality of residuals and examined the dispersion of fitted versus simulated residuals using the DHARMa package such that dispersion values closer to 1 and p-values greater than 0.05 indicate no significant overdispersion, and hence a good model fit (Hartig and Lohse, 2022).

3. RESULTS

3.1. Microclimatic profiles

Forest and bamboo had a lower mean temperature and higher mean relative humidity than jhum and abandoned jhums. Moreover, the variances in both temperature and relative humidity were higher in jhum and abandoned jhum than forest and bamboo. (Table 1, Figure 2 with differences and p-values using ANOVA followed by Tukey's post-hoc test).

Table 1: Mean temperature and relative humidity (± standard deviation) of four LULC types.

LULC types	Mean temperature (℃)	Mean relative humidity (%)
Forest	11.53 ± 3.86	85.13 ± 11.89
Bamboo	11.21 ± 4.58	82.33 ± 14.50
Jhum	15.64 ± 9.92	74.11 ± 27.20
Abandoned jhum	14.60 ± 10.62	75.62 ± 27.88

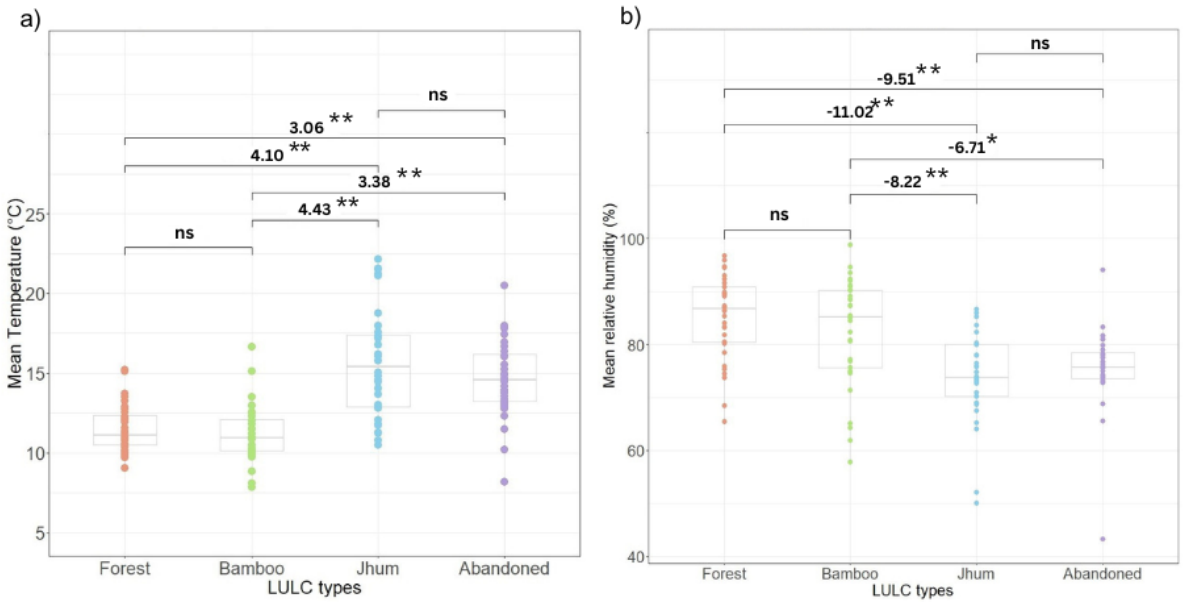

Figure 2: Box plots of four LULC types over the entire sampling time a) mean temperatures (℃) and b) mean relative humidity (%) showing significant differences with t-values (**P<0.001****, **P<0.05***, ns= non-significant). Each dot represents a sample site. Forests and bamboo were significantly cooler and wetter than jhum and abandoned jhum.

In the pre-winter, both forest and bamboo sites were cooler and wetter than jhum and abandoned jhum sites. However, in post-winter, forest and bamboo were cooler than jhum and abandoned jhum, but only forest was significantly wetter than jhum and abandoned jhum (refer to Supplementary for summary statistics, Table S2; seasonal comparisons of mean temperature and mean relative humidity using ANOVA followed by Tukey's post-hoc test, Figure S3, Figure S4).

3.2. Species richness

The α-diversity curve was the highest for forest, followed by bamboo, jhum and abandoned jhum across the entire sampling time (Figure 3a). The sample completeness plot representing the sampling effort approaches a near-plateau first for bamboo, then for

forest, followed by jhum and abandoned jhum (Figure 3b). The coverage-based R/E curve which plots richness estimates based on standardised sample coverage was the highest for forest, followed by bamboo, then with an overlap between jhum and abandoned jhum, generally indicating that more sampling will reveal additional species across these habitats (Figure 3c).

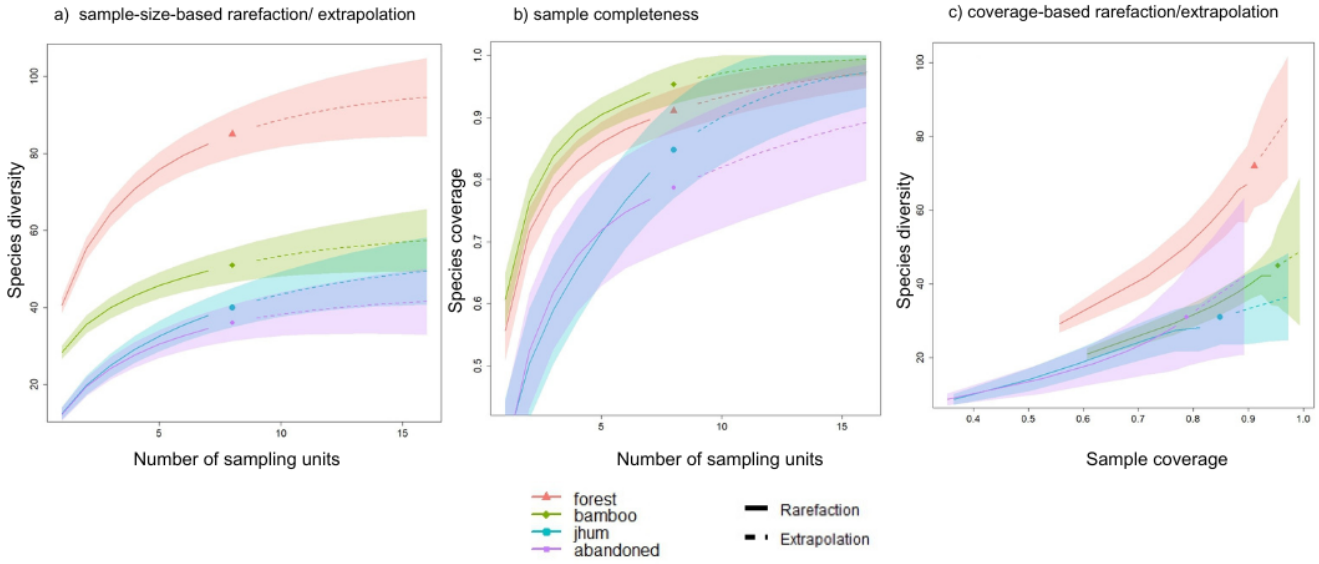

Figure 3: iNEXT plots with 95% confidence intervals for four habitats: a) sample-size based R/E showing richness was the highest for forest, second highest for bamboo, then jhum which was closely followed by abandoned jhum, b) sample completeness indicating bamboo, forest, and abandoned jhum approaches a near-plateau, and c) coverage-based R/E plot indicating generally all habitats will reveal more species with continued sampling.

When treating pre-winters and post-winters sampling times separately, the sample-size based R/E curves followed similar patterns as that across the entire sampling time. However, there was an overlap between jhum and abandoned jhum in the pre-winters (Supplementary, Figure S5a and Figure 6a). In the case of sample completeness, all habitats approached a near plateau (Supplementary file, Figure S5b, Figure S6b). The coverage-based curves of both pre-winters and post-winters also indicate that more sampling will reveal additional species in the habitats (Supplementary file, Figure S5c, Figure S6c).

In terms of the overall β-diversity, communities within jhum (β_{J}=0.85) and within abandoned jhum (β_{A}=0.83) varied more compared to those within the forest (β_{F} =0.80) and within bamboo sites (β_{B} =0.77). These patterns were also evident from the NMDS

plot which showed larger polygons of jhum and abandoned jhum signifying variation in community composition at each site (Figure 4). There was also an overlap between jhum and abandoned jhum bird communities.

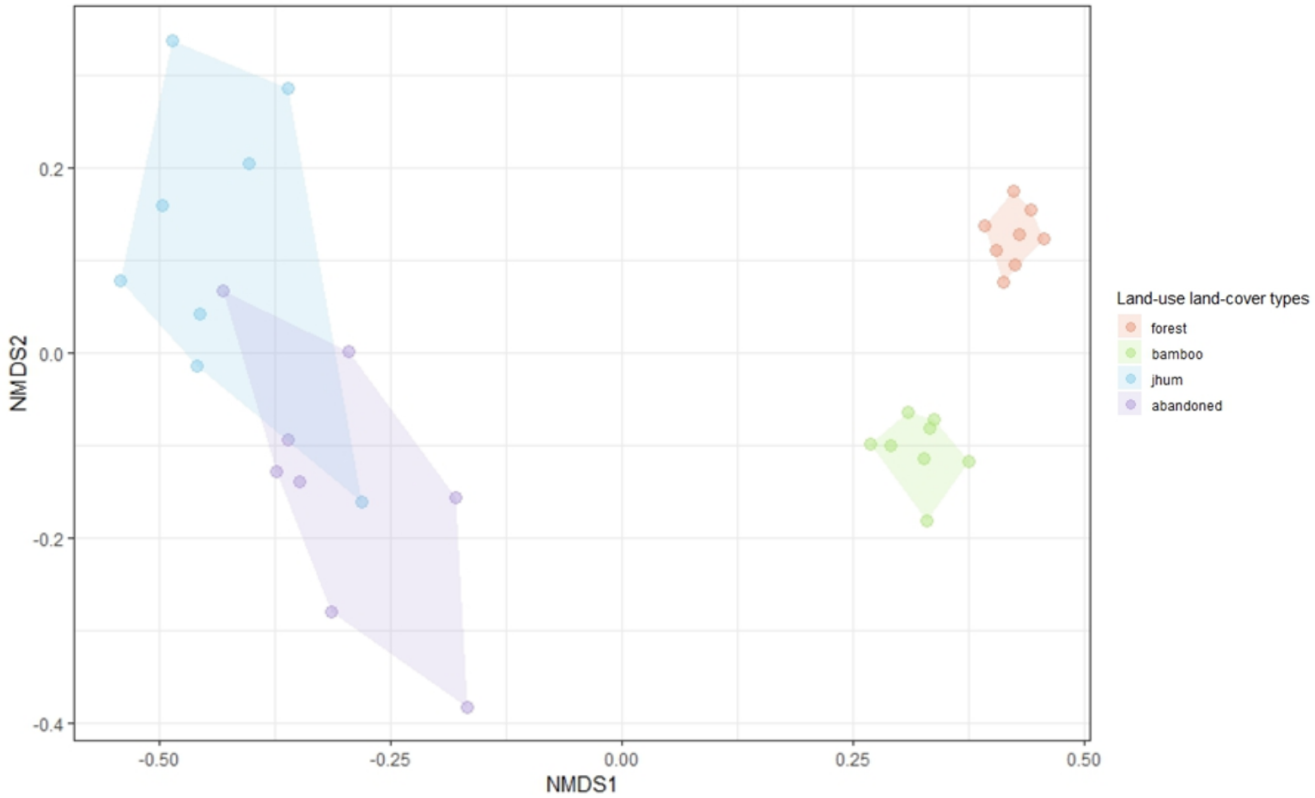

Figure 4: Non-metric dimensional scaling (NMDS) plot depicting overlap between the composition of jhum and abandoned jhum communities, and no overlap with or between those of forest and bamboo. Each dot represents a sample site and the size of each polygon signifies the proportion of within-habitat dissimilarities. The NMDS stress plot had a high linear fit ($R^2 = 0.96$) indicating a good fit.

Treating seasons separately, we find that the communities within jhum (pre-winter, β_J =0.89; post-winter, β_J =0.89) and abandoned (pre-winter, β_A =0.88; post-winter, β_A =0.88) were consistently variable compared to within forest (pre-winter, β_F =0.85; post-winter, β_F =0.85) and within bamboo (pre-winter, β_B =0.82; post-winter, β_B =0.82). There was also a clear overlap within pre-winter and post-winter community compositions of forest and bamboo sites, and a slight overlap within the seasonal compositions of abandoned jhum as seen in the NMDS plot (Supplementary file, Figure S7). However, the bird communities of jhum in pre-winter and post-winter were completely different, and there was an overlap between post-winter jhum and post-winter abandoned jhum.

3.3. Functional space and functional diversity

We observed that the patterns of distribution of functional traits in space in each of the four habitats had prominent areas of functional hotspots (in red colour) (Figure 5). In addition to darker-coloured areas of high concentration, there were also smaller clusters of lighter-coloured areas with low concentration of functional traits.

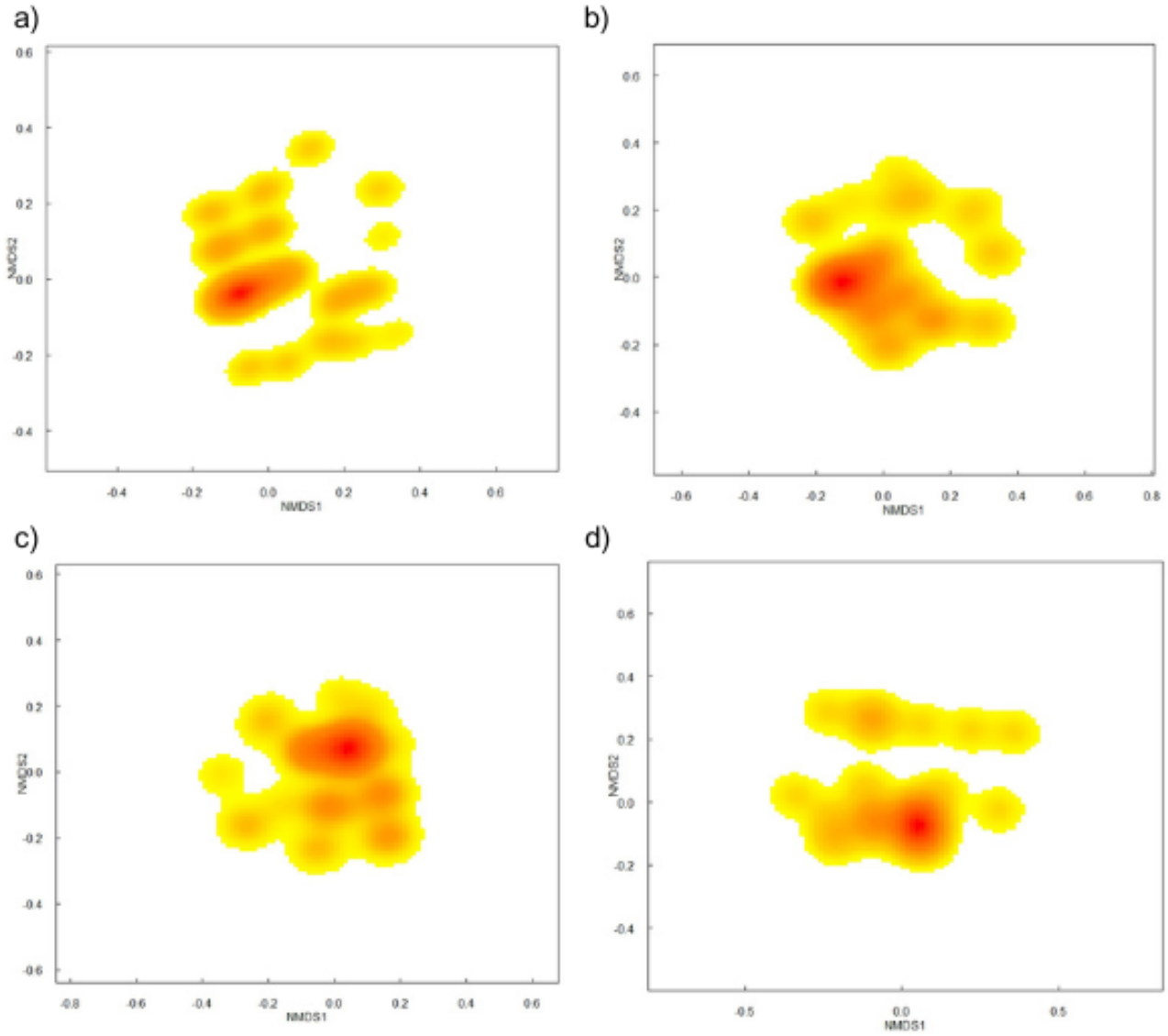

Figure 5: Functional trait space of four LULC types summarising first and second NMDS axes (NMDS1 and NMDS2) described by body mass, bill size, body size, primary diet, and primary lifestyle. Darker-coloured areas represent high probabilistic distribution of traits (in red) and lighter-coloured areas represent low probabilistic distribution of traits (in yellow) in a) forest, b) bamboo, c) jhum, and d) abandoned jhum.

When separating by seasons, we found that the functional trait space of the forest was similar to that of bamboo with a combination of high, moderate and low concentration areas (Supplementary, Figure S7). Jhum and abandoned jhum at times showed relatively smaller functional spaces but continued to have functional hotspots.

3.4. Phylogenetic diversity

Out of the 84 species used in phylogenetic diversity (PD) and phylogenetic species' richness (PSR) analysis, the highest number of genera were found in forests (37), followed by bamboo (25), jhum (23), and abandoned jhum (19). Graphically, average PD and PSR overall were the highest in forest, followed by bamboo, and jhum, and was the lowest in abandoned jhum (Figure 6a, b).

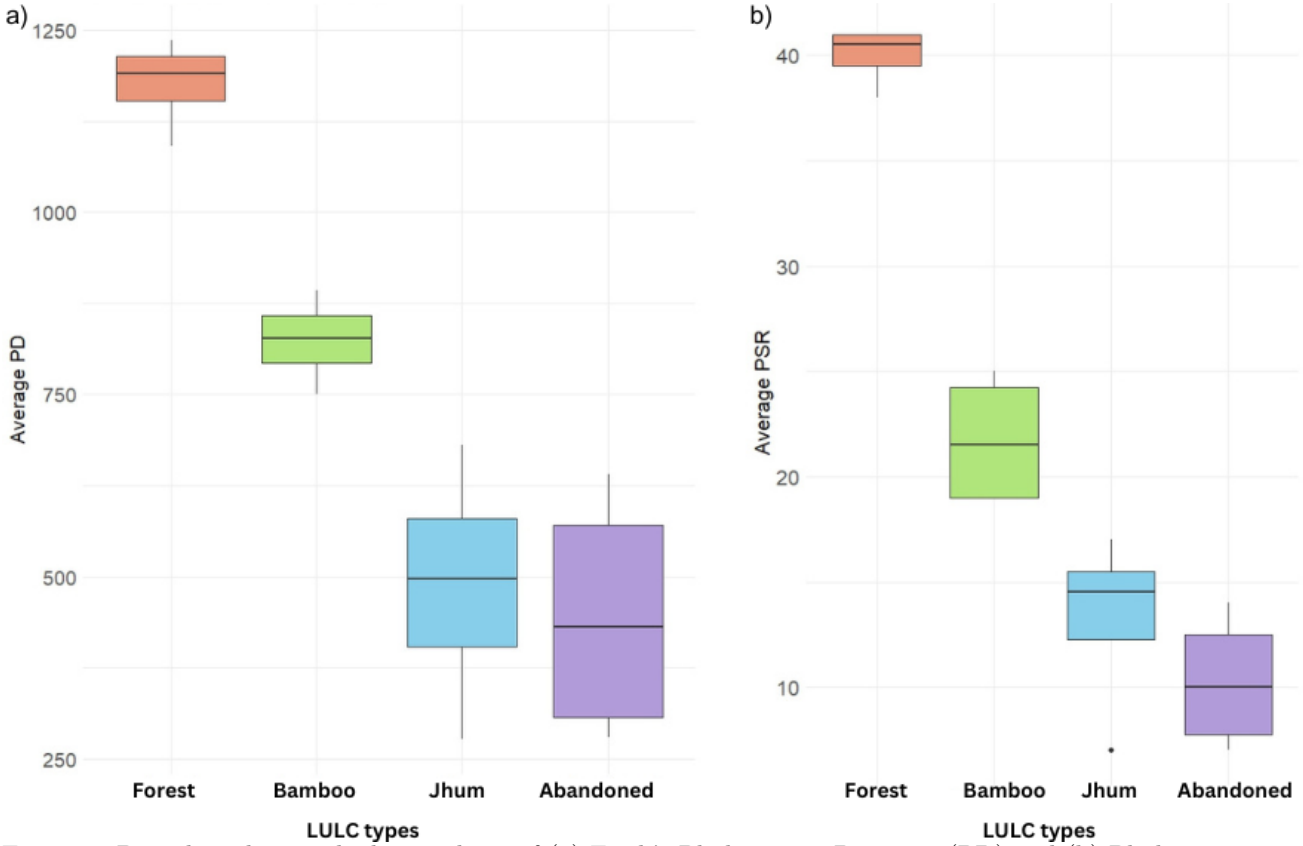

Figure 6: Box plots showing higher medians of (a) Faith's Phylogenetic Diversity (PD) and (b) Phylogenetic species' richness (PSR) for the forest, followed by bamboo, jhum, and abandoned. PD for jhum and abandoned were more varying than for forest and bamboo. PSR for all non-forest habitats were more varying than forest.

For the seasonal comparisons, forest and bamboo consistently had higher PD and PSR.

However, in pre-winters, PD was lower in jhum than abandoned (Supplementary file, Figure S9a) and was the opposite in post-winters (Supplementary file, Figure S10a). PSR was higher in jhum in post-winter than the pre-winters but remained roughly similar for abandoned (Supplementary file, Figure 9b, Figure 10b).

The communities in forest and bamboo comprised both closely related and distantly related species (Supplementary file, Figure S11, Figure 12, respectively), whereas the communities of jhum and bamboo were generally comprised of more closely related than distantly related species (Supplementary file, Figure S13 and S14, respectively).

3.5. Relationships between diversity and microclimatic variation

Mean temperature and mean relative humidity were found to be highly correlated according to Pearson's correlation test (overall, correlation= 72.97%, **P<0.05**, within seasons correlation= 64.79%, **P<0.001**). Hence, they were treated in separate GLMMs.

Species richness was higher in the post-winter season and had a significant negative relationship with bamboo, jhum, and abandoned jhum (Figure 7, 8). There was a trend of richness declining with increasing mean temperature, but the relationship was not significant (Table 2). Species richness had a significant positive relationship with mean relative humidity (Table 4). Model performance in Tables 3 and 5 shows that the candidate model performed better than other models.

Table 2: Summary statistics with standard error (S.E.), and degree of freedom (df) with pre-winter as a reference season and forest as a reference LULC type showing α-diversity was higher in post-winter season, and had a small but no significant relationship with mean temperature (model (i)). Significant results ($P < 0.05$) are highlighted in **bold***.

Models	**Estimate**	**S.E.**	**df**	**t-value**	***P***
(i) $\alpha \sim$ mean temp + season + LULC + (1|site)					
Intercept	39.44	3.17	53.74	12.40	**<0.001***
mean temp	-0.10	0.14	95.98	-0.75	> 0.05
post-winter	1.43	0.71	93.97	2.00	**<0.05***
abandoned	-27.50	3.78	28.69	-7.26	**<0.001***
bamboo	-12.11	3.76	27.96	-3.22	**<0.05***
jhum	-27.25	3.80	29.29	-7.15	**<0.001***
(ii) $\alpha \sim$ mean temp + LULC + (1|site)					
Intercept	40.62	3.13	51.34	12.95	**<0.001***
mean temp	-0.11	0.14	97.06	-0.80	> 0.05
abandoned	-27.47	3.78	28.71	-7.25	**<0.001***
bamboo	-12.11	3.76	27.96	-3.22	**<0.05***
jhum	-27.21	3.80	29.33	-7.14	**<0.001***
(iii) $\alpha \sim$ mean temp + season + (1|site)					
Intercept	23.83	3.10	74.03	7.67	**<0.001***
mean temp	-0.18	0.14	96.70	-1.33	>0.05
post-winter	1.42	0.71	93.67	1.98	>0.05

Table 3: Model performance of each GLMM using mean temperature. The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
(i) $\alpha \sim$ mean temp + season + LULC + (1—site)	774.89	0.00	0.81
(ii) $\alpha \sim$ mean temp + LULC + (1—site)	777.74	2.86	0.19
(iii) $\alpha \sim$ mean temp + season + (1—site)	820.72	45.84	0.00
$\alpha \sim 1 +$ (1—site)	821.36	46.48	0.00

Table 4: Summary statistics with standard error (S.E.), and degree of freedom (df) with pre-winter as a reference season and forest as a reference LULC type showing α-diversity was higher in post-winter season, with a positive relationship with mean relative humidity (RH). LULC types of abandoned jhum, bamboo, and jhum had a significant negative relationship. Significant results ($P < 0.05$) are highlighted in **bold***.

Models	**Estimate**	**S.E.**	**df**	**t-value**	***P***
(i) $\alpha \sim$ mean RH + season + LULC + (1|site)					
Intercept	23.18	4.89	117.40	4.73	**<0.001***
mean RH	0.16	0.04	99.13	3.68	**<0.001***
post-winter	2.59	0.74	94.95	3.50	**<0.001***
abandoned	-26.24	3.77	28.71	-6.95	**<0.001***
bamboo	-11.61	3.74	28.05	-3.09	**<0.05***
jhum	-25.85	3.78	28.29	-6.83	**<0.001***
(ii) $\alpha \sim$ mean RH + LULC + (1|site)					
Intercept	30.79	4.54	112.39	6.78	**<0.001***
mean RH	0.09	0.04	99.79	2.30	**<0.05***
abandoned	-26.88	3.78	28.66	-7.14	**<0.001***
bamboo	-11.80	3.74	28.05	-3.15	**<0.05***
jhum	-26.59	3.77	28.89	-7.04	**<0.001***
(iii) $\alpha \sim$ mean RH + season + (1|site)					
Intercept	5.53	4.51	124.45	1.22	>0.05
mean RH	0.18	0.04	96.95	4.10	**<0.001***
post-winter	2.73	0.74	94.30	3.68	**<0.001***

Table 5: Model performance of each α GLMM using mean RH (relative humidity). The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
(i) $\alpha \sim$ mean RH + season + LULC + (1—site)	764.97	0.00	1.00
(ii) $\alpha \sim$ mean RH + LULC + (1—site)	775.59	10.62	0.00
(iii) $\alpha \sim$ mean RH + season + (1—site)	808.84	43.87	0.00
$\alpha \sim 1 + (1$—site)	821.36	56.40	0.00

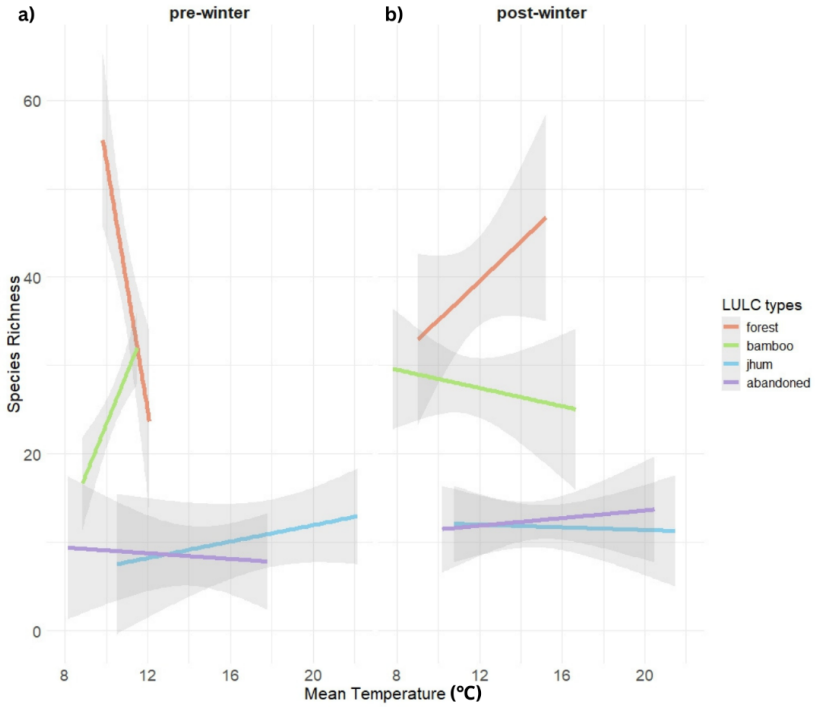

Figure 7: There was a trend of a negative relationship between species richness and mean temperature. In pre-winter (a), richness in the forest tended to decline with increasing mean temperature, but was the opposite for bamboo birds; (b) in post-winter, richness increased with increasing mean temperature in the forest, and decreased in bamboo. Species richness in jhum and abandoned jhum had an almost similar relationship with mean temperature.

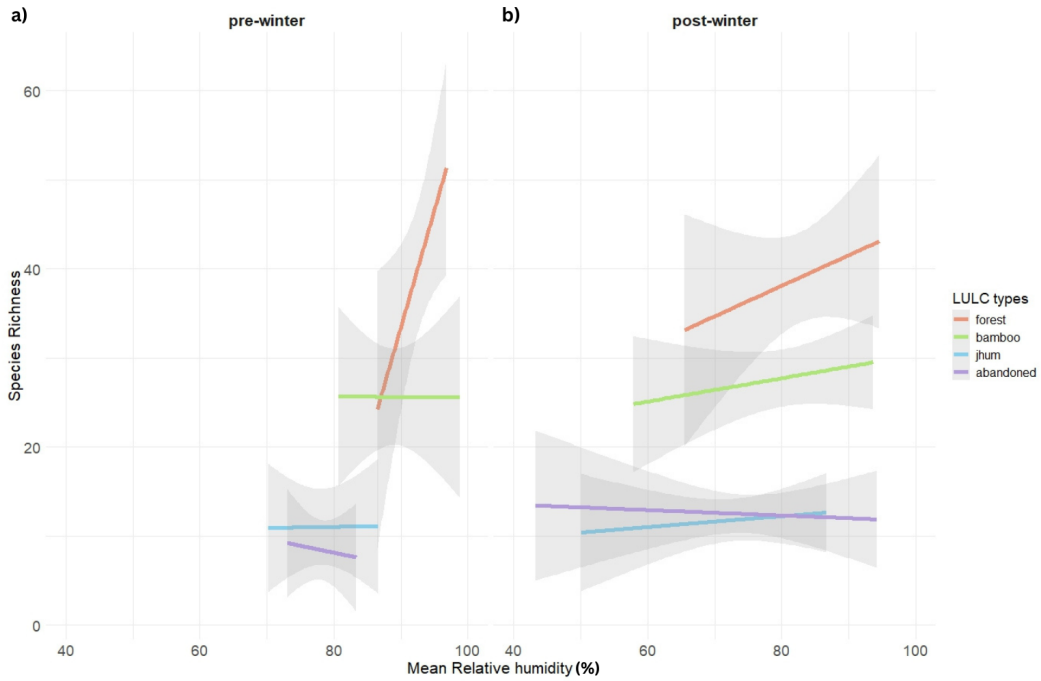

Figure 8: Species richness increased with mean relative humidity (RH). In the pre-winter (a), richness increased sharply with increasing mean RH in forest, and decreased in abandoned jhum while that of bamboo and jhum appeared stable; (b) in the post-winter, richness in forest and bamboo increased with increasing mean RH, but slightly decreased or remained roughly the same in jhum and abandoned jhum.

We found a significant negative relationship between FRich and mean relative humidity (Table 6). Model performance is shown in Table 7.

Table 6: Summary statistics with standard error (S.E.) with pre-winter as a reference season and forest as a reference LULC type showing FRich had a significant positive relationship with mean temperature, and a significant negative relationship with mean relative humidity (RH), and a positive relationship with jhum and abandoned jhum. Significant results ($P < 0.05$) are highlighted in **bold*.**

Fixed effects	**Estimate**	**S.E.**	**z-value**	**P**
(i) FRich ~ mean RH + (1—year)				
Intercept	1.86	0.41	4.51	**<0.001***
mean RH	-0.01	0.01	-3.50	**<0.001***
(ii) FRich ~ mean temp + (1—year)				
Intercept	-0.15	0.23	-0.66	>0.05
mean temp	0.04	0.01	2.50	**<0.05***
(iii) FRich ~ LULC + (1—year)				
Intercept	0.25	0.06	3.89	**<0.001***
abandoned	0.24	0.09	2.61	**<0.05***
bamboo	0.10	0.09	1.16	>0.05
jhum	0.31	0.09	3.34	**<0.001***
(iv) FRich ~ season + (1—year)				
Intercept	0.43	0.06	6.88	**<0.001***
post-winter	-0.02	0.08	-0.25	>0.05

Table 7: Model performance of each FRich GLMM. The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
(i) FRich ~ mean RH (1—year)	-7.37	0.00	0.81
(ii) FRich ~ mean temp + (1—year)	-3.53	3.84	0.12
FRich ~ 1 + (1—year)	-1.89	5.49	0.05
(iii) FRich ~ season + (1—year)	1.69	9.06	0.01
(iv) FRich ~ season + (1—year)	1.71	9.08	0.01

We found no significant relationships between FDiv and any of the variables (Table 8). Model performance is shown in Table 9.

Table 8: Summary statistics with standard error (S.E.) with pre-winter as a reference season and forest as a reference LULC type showing FDiv had no significant relationships with mean temperature, mean relative humidity (RH), season, and of the LULC types. Significant results ($P < 0.05$) are highlighted in **bold***.

Fixed effects	**Estimate**	**S.E.**	**z-value**	**P**
(i) log(FDiv) ∼ mean temp + (1—year)				
Intercept	-0.38	0.12	-3.15	**<0.001***
mean temp	-0.01	0.01	-0.13	>0.05
(ii) log(FDiv) ∼ mean RH + (1—year)				
Intercept	-0.66	0.23	-2.83	**<0.001***
mean RH	0.01	0.01	1.14	>0.05
(iii) log(FDiv) ∼ season + (1—year)				
Intercept	-0.36	0.025	-14.44	**<0.001***
post-winter	-0.06	0.03	-1.81	>0.05
(iv) log(FDiv) ∼ LULC + (1—year)				
Intercept	-0.34	0.03	-9.67	**<0.001***
abandoned	-0.05	0.05	-1.09	>0.05
bamboo	-0.04	0.05	-0.90	>0.05
jhum	-0.02	0.05	-0.52	>0.05

Table 9: Model performance of each FDiv GLMM. The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
FDiv ∼ 1 + (1—year)	-27.99	0.00	0.46
(iii)FDiv ∼ season (1—year)	-27.35	0.64	0.33
(ii) FDiv ∼ mean RH + (1—year)	-25.61	2.38	0.92
(i) FDiv ∼ mean temp + (1—year)	-24.37	3.62	0.07
(iv) FDiv ∼ lulc + (1—year)	-16.01	11.99	0.00

We found a significant negative relationship between PD and mean temperature (Table 10). Model performance is shown in Table 11.

Table 10: Summary statistics with standard error (S.E.) with pre-winter as a reference season and forest as a reference LULC type showing PD had a significant negative relationship with mean temperature. Significant results ($P < 0.05$) are highlighted in **bold***.

Fixed effects	**Estimate**	**S.E.**	**z-value**	**P**
(i) log(PD) ~ mean temp + (1—year)				
Intercept	8.78	0.48	18.26	**<0.001***
mean temp	-0.17	0.03	-4.83	**<0.001***
(ii) log(PD) ~ LULC + (1—year)				
Intercept	7.06	0.12	57.60	**<0.001***
abandoned	-1.03	0.17	-5.95	**<0.001***
bamboo	-0.35	0.17	-2.06	**<0.05***
jhum	-0.93	0.17	-5.37	**<0.001***
(iii) log(PD) ~ mean RH + (1—year)				
Intercept	2.42	1.11	2.16	**<0.05***
mean RH	0.05	0.01	3.64	**<0.001***
(iv) log(PD) ~ season + (1—year)				
Intercept	6.40	0.17	37.62	**<0.001***
post-winter	0.16	0.24	0.67	>0.05

Table 11: Model performance of each PD GLMM. The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
(i) PD ~ mean temp + (1—year)	19.73	0.00	0.69
(iv) PD ~ lulc + (1—year)	21.79	2.06	0.25
(ii) PD ~ mean RH + (1—year)	24.45 4.72	0.06	
PD ~ 1 + (1—year)	30.49	10.75	0.00
(iii)PD ~ season (1—year)	33.68	13.95	0.00

We found a significant negative relationship between PSR and LULC types of abandoned jhum, bamboo, and jhum (Table 12). Model performance is shown in Table 13.

Table 12: Summary statistics with standard error (S.E.) with pre-winter as a reference season and forest as a reference LULC types of abandoned jhum, bamboo, and jhum. Significant results ($P < 0.05$) are highlighted in **bold***

Fixed effects	**Estimate**	**S.E.**	**z-value**	**P**
(iv) PSR ~ LULC + (1—year)				
Intercept	3.68	0.07	46.66	**<0.001***
abandoned	-1.36	0.17	-7.78	**<0.001***
bamboo	-0.60	0.13	-4.57	**<0.001***
jhum	-1.10	0.15	-6.97	**<0.001***
(i) PSR ~ mean temp + (1—year)				
Intercept	5.60	0.36	15.32	**<0.001***
mean temp	-0.19	0.02	-6.82	**<0.001***
(ii) PSR ~ mean RH + (1—year)				
Intercept	-1.41	0.66	-2.13	**<0.05***
mean RH	0.05	0.01	6.87	**<0.001***
(iii) PSR ~ season + (1—year)				
Intercept	3.01	0.07	38.48	**<0.001***
post-winter	0.08	0.10	0.81	>0.05

Table 13: Model performance of each PSR GLMM. The best-performing model is highlighted in **bold.**

GLMMs	**AIC**	**ΔAIC**	**Weight**
(i) PSR ~ lulc + (1—year)	101.47	0.00	1.00
(ii) PSR ~ mean temp + (1—year)	135.60	34.12	0.00
(iii) PSR ~ mean RH + (1—year)	141.80	40.32	0.00
PSR ~ 1 + (1—year)	184.99	83.52	0.00
(iv)PSR ~ season (1—year)	187.41	85.94	0.00

The fitted versus simulated residuals of all models had dispersion values close to 1 and p-values less or slightly greater than 0.05 indicating no or little evidence of overdispersion and an overall good model fit. All models converged successfully.

4. DISCUSSION

We demonstrate that the bird communities of a mosaic landscape in the eastern Indian Himalaya depict complex responses to LULC changes as assessed using multiple metrics. We find that while species diversity and phylogenetic diversity were higher in forest and bamboo, the functional diversity was higher in jhum and abandoned jhum. We also found that the bird communities have a consistent relationship with temperature and humidity both overall and seasonally. Our results signify that the bird communities are not only tracking their thermal but also their hygric niches across the four habitats, albeit with varying intensities.

Species diversity

It is predicted that temperature and evapotranspiration rates drive high species richness patterns of tropical mountain birds (Ruggiero and Hawkins, 2008). Globally, bird species richness is predicted to increase linearly with temperature and precipitation until it hits a threshold (McCain, 2009). At regional scales, elevational-gradient studies on bird communities of wet tropical mountains have revealed similar patterns in association with temperature but anomalies with precipitation (e.g., in Ecuadorian Andes (Santillán et al., 2020); in Tanzania (Dulle et al., 2016)). In the eastern Indian Himalaya, bird assemblages are predicted to be limited by temperature (Srinivasan et al., 2018, 2019), although the role of water-related conditions such as humidity, rainfall, and precipitation in the region in directly shaping bird community patterns has generally been overlooked or not detected.

In our locally-focused study in the eastern Indian Himalaya, we found a trend of species richness declining with increasing temperature, although it was a non-significant relationship, and a significant positive relationship with mean relative humidity- deviating from the general global predictions. In the pre-winter season, forest birds exist in cool

and wet conditions and warm and wet conditions in the post-winter. Bamboo birds exist in warm and wet conditions throughout both seasons. Jhum birds exist in warmer and drier conditions. Abandoned jhum birds exist in cool and dry conditions in pre-winter, but warm and dry conditions in post-winter.

In the tropical mountains, forest-dependent birds with narrow physiological tolerances are likely to face high costs to adapt to alterations in temperature and humidity (Londoño et al., 2017), hence they tend to avoid drier and open agricultural areas, which are usually dominated by species with higher persistence and colonising traits (Frishkoff et al., 2016). However, some forest-dependent eastern Himalayan birds also forage in relatively warmer and less humid selectively logged forests, although the behaviour is peculiar to specific guilds (Aggarwal et al., 2023). On the other hand, species with wider physiological tolerances are expected to adapt faster to both habitat and climatic alterations (Barnagaud et al., 2012). Our findings show forest-dependent and bamboo-dependent birds had restricted tolerances to microclimatic variations as compared to jhum and abandoned jhum bird communities, which can also be extended to predicting vulnerabilities due to changing climate.

Functional diversity and space

We found congruent functional trait spaces across the four LULC types with slight seasonal variations, which may indicate the presence of functionally redundant species performing similar ecological functions (Rosenfeld, 2002). Functional redundancy contributes to an overall resilient ecosystem since the ecological functions performed by disappearing species can be substituted by new recruits, however the potential shifts in roles due to environmental changes in the future cannot be ignored (Fetzer et al., 2015). For example, in the Brazilian Atlantic forests, new colonizers did not directly compensate for the loss of the original forest-dependent species resulting in larger functional distances (Fuzessy et al., 2024). Additionally, we found higher functional richness in jhum and abandoned jhum. The closer spatial connectivity with natural habitats is likely responsible for maintaining

overall functional diversity in jhum and abandoned jhum.

Previously, temperature has been noted to have a negative effect on the functional diversity of birds of eastern Himalaya (Penjor et al., 2022). However, we report that functional richness increased with mean temperature and decreased with mean relative humidity since FRich was higher in drier and warmer habitats. Moreover, we found an overlap between bird assemblages of jhum and abandoned jhum, given the similarity of the habitat type, signifying overlaps in their functional trait spaces as well. Our results indicate that while species richness declines, functional richness is conserved in open habitats of a mosaic landscape.

Phylogenetic diversity

We found that forests harbour far greater phylogenetic diversity and phylogenetic species richness than any other habitat with both closely related and distantly related species. Higher phylogenetic diversity indicates minimum niche overlap and competition (Webb et al., 2002), equating to higher ecosystem functioning with the presence of much more complex multi-trophic interactions (Srivastava et al., 2012). Thus, forest bird communities play a larger role in maintaining overall ecosystem stability (Cadotte et al., 2012), a conclusion that can be extended to Dibang Valley. On the other hand, tropical agricultural systems lack phylogenetic diversity and are dominated by more closely related than distantly related species (Frishkoff et al., 2014), which is similar to our findings as jhum and abandoned jhum had a lack of unique community-level phylogenetic relationships. While functional diversity is retained with the presence of neighbouring natural habitats in our study area, we determine that phylogenetic diversity is more complicated to maintain.

At a global scale, phylogenetic diversity is expected to have a negative relationship with temperature (e.g., in terrestrial mammals (Barreto et al., 2019)). In the tropics, precipitation is attributed to be an important predictor of phylogenetic diversity in some families and clades (e.g., plants, birds (Paz et al., 2021)), and areas with higher precipitation have higher phylogenetic diversity (e.g., plants in South America (Neves

et al., 2020)). We found similar patterns in our study area since phylogenetic diversity and phylogenetic species richness were higher in cooler and wetter habitats, similar to patterns observed for α-diversity. Our findings highlight that the bird communities of forests, followed by bamboo, largely have cool- and wet-adapted clades, whereas that of jhum and abandoned jhum have clades adapted to dry and warm conditions.

Conservation implications

Indigenous people's lands across the tropics support high numbers of forest-dependent vertebrate species (Sze et al., 2024) and even have lower deforestation rates than the protected areas (Porter-Bolland et al., 2012). Moreover, indigenous communities protect forests based on taboos and cultural values, yet the significance of these practices in maintaining local biodiversity is often overlooked (Asante et al., 2017). During fieldwork, it was noted that the Idu-Mishmis preserve sacred forest sites, where many bird species were also sighted, further underscoring the significance of indigenous beliefs in the protection of biodiversity and their habitats. We found that jhum and abandoned jhum sites were overall "wildlife-friendly" and on a few occasions, there were fresh signs of the presence of Indian muntjac (Muntiacus muntjak) and Himalayan black bear (Ursus thibetanus). It is also possible to improve phylogenetic diversity in these sites to an extent with additional tree cover (Rurangwa et al., 2022). While, the natural habitats with little or no disturbance are prime centres of tropical biodiversity (Gibson et al., 2011), it is also worth noting that the heterogeneous habitats support unique species composition. The mosaic in community lands examined here provides varying microclimatic conditions that maintain diversity and niches of avian species in the eastern Indian Himalaya.

Author contributions

AD and SC formulated the idea and designed the study. AD acquired the field grants, secured the permits, liaised with the Idu-Mishmi community, conducted the fieldwork,

analysed the data, and wrote the original manuscript. SC provided feedback, edits on drafts.

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Supplementary

Table S1: Loading values of Principal Component Analysis (PCA) for ecological traits for species observed across all four LULC types with (a) "foraging" traits and (b) "locomotory" traits. The percentage variation explained by each PC is shown in parentheses.

Trait	**PC1 (89.6%)**	**PC2 (8.7%)**	**PC3 (1.7%)**
(a) "Foraging" traits			
Beak length	0.55	0.81	0.15
Beak width	0.58	-0.51	0.63
Beak depth	0.59	-0.26	-0.76
(b) "Locomotory" traits			
Tarsus length	0.55	0.79	0.25
Wing length	0.60	-0.16	-0.77
Tail length	0.57	-0.58	0.57

Table S2: Mean temperature and relative humidity (± standard deviation) of four LULC types for two pre- and post-winters.

LULC types	**Temperature (°C)**		**Relative humidity (%)**	
	Pre-winter	Post-winter	Pre-winter	Post-winter
Forest	11.21 ± 1.48	11.85 ± 1.52	87.56 ± 7.33	82.71 ± 7.94
Bamboo	11.03 ± 1.18	11.38 ± 2.35	83.11 ± 7.87	81.55 ± 12.43
Jhum	16.63 ± 3.63	14.65 ± 3.04	74.92 ± 6.34	73.30 ± 10.49
Abandoned jhum	13.92 ± 2.43	15.28 ± 2.26	77.19 ± 5.92	74.04 ± 9.05

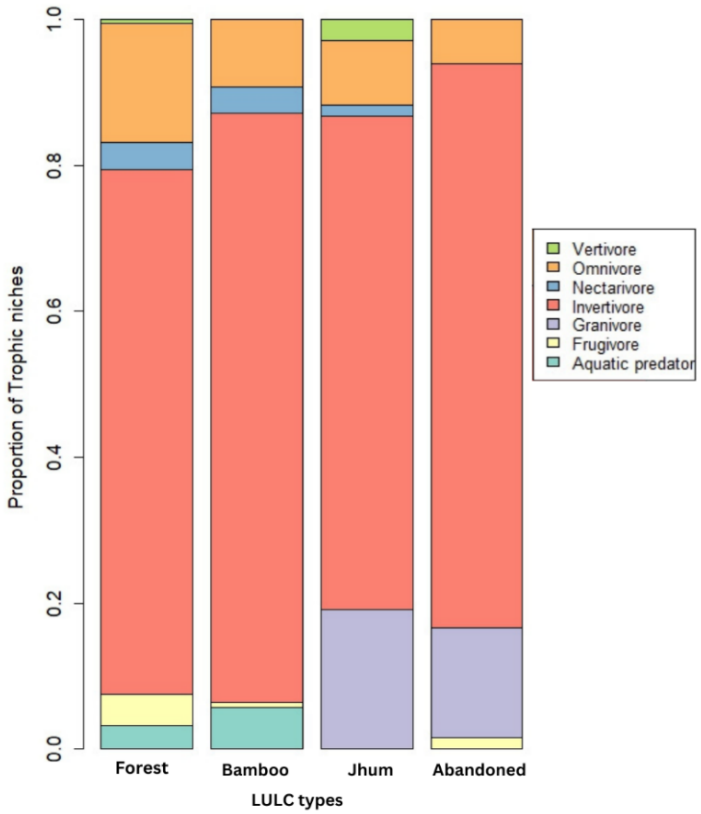

Figure S1: Proportion of trophic niche from group (c) on dietary traits for four LULC types

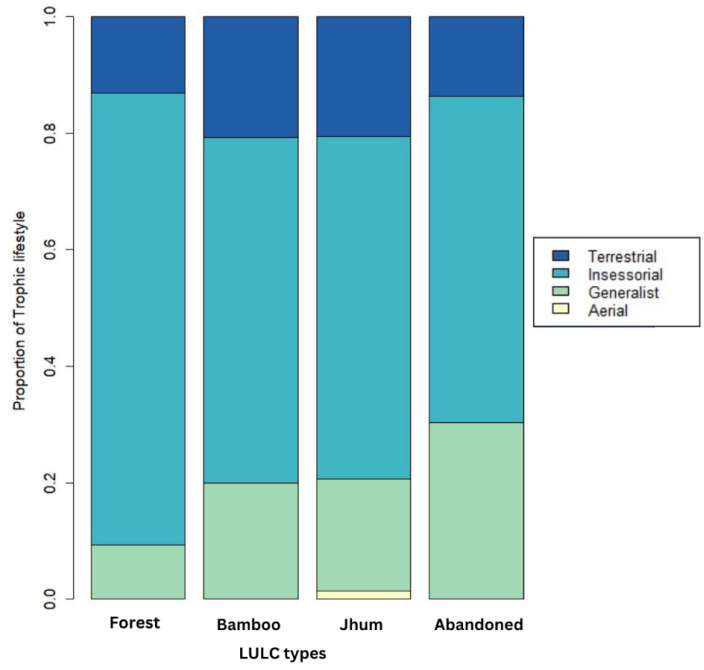

Figure S2: Proportion of primary lifestyle from group (c) on dietary traits for four LULC type

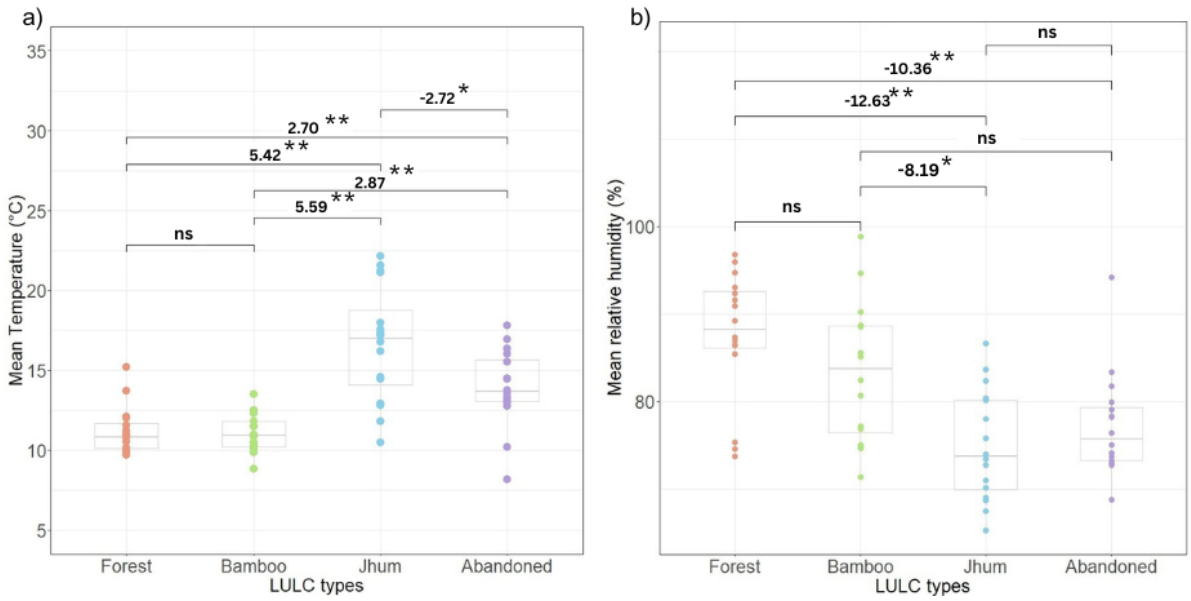

Figure S3: Box plots of four LULC types of pre-winter seasonal a) mean temperatures (℃) and b) mean relative humidity (%) showing significant differences with t-values (**P<0.001****, **P<0.05*** ns= non-significant). Each dot represents a sample site. Forests and bamboo were significantly cooler and wetter than jhum and abandoned jhum.

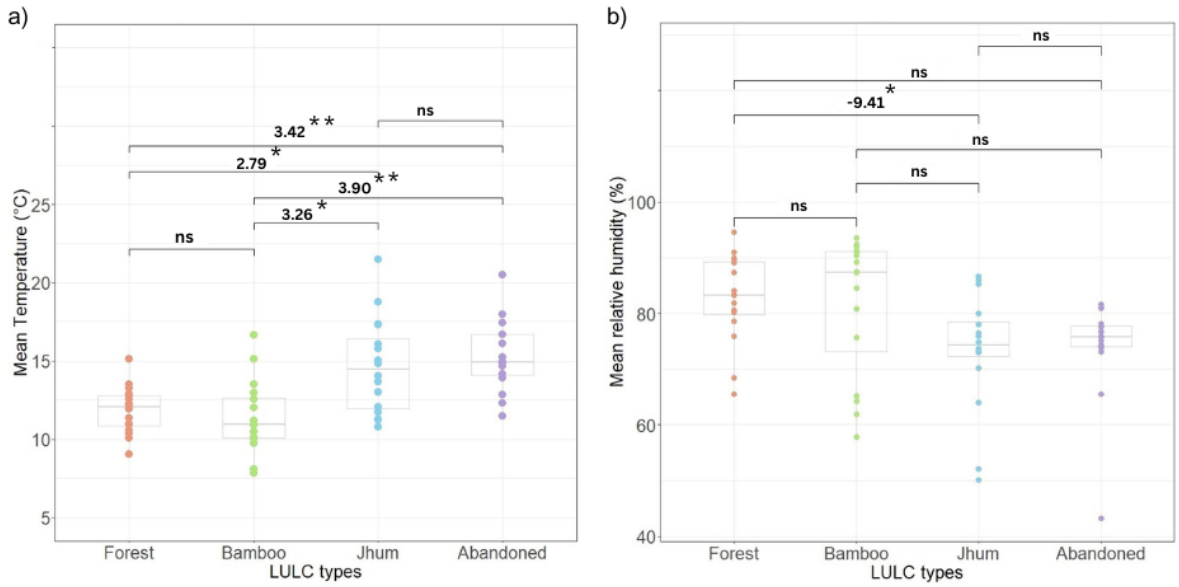

Figure S4: Box plots of four LULC types of post-winter seasonal a) mean temperatures (℃) and b) mean relative humidity (%) showing significant differences with t-values (**P<0.001****, **P<0.05***, ns= non-significant). Each dot represents a sample site. Forests and bamboo were significantly cooler than jhum and abandoned jhum, but only forests were wetter than jhum and abandoned jhum.

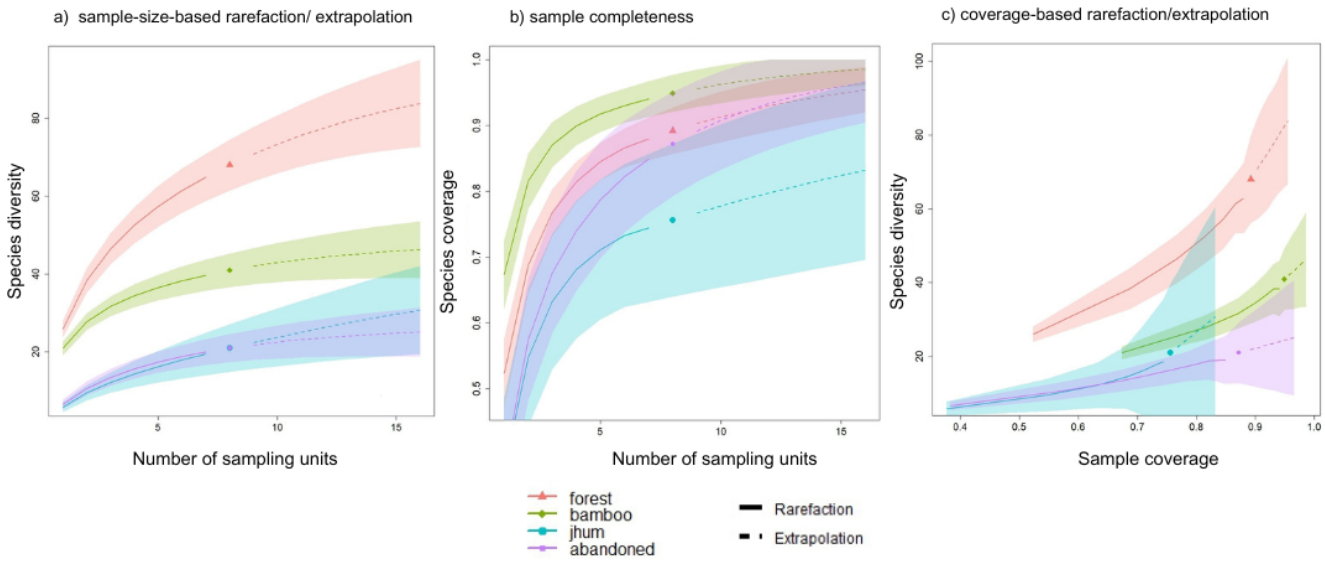

Figure S5: iNEXT plots with 95% confidence intervals for four habitats in two pre-winters combined: a) sample-size based R/E showing richness was the highest for forest, second highest for bamboo, then an overlap between jhum and abandoned jhum, b) sample completeness indicating bamboo, forest, and jhum reached a near plateau, and c) coverage-based R/E plot indicating generally all habitats will reveal more species with continued sampling.

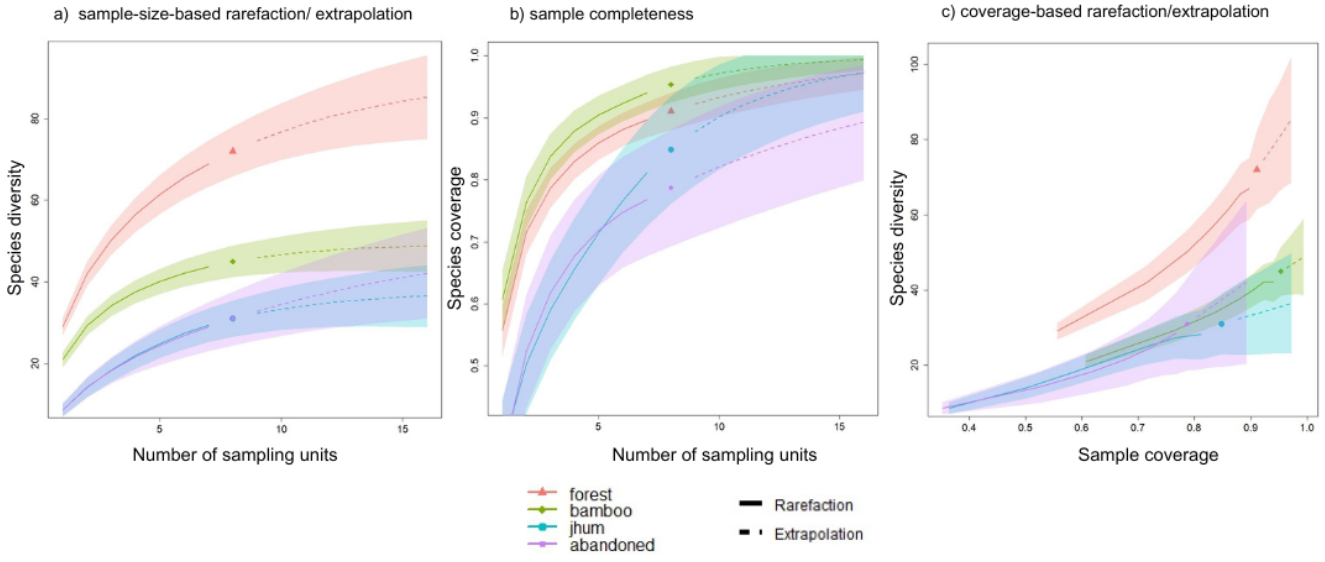

Figure S6: iNEXT plots with 95% confidence intervals for four habitats in two post-winters combined: a) sample-size based R/E showing richness was highest for forest, second highest for bamboo, then an overlap between jhum and abandoned jhum, b) sample completeness indicating bamboo, forest, and abandoned jhum reached a near plateau, and c) coverage-based R/E plot indicating generally all habitats will reveal more species with continued sampling.

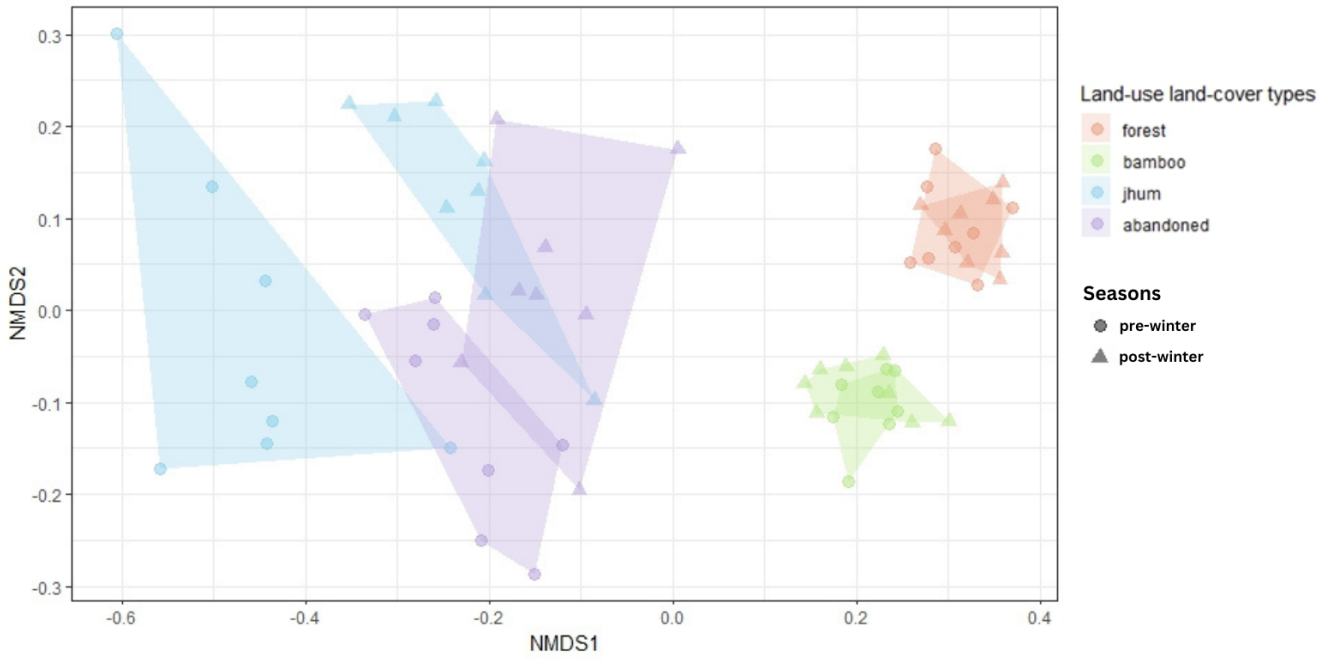

Figure S7: Non-metric dimensional scaling (NMDS) plot at a seasonal scale depicting overlap between compositions of pre- and post-winter forest, pre- and post-winter bamboo, and a slight overlap between pre- and post-winter abandoned jhum. There was no overlap between seasonal jhum bird communities indicating unique compositions in pre- and post-winter, however, post-winter of jhum and post-winter of abandoned jhum were similar. Each dot represents sample site and the size of each polygon signifies proportion of within-habitat dissimilarities. The NMDS had a good fit according to the stress plot ($R^2 = 0.94$).

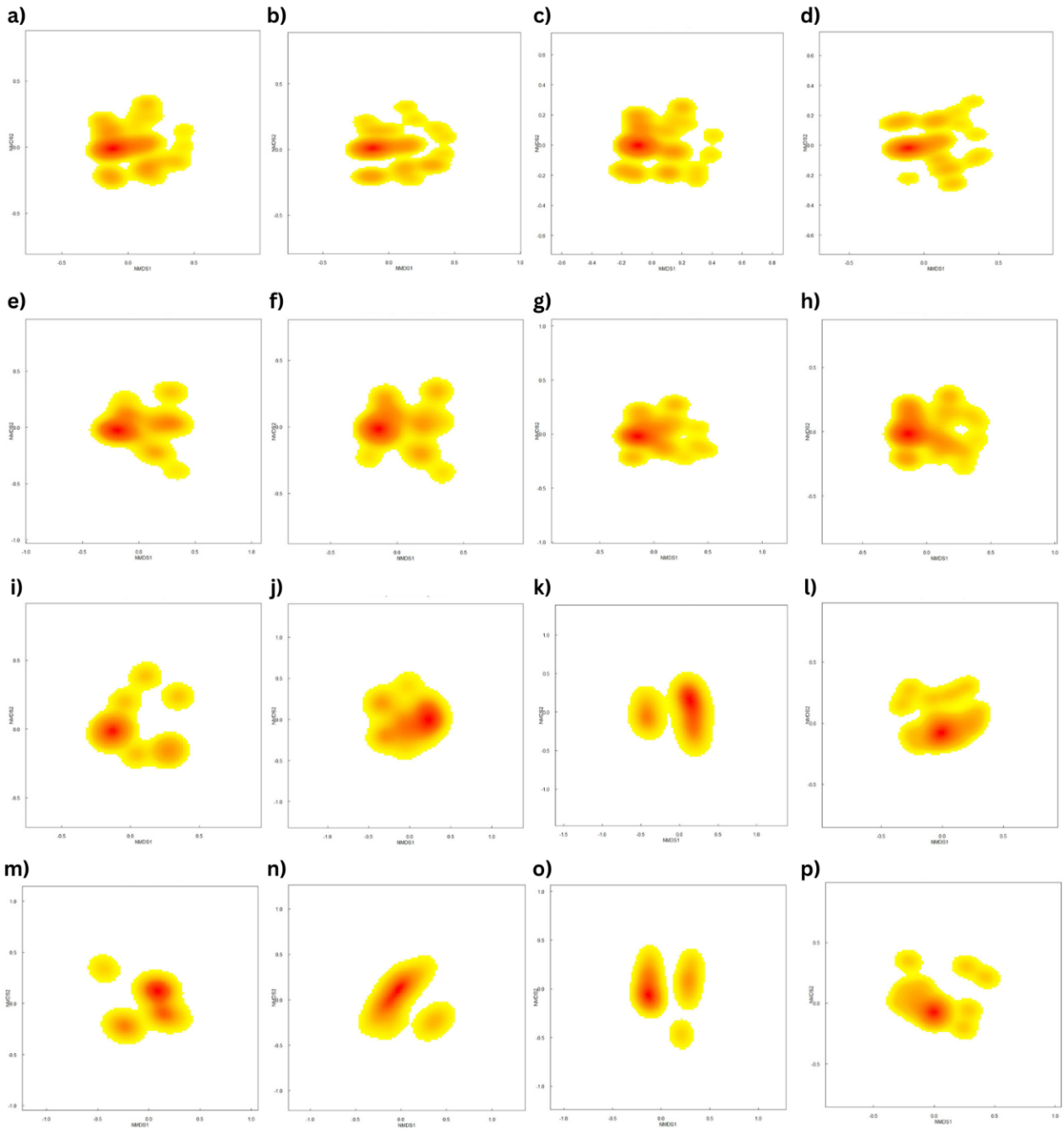

Figure S8: Functional trait space of four LULC types across each sampling season summarising first and second NMDS axes (NMDS1 and NMDS2) described by body mass, beak shape, body shape, primary diet, and primary lifestyle. Darker-coloured areas represent high probabilistic distribution of traits (in red) and lighter-coloured areas represent low probabilistic distribution of traits (in yellow). The plots are arranged in increasing order of sampling season for each season (pre-winter in year 1, post-winter in year 1, pre-winter in year 2, post-winter in year 2) from left to right for forest (first row- a to d), b) bamboo (second row- e to h) c) jhum (third row- i to l), and d) abandoned jhum (fourth row- m to p).

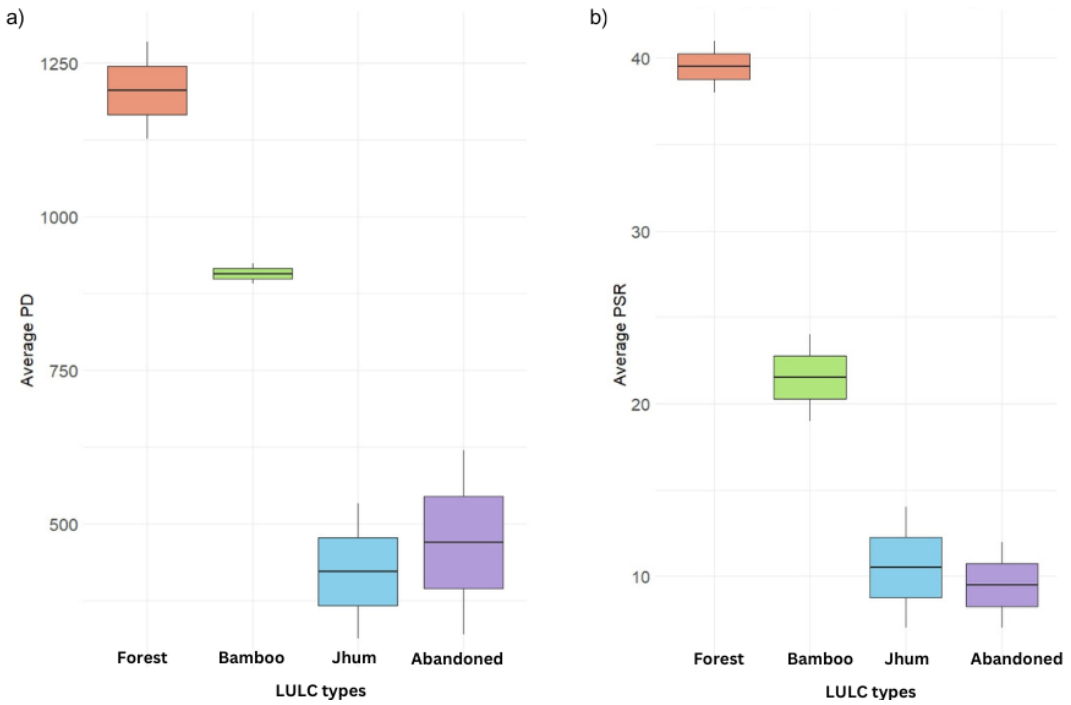

Figure S9: Box plots for pre-winter season showing higher medians of (a) Faith's Phylogenetic Diversity (PD) and (b) Phylogenetic species' richness (PSR) for forest, followed by bamboo. Abandoned jhum had higher PD than jhum, whereas jhum had higher PSR than abandoned. Both jhum and abandoned jhum had higher variations in PD and PSR.

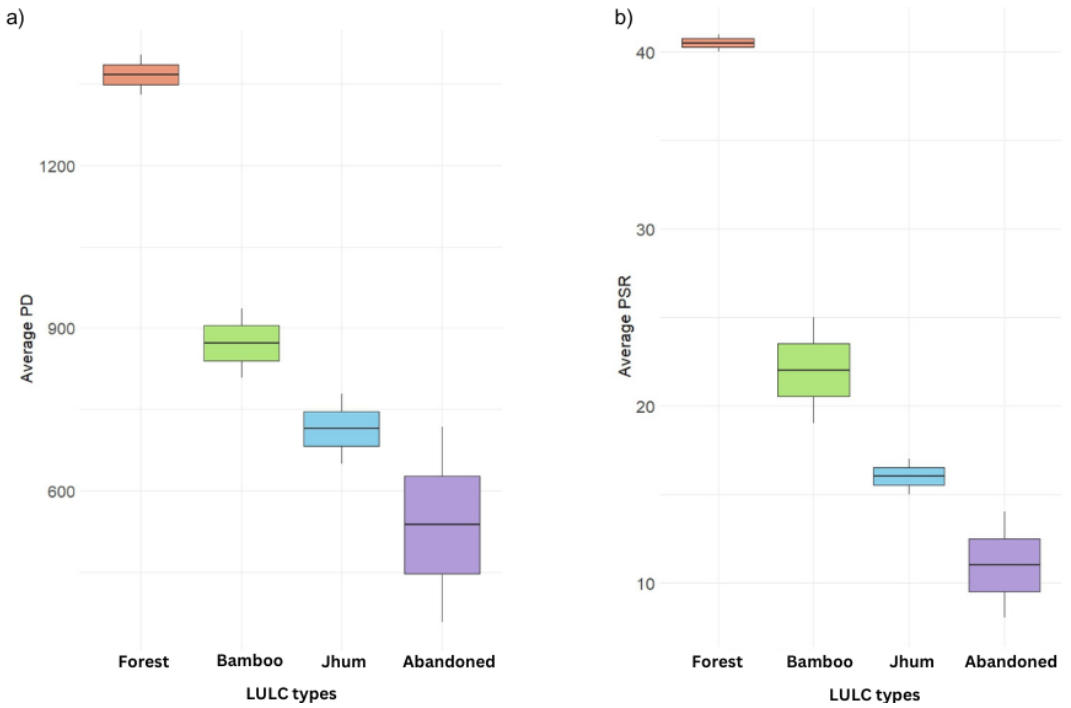

Figure S10: Box plots for post-winter season showing higher medians of (a) Faith's Phylogenetic Diversity (PD) and (b) Phylogenetic species' richness (PSR) for forest, followed by bamboo. Abandoned jhum showed the highest variation of PD. Both bamboo and abandoned jhum showed higher variations in PSR.

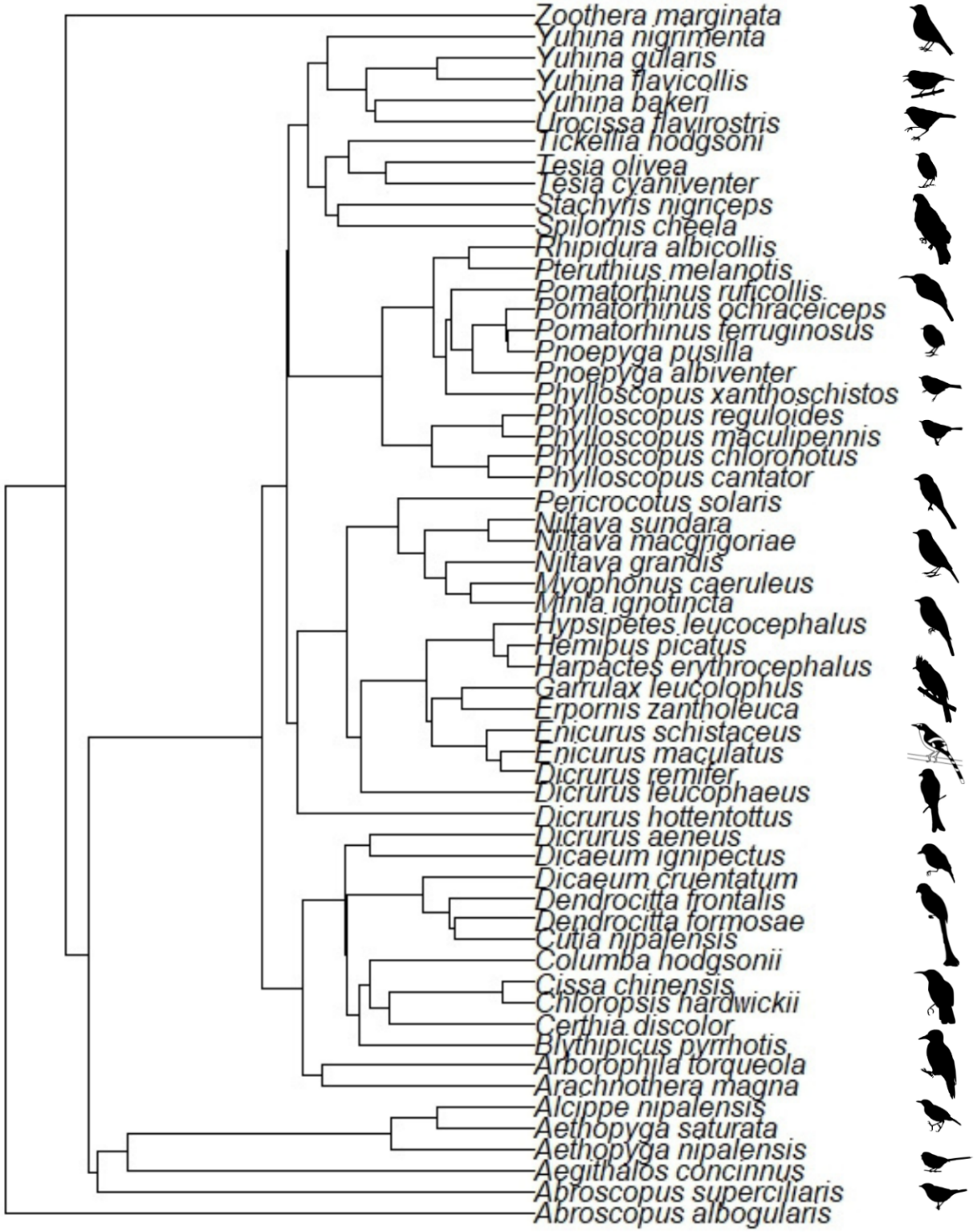

Figure S11: Phylogenetic tree of bird communities observed in forest indicating presence of both closely related and distantly related species.

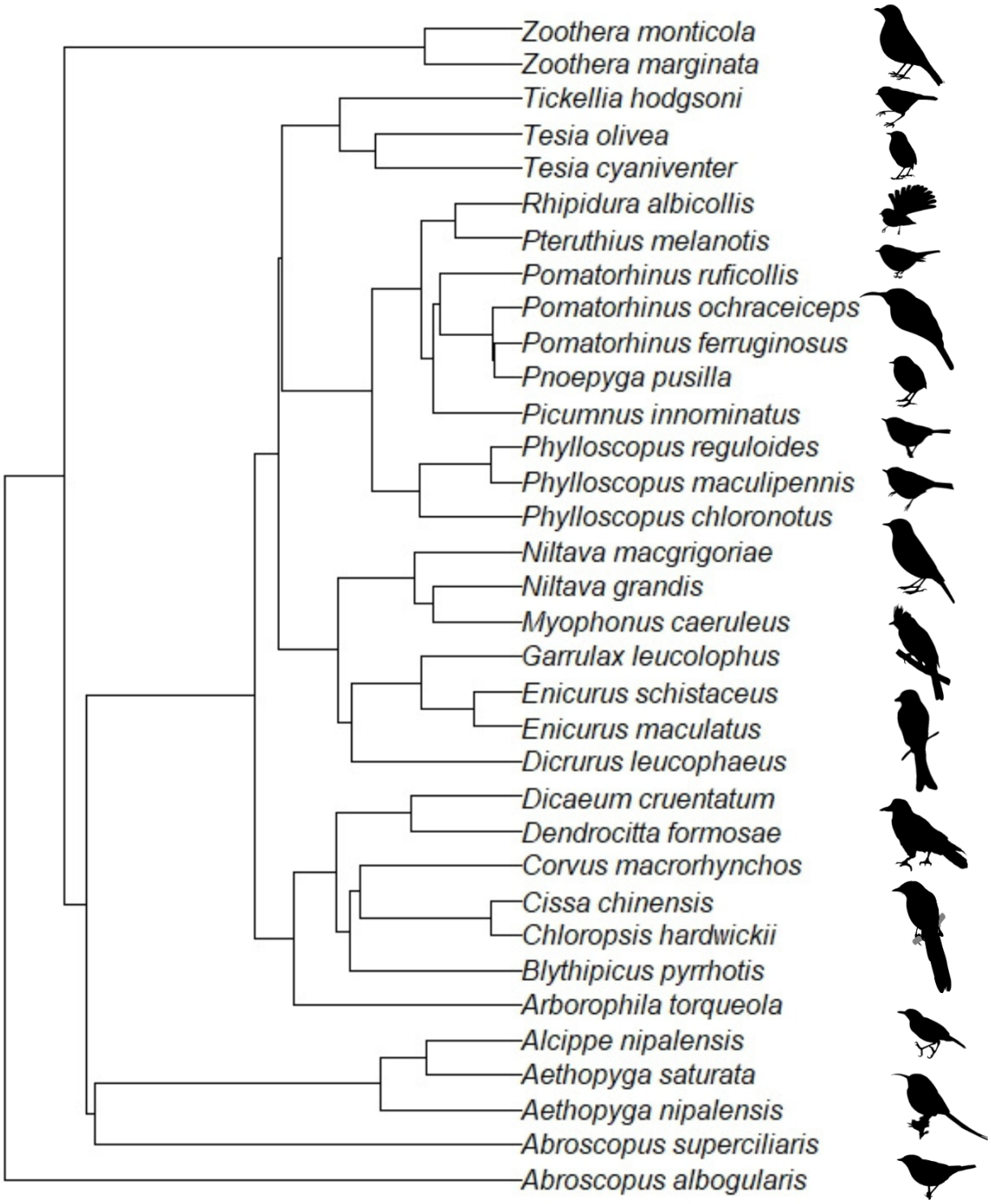

Figure S12: Phylogenetic tree of bird communities observed in jhum indicating a higher presence of closely related than distantly related species.

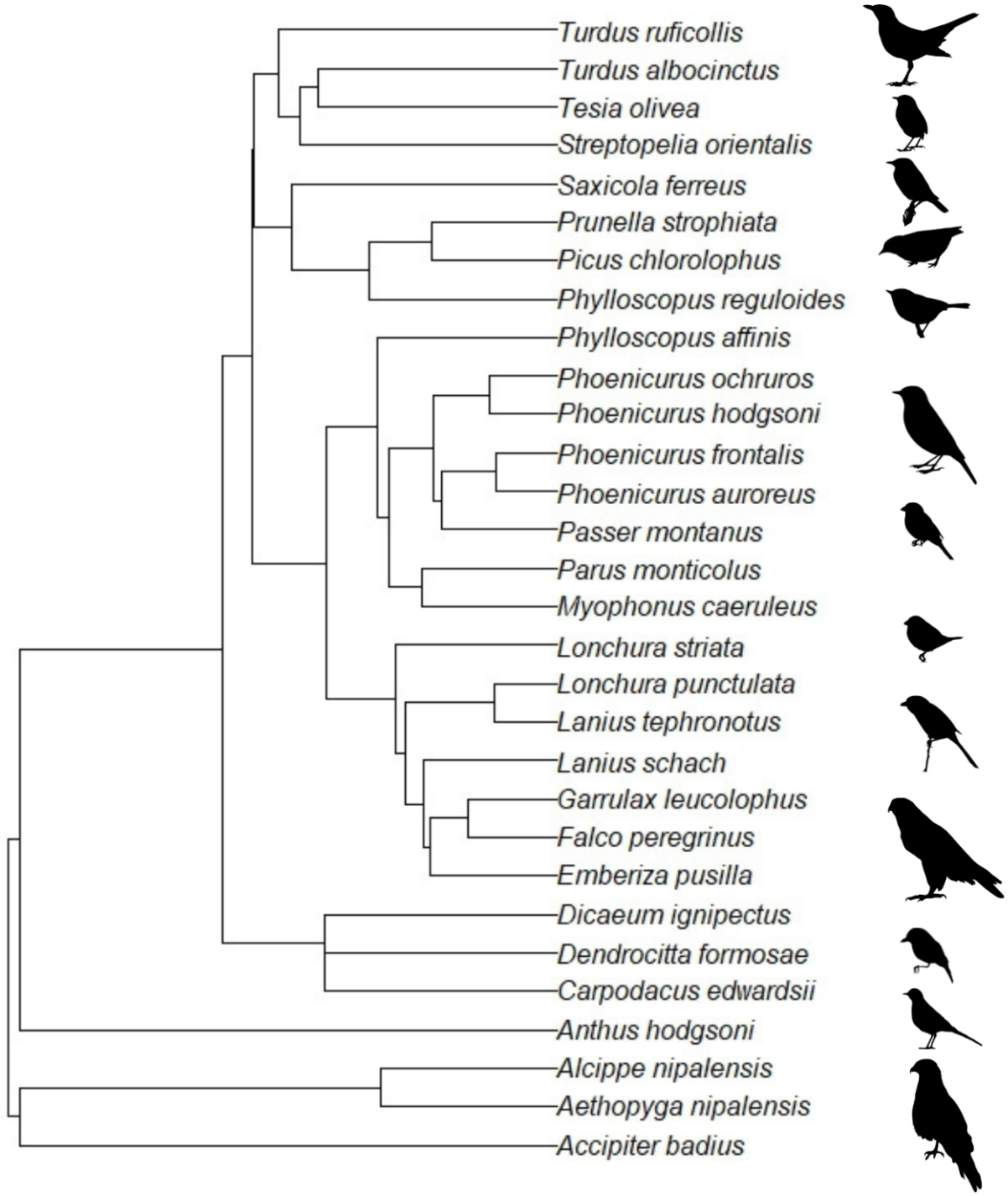

Figure S13: Phylogenetic tree of bird communities observed in abandoned jhum indicating a higher presence of closely related than distantly related species.

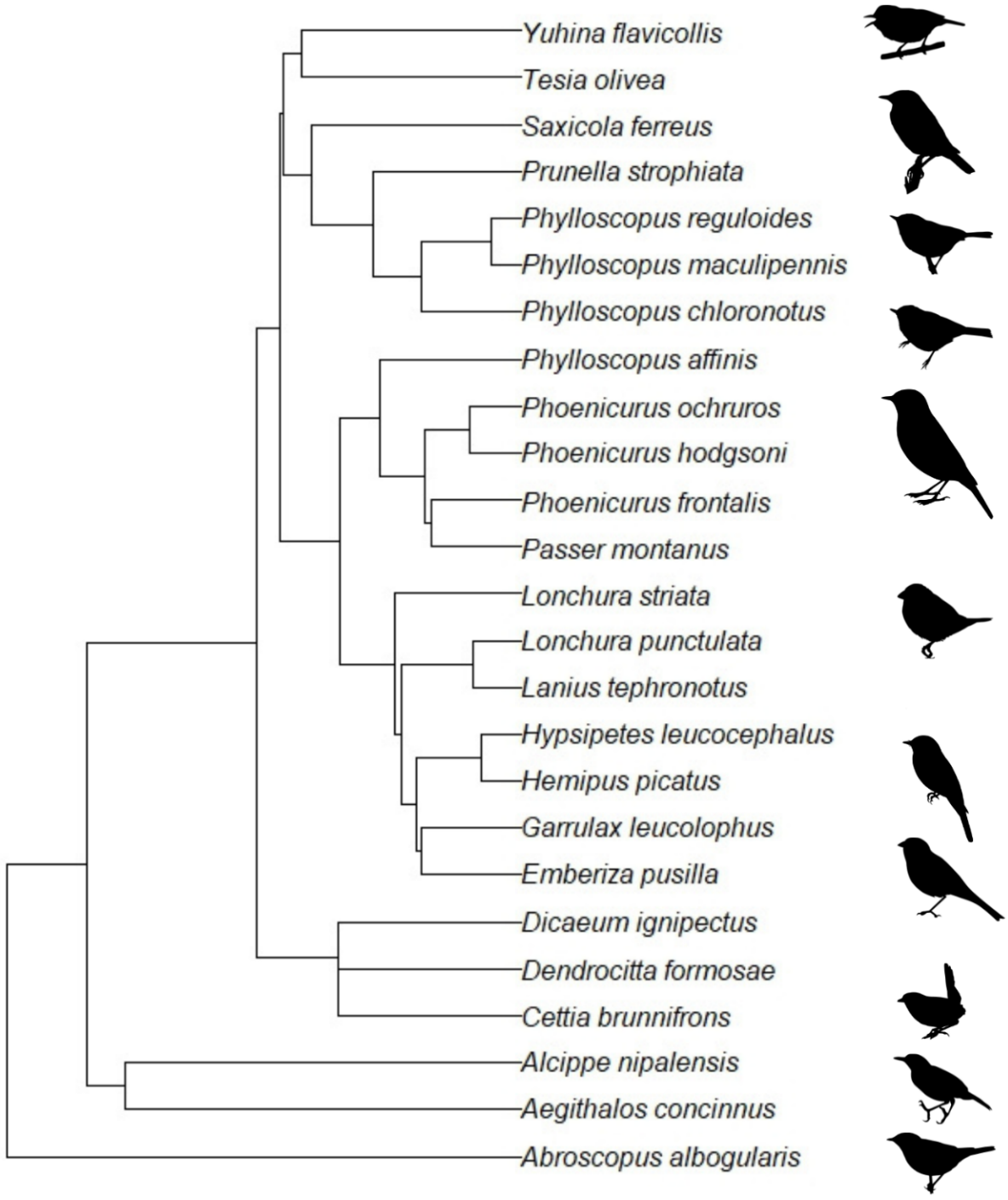

Figure S14: Phylogenetic tree of bird communities observed in bamboo indicating presence of both closely related and distantly related species.

Chapter 4

The effects of small-scale disturbance on avian communities of an eastern Himalayan tropical forest

Aavika Dhanda[1], Sonya Clegg[1]

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ABSTRACT

Large-scale forest disturbance can result in altered patterns of species richness and community composition eventually leading to biotic homogenisation. However, patchy, small-scale forest disturbance could maintain or even increase species richness at least in the short-term due to increased vegetation gaps. We surveyed bird species occupying community-owned forest in Dibang Valley of eastern Indian Himalaya, and we compared multiple aspects of relationships between avian diversity and forest vegetation, before and after the onset of small-scale disturbance. There were no significant shifts in alpha or beta diversity measures, nor were there any significant changes in body mass composition and trophic groups across the two stages. However, there were some subtle effects of small-scale disturbance on avian communities. First, bioindicator species identified pre- and post- disturbance belonged to different trophic guilds indicating a potential shift in habitat health. Furthermore, the negative relationship between foliage height diversity and α-diversity was weakened in the post-disturbance, such that α-diversity is higher when FHD is low. Finally, there was a significant increase in sub-canopy invertivore species from the pre- to post-disturbance stage which was not explained by vegetation variables. Hence, while the broad patterns of bird community composition are stable, there are nuanced species and community responses to small-scale disturbance. Our findings emphasize the importance of using multiple metrics to evaluate the effects of disturbances on bird communities, and highlights the role of secondary forests in maintaining local biodiversity.

1. INTRODUCTION

Tropical forests are continuously facing degradation due to human-mediated activities such as selective logging, cash cropping, forest fires, road expansions, and livestock grazing. These activities severely affect forest-reliant species (Wright, 2010; Wimmer et al., 2013).

At a large-scale, forest degradation and modifications lead to biotic homogenisation and loss of functional diversity (Ibarra and Martin, 2015). Winner-loser outcomes can result with more resilient 'winner' species (often assumed to be generalists) widening their distributions and replacing more vulnerable 'loser' species (often assumed to be specialists) with narrow distributions and ecological requirements (Tabarelli et al., 2012). Outcomes can be influenced by species' traits including trophic niche and body mass, and the scale of disturbances to which they are exposed. For example, it is recognised that the specialist understorey insectivores are vulnerable to the effects of deforestation in the tropical rainforests (Powell et al., 2015), and these are generally smaller-bodied species that are sensitive to microhabitat changes following fragmentation (Visco et al., 2015). In the Atlantic forests of Argentina, terrestrial granivores are 'winners' following fragmentation (Giraudo et al., 2008) while in Malaysian Borneo, large-bodied species occupying higher trophic positions and foraging heights are 'losers' following selective logging (Hamer et al., 2015). Changing, trait-related species composition is then reflected in modified community patterns (e.g., in forest fragments of Ecuador, Cook et al., 2020). At a large-scale, species richness is expected to decline and turnover rates may increase resulting in high dissimilarity between community composition of disturbed vs undisturbed forests (Jones et al., 2021). Moreover, disturbed forests are likely to have fewer bioindicator species, which are used to assess the health of an ecosystem, as compared to undisturbed sites (Shahabuddin and Kumar, 2006). However, at smaller-spatial scales, disturbances can maintain or even, increase overall diversity for a transient period (Hamer and Hill, 2000). Furthermore, species with so-called 'winning' ecological traits are likely to benefit more than the others (Gray et al., 2007)- an effect which may be overlooked by broad diversity patterns. Investigating the nuanced effects of small-scale disturbances on forest species can reveal the spatial thresholds at which community composition is altered or remain conserved.

Small-scale disturbance can lead to an increased species diversity owing to an introduction of edge species following creation of gaps in vegetation. Forest fragmentation results in gap formation which creates ecological edges between disturbed and non-disturbed

habitats with increased light availability, unique microclimatic conditions, and changing vegetation structures (Tabarelli et al., 2008). Once disturbed, these remnant forest patches have reduced canopy cover, an increased growth of edge shrub species and trees (Echeverría et al., 2007), and a higher abundance of lianas (woody vines) along the forest edges (Laurance et al., 2001). Fragmentation leads to the loss of understorey plant diversity, thereby altering the course of natural regeneration of forests (Benítez-Malvido and Martínez-Ramos, 2003). These newly-created edge habitats may be occupied by new species and in particular, by non-forest dependent species which benefit from widening of ecotones (Morante-Filho et al., 2018). These newer additions may arrive from neighbouring habitat patches resulting in positive responses and an increased species richness (Reino et al., 2009; Forsman et al., 2010).

Vegetation alteration after small-scale disturbance can thus lead to nuanced patterns with consequences for community composition. While at the outset, vegetation alteration is expected to increase species diversity, the effects may be short-lived and lead to a decline as competitively dominant species outtake inferior species (Sheil and Burslem, 2003). The underlying patterns may be overlooked by diversity metrics but can be better understood by analysing species traits (Rosenfield and Müller, 2020).

Along with community composition and species trait assessment, detection of bioindicator species can be an essential tool in evaluating and monitoring the effects of disturbances on forest ecosystems (King et al., 2021). Bioindicator species are species with high fidelity to a certain type of environment, are easily observable, and are thus good representatives of changes (Gerhardt, 2002). Identifying bioindicators can be an efficient tool to study the impacts of disturbances and are crucial during ecological restoration as these may be early responders to reverting of natural ecological processes (Chowfin and Leslie, 2021).

Tropical forest cover in the Indian state of Arunachal Pradesh in eastern Himalaya has been decreasing at an alarming rate due to both natural causes such as landslides and soil erosion, and human-induced causes such as encroachment and urbanisation (Ronald et al., 2023). The large-scale deforestation in Arunachal Pradesh is expected

to have unprecedented impacts on the endemic and understudied biodiversity of the region (Pandit et al., 2007). The resultant secondary forests, however, continue to provide ecosystem services and maintain local biodiversity (Vishwakarma et al., 2021). In particular, "community forests" owned and managed by the local communities outside the protected areas contribute significantly towards sustaining both local and regional biodiversity in Arunachal Pradesh (Velho et al., 2016). It is thus crucial to investigate biodiversity patterns in community forests for an improved understanding of eastern Himalayan ecosystems..

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While conducting an ecological study of birds of Dibang Valley in Arunachal Pradesh from 2021 to 2023, some primary forest sites were observed to be undergoing small-scale disturbance. We continued sampling in these now-secondary forest sites to assess the short-term impacts of small-scale disturbance on bird communities and relate these to vegetation parameters. We ask, 1) how does α- and β- diversity, and detected bioindicator species differ after disturbance?; 2) how do species traits of trophic groups and body mass vary after disturbance?; and 3) how does α- diversity relate to site-specific vegetation parameters (canopy cover, leaf litter and forest height diversity)?

2. METHODS

2.1. Study area

Dibang Valley district in Arunachal Pradesh is situated in the eastern Indian Himalaya, a global biodiversity hotspot (Myers et al., 2000). Dibang Valley is part of the Dihang-Dibang Biosphere Reserve, the only biosphere reserve in the eastern Indian Himalaya. The district has a wide variety of habitat types such as tropical evergreen forest, subtropical evergreen forest, temperate broadleaved forest, temperate coniferous forest, alpine grasslands, and jhum (slash and burn) agricultural lands (Singh, Singh and Tiwari, 2013). Although termed 'temperate', forests of eastern Himalaya are characteristically more akin to tropical systems since they are dominated by evergreen trees (Singh, 2014).

Dibang Valley is mainly inhabited by the indigenous Idu-Mishmi community, who manage and own (individually and/or collectively) the majority of habitats. Dri Valley surrounding Dri River in Dibang Valley, consists mainly of temperate broadleaf and temperate coniferous forests. Many parts of Dri Valley are undergoing landscape changes both at smaller-spatial scales mainly due to changes in agricultural patterns, and at larger-spatial scales due to developmental projects such as construction of roads, highways, and hydroelectric dams.

We identified five sites of temperate broadleaf forest, all within the elevation of 1280-1480 metres above sea level that experienced a combination of small-scale disturbances between surveys in 2021-2022 (pre-disturbance stage) and 2022-2023 (post-disturbance stage). The sites were dominated by tree species belonging to Actinidaceae and Rubiceae families such as Eastern Gogan *(Saurauia roxburghii)*, Narrow-Leaf Morinda *(Morinda angustifola)*, and East Himalayan Mussaenda *(Mussaenda roxburghii)*. These sites were neighboured by intact primary forests (Figure 1).

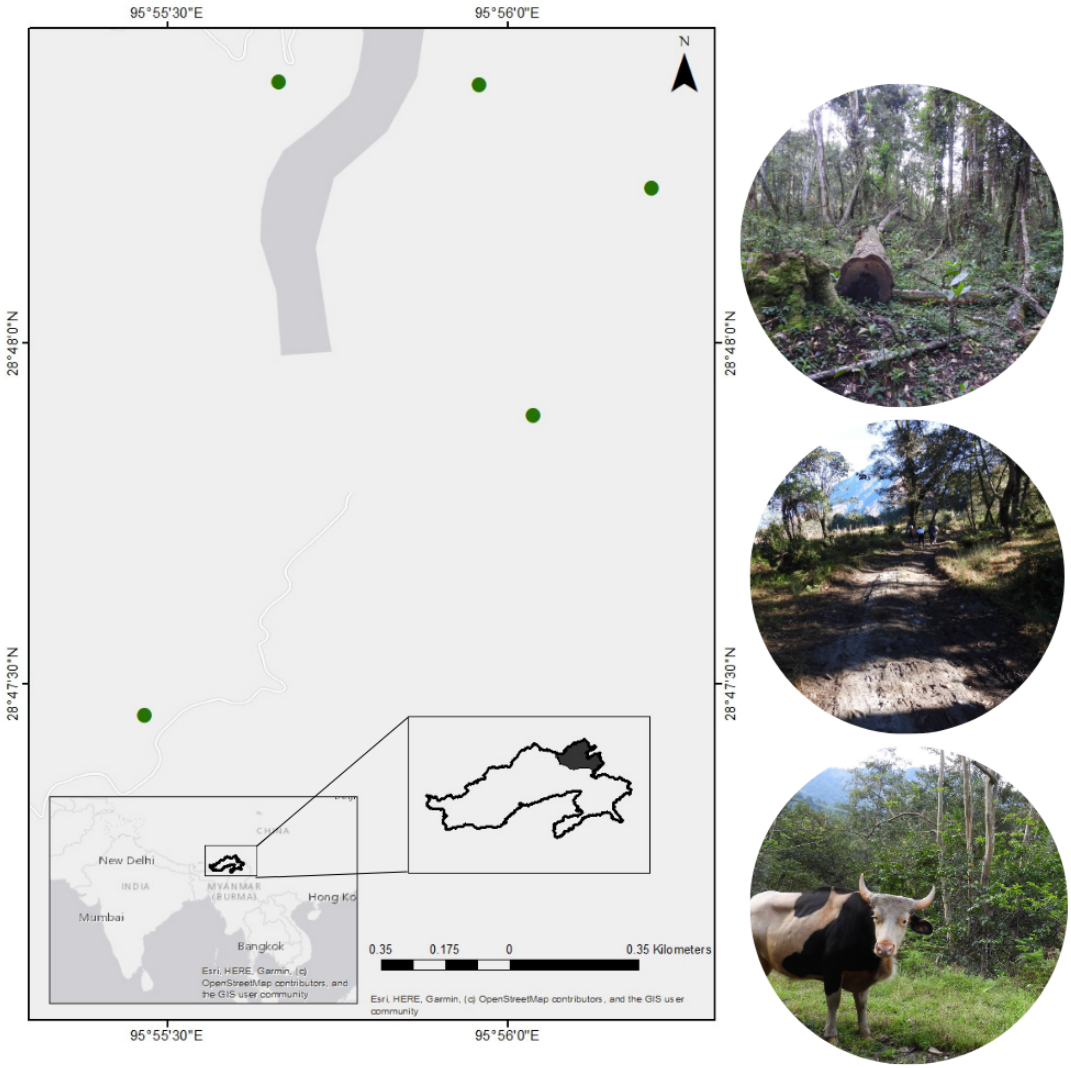

Figure 1: Sampled forest sites undergoing small-scale disturbance due to selective logging, a rural road widening project, and grazing in Dibang Valley, Arunachal Pradesh

Selective felling of two or three old-growth trees for the purpose of selling was seen in two individually-owned forest sites, while disturbances due to a nearby rural road-widening project, and intensified cattle grazing were observed in the remaining sites. Mithun or gayal *(Bos frontalis)* is a free-ranging, semi-domesticated animal that may be seasonally directed towards selected forests to limit their grazing activity within specific village boundaries. Additionally, lopping of branches was also observed in sites undergoing grazing and those near the road-widening project. Due to the opportunistic nature of this study, we did not have replicated sites with exactly the same type of disturbance and therefore could only compare bird community characteristics between forest sites of pre- and post-disturbance sampling stages. However, the overall vegetation changes in the

post-disturbance stage were similar amongst the five sites undergoing a combination of disturbances (Supplementary, Table S1 for summary of vegetation variables).

2.2. Study design and bird surveys

The forest sites were a minimum of 250 metres from each other to avoid observing the same individuals birds at different sites (Ralph, Droege and Sauer, 1995). At each site, bird species were detected both visually and aurally in a fixed radius of 30 metres during a 15-minute standard point count. point counts were conducted only on clear sky mornings and from 06300 to 09300 hours. All sites were visited multiple times to increase species' detection and to improve richness estimates (Robinson and Curtis, 2020). Repeat surveys in each of the five sites comprised of two point counts undertaken at least seven to 10 days apart in pre-peak winter season (mid-October to mid-December) and again in post-peak winter season (mid-February to mid-March) in both 2021-2022 and 2022-2023, resulting in 20 point counts in each of the pre- and post-disturbance stages.

All point count surveys were complemented with recordings from AudioMoth (Open Acoustic Devices, United Kingdom) a passive acoustic monitoring device. Passive acoustic methods can account for uncommon and imperfectly detected species which are often missed during point count surveys (Metcalf et al., 2022). An AudioMoth recorder was deployed in a waterproof case and left unattended for an hour after every point count at a default setting of 48kHz and medium gain, resulting in a total of 40 one-hour recordings in total. All recordings were manually annotated in Raven Pro 1.6 software (Cornell Lab of Ornithology, NY, USA) using a subsampling approach (Levine and De Robertis, 2019). Subsampling is a flexible and efficient method which involves intermittent listening to specific periods of an acoustic recording that minimises high levels of false identifications, and increases overall efficiency for species richness estimates (Wimmer et al., 2013; La and Nudds, 2016). For each recording, annotations were performed in phases such that only the first and third quarter were annotated, resulting in a total of 20 hours of subsampled recordings. All point counts and AudioMoth annotations were conducted

by AD to maintain consistency and to avoid observer differences. Calls and songs in recordings were identified based on the AD's field observations, and by comparing them with those available online on xeno-canto (https://xeno-canto.org/) and Birds of the World (https://birdsoftheworld.org/). A few calls were also identified with the help of local people, and by ornithologists with field experience on birds of Arunachal Pradesh.

2.3. Vegetation parameters

A bird community composition can be influenced by vegetation characteristics (Davis et al., 2016). We quantified vegetation parameters of heights of structures (understorey, mid-canopy, and high-canopy), canopy cover, and leaf litter in the sites following the standard vegetation sampling protocols for bird studies (Bibby, Burgess and Hill, 1992). The vertical vegetation structure of temperate broadleaved forests in Dri Valley is comprised of three stratifications- understorey, sub-canopy and high-canopy. A circular radial plot of 12.62 metres was laid at every visit and five equidistant points were set to take measurements of heights of understorey, and of mature trees of GBH (girth at breast height) $\geq$30 cm forming high-canopy and sub-canopy. Although tree heights did not vary at each visit within seasons, the understorey height was variable between visits. Bird diversity is expected to have a positive relationship with foliage height diversity (FHD) (MacArthur, MacArthur and Preer, 1962). Therefore, we calculated FHD with vertical measurements of three structures using Shannon-Weiner Index at each visit (e.g., Terborgh, 1977). FHD was scaled from 0 to 1 for pre-disturbance and post-disturbance stages such that higher values signify greater vegetation complexity. Canopy cover was estimated within the same circular radial plot of 12.62 metres as the percentage of grids fully covered on densitometer (a mirror partitioned with 26 equal-sized grids placed under the canopy). Average leaf litter percentage was visually estimated across five 1x1 metre quadrats laid on the forest floor.

2.4. Statistical analysis

All analyses were performed in R base software version 4.2.3 (R Core Team, 2020) using RStudio Desktop version 2023.03.0+386. R script, data files, and bird checklist are provided at github.com/aavikad/small-scale-disturbance-dibang-v1-0. All detections were converted to presence-absence format (0s and 1s) since rare and uncommon species are often underestimated in estimation of species richness while common and more abundant species inflate patterns (Lennon et al., 2004). Such biases can lead to modelling errors which can be minimised by using presence-absence data (Cunningham and Lindenmayer, 2005). We used three measures to compare bird communities in pre- and post-disturbance stages- i) change in bioindicator species (species strongly associated to forests), ii) α-diversity (site-specific richness), iii) β-diversity (community dissimilarity).

2.4.1 Body size, trophic niche, and bioindicator analyses

We collated two types of species' trait data- body mass and trophic niche from the AVONET database (Tobias et al., 2022). There were six classifications of trophic niches- vertivore, omnivore, nectarivore, invertivore, frugivore, and aquatic predator. We complimented these trophic niches with two years of field observations on vertical vegetation stratifications (understorey, mid-canopy, and high-canopy) that species usually tend to occupy in forests of Dri Valley. We thus created a new classification of trophic group comprising of 10 classes- high-canopy frugivore, high-canopy invertivore, high-canopy nectarivore, high-canopy omnivore, sub-canopy invertivore, sub-canopy omnivore, sub-canopy vertivore, understorey aquatic predator, understorey invertivore, and understorey omnivore. For the trait analysis, we first log-transformed body mass for a proportional estimate and then compared them using Wilcoxon rank sum-test due to their non-normal distributions (Wilcoxon, 1945). We then used Fligner test to compare variances in body mass between two sampling stages (Fligner and Killeen, 1976). We used Fisher's exact test with simulated p-value suited to smaller data size to compare the proportions

of species occupying all the 10 trophic groups across two stages (Fisher, 1922). Sub-canopy invertivores represented the largest trophic group, and we examined the effects of disturbances on this group in more detail (refer to Methods section 2.4.2).

We detected bioindicator species for each of the sampling stages using IndVal analysis with Pearson's phi coefficient in indicspecies package (Cáceres, Jansen and Dell, 2023). The IndVal analysis measures the association between species and the selected sampling stage by assigning a positive index values based on fidelity and specificity such that species with the highest values are called bioindicators of that habitat.

2.4.2. Diversity estimates

To estimate α-diversity, we used a presence/ absence matrix consisting of forest sites (referred to as sampling units) in columns and species in rows to perform coverage-based rarefaction/extrapolation (R/E) analysis. Coverage-based R/E allows standardisation of sampling effort (Roswell et al., 2021) based on completeness and not by equal size which may otherwise yield biased richness estimates for different habitats since detecting new species can vary from one habitat to another (Chao and Jost, 2012). We performed R/E using iNEXT package with 'incidence_raw' datatype for Hill numbers order q=0 (species richness) (Hsieh, Ma and Chao, 2016) and extracted coverage-based rarefied diversity estimates (α_{rarefied}) for each site in both pre- and post-disturbance sampling stages.

To estimate α-diversity of sub-canopy invertivores ($\alpha_{\text{sub-canopy}}$), we applied second-order incidence-based jackknife method, a powerful non-parametric test which avoids underestimation of species richness in smaller sample sizes and is expected to perform better with fewer biases than other ecological methods of the same class such as first-order jackknife and bootstrapping (Hellmann and Fowler, 1999). The α_{rarefied} and $\alpha_{\text{sub-canopy}}$ estimates were used subsequently as response variables in different generalised linear mixed models (Methods Section 2.4.3).

We estimated the between-sampling stage diversity (β- diversity) to test whether

the community composition of post-disturbance stage was different from that of pre-disturbance stage. We used vegan package to create a Jaccard distance matrix with presence/ absence data, and then tested the significance of variability given the distance matrix by applying PERMANOVA method using adonis2 function (Oksanen et al., 2009). The method gives values ranging from 0 to 1 such that lower values indicate the factors explain none of the variations while higher values indicate factors explain all the variations (Anderson, 2017). We used nonmetric multidimensional scaling (NMDS) to visualise overlap between the pre- and post-disturbance stages community compositions.

2.4.3. Effects of vegetation on α-diversity

Generalised linear mixed models (GLMMs) were specified using α_{rarefied} and ($\alpha_{\text{sub-canopy}}$) as the response variables, vegetation (canopy cover %, leaf litter %, FHD) as predictor variables, and the interactions between each vegetation variable and stage. We used using lmer function for α_{rarefied} and glmmTMB function for $\alpha_{\text{sub-canopy}}$ in lmerTest package with Gaussian family (Kuznetsova et al., 2020). Because canopy cover % and leaf litter % were highly correlated (Pearson correlation test, $r = 83\%$, P<0.001), they were included in separate models (refer to Supplementary, Figure S1 for correlation matrix). Site was included as a random effect to account for non-independence as each forest site was visited repeatedly four times.

The best model to explain variation in α_{rarefied} and $\alpha_{\text{sub-canopy}}$ was identified by applying Akaike Information Criteria (AIC) method (McDonald, 1989) using AICcmodavg package (Mazerolle, 2023). Dispersion of fitted versus simulated residuals of candidate model was performed using DHARMa package such that models with dispersion values closer to 1 and p-values greater than 0.05 do not have evidence of overdispersion (Hartig and Lohse, 2022). Normality of residuals in candidate model was also examined.

3. RESULTS

A total of 473 records of 73 species were observed from point counts and AudioMoths recordings over the course of the study. Of these, 57 species were observed in the pre-disturbance sampling stage, 61 in the post-disturbance sampling stage, and 45 species were common to both sampling stages.

3.1. Body size, trophic niche, and bioindicator species

There were no statistically significant differences in the mean and variances of body mass when comparing pre- and post-disturbance sampling stages (Wilcoxon rank sum test with continuity correction of mean body mass $W = 4551.5$, $P>0.05$; Fligner-Killeen test of homogeneity of variances of body mass, $\chi^2 = 1.77$, $P>0.05$). However, visual comparison of body mass distributions showed a slight tendency for loss of larger-bodied species and an addition of smaller-bodied species in the post-disturbance stage (Figure 2a). There was no statistically significant difference in the overall proportions of trophic groups (Fisher's exact test, $\chi^2 = 0.037$, $P>0.05$) though loss of understorey omnivores and introduction of sub-canopy vertivores in the post-disturbance stage was indicated (Figure 2b).

Bioindicator species identified by the Indicator Value Index were Pygmy Cupwing (Pnoepyga pusilla) and Yellow-billed Blue Magpie (Urocissa flavirostris) for the pre-disturbance stage, and Black Bulbul (Hypsipetes leucocephalus) for the post-disturbance stage.

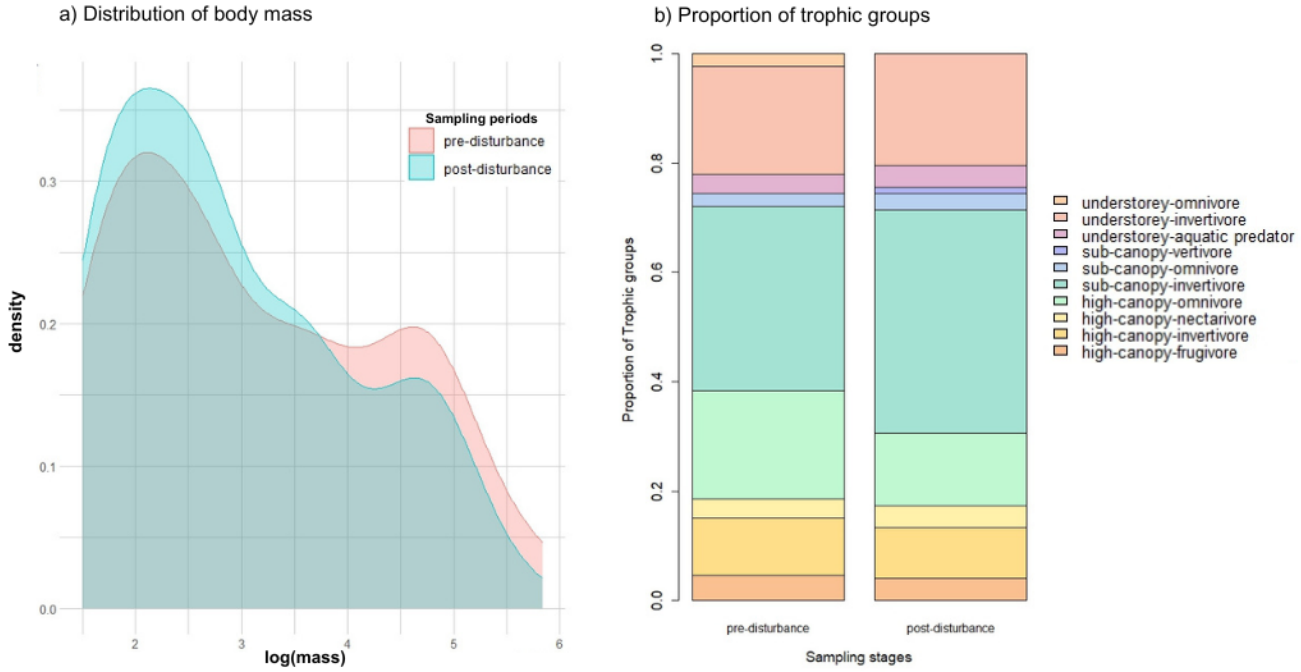

Figure 2: Pre- and post-disturbance comparisons of a) species' body mass distributions, showing tendency for loss of large-bodied species and gain of small-bodied species in the post-disturbance stage; and b) proportions of trophic groups showing similar overall proportions but a loss of understorey-omnivores and gain of sub-canopy vertivores in the post-disturbance stage.

3.2. α- and β-diversity

The sample-size based rarefaction/extrapolation (R/E) curve shows an overlap between diversity (α_{rarefied}) of pre-and post-disturbed sampling stages (Figure 3a). The sample completeness curve representing sampling effort approaches a plateau for both stages (Figure 3b). The coverage-based curve continues to increase and indicates that the expected total diversity is higher than the observed but is comparable across the sampling stages (Figure 3c). The richness of sub-canopy invertivores ($\alpha_{\text{sub-canopy}}$) was higher in the post-disturbance than the pre-disturbance stage (Figure 4).

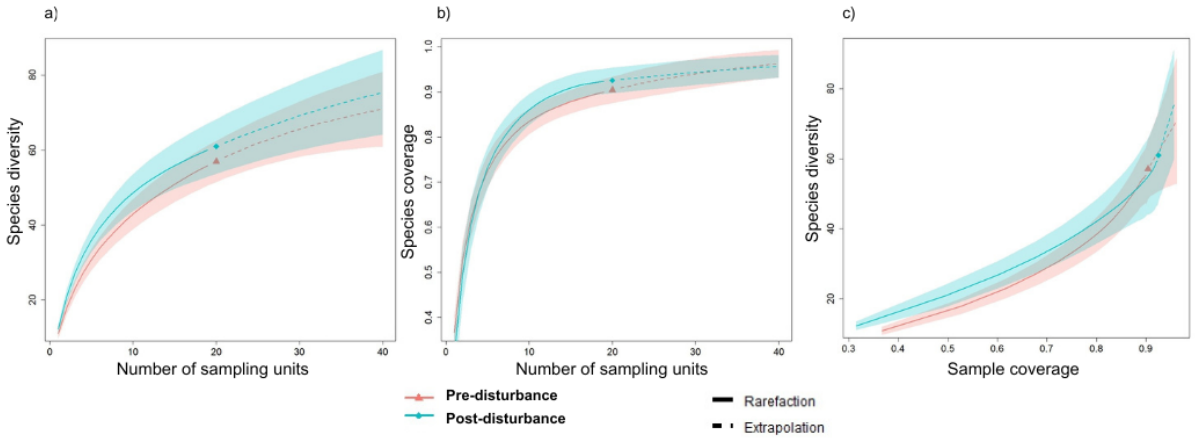

Figure 3: a) sample-based, b) sample-completeness, and c) coverage-based rarefaction/extrapolation curves at 95% confidence intervals showing overlaps between pre- and post-disturbance sampling stages.

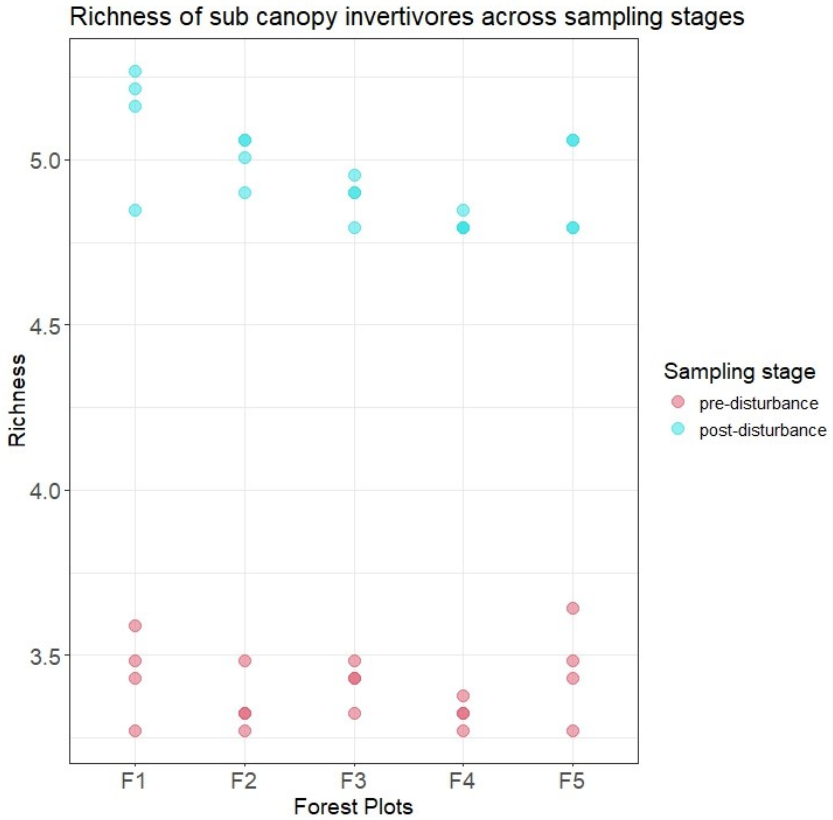

Figure 4: Species richness estimates of sub-canopy invertivores ($\alpha_{\text{sub-canopy}}$)) were higher in the post-disturbance stage. Each dot represents a site visit and overlapping values are indicated by darker dots.

The community communities in pre- and post-disturbance sampling stages were not significantly dissimilar (PERMANOVA, $R^2 = 0.036$, P>0.05). The large overlap in community composition is visualised in the NMDS plot, though some species were unique to pre- or post-disturbance sampling stage (Figure 5).

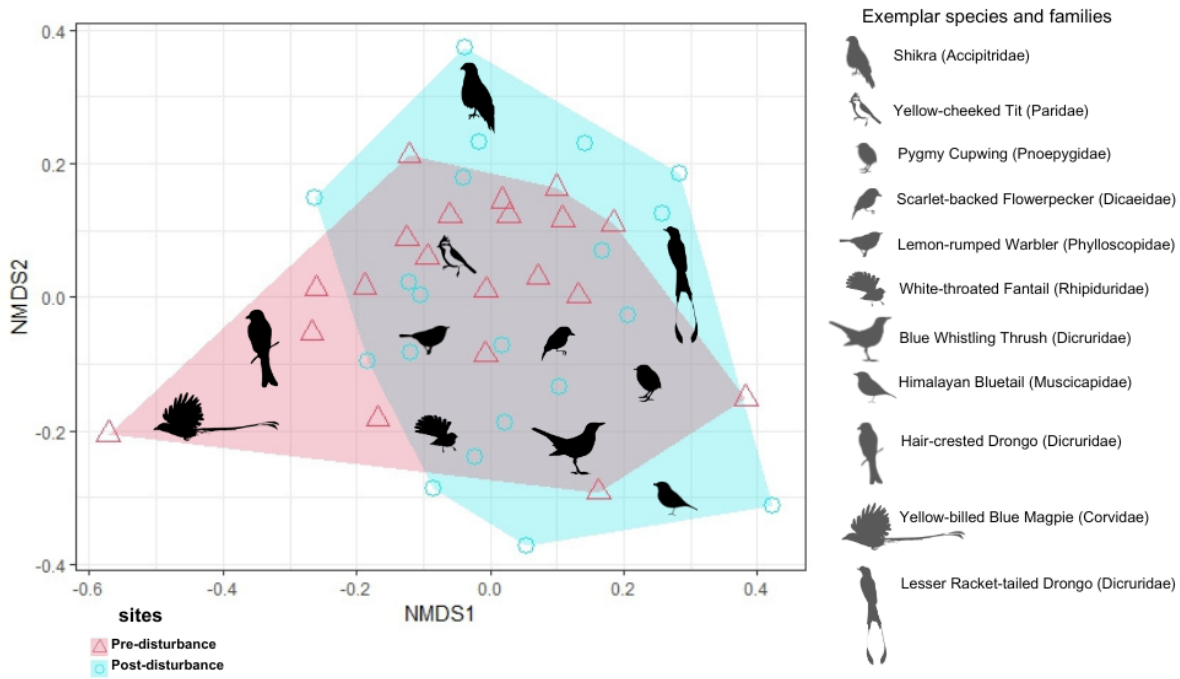

Figure 5: NMDS plot of forest bird communities and in pre- and post-disturbance sampling stages with exemplar species (bird images from https://www.phylopic.org/). Each triangle or circle represent site visit.

3.3. Effects of vegetation on $\alpha-$diversity

We found a statistically significant negative relationship between α_{rarefied} and FHD and a statistically positive interaction with FHD in the post-disturbance stage. There was a trend of a negative relationship between species richness and canopy cover %, although it was not significant (summary statistics in Table 1; refer to Supplementary, Figure S2). The model with FHD and leaf litter as predictor variables was the best performing with the lowest AIC score (model (i), Table 2) and converged successfully. The dispersion value of the candidate model was 0.95 with p-value = 0.90 indicating no overdispersion.

There was a significant positive impact of post-disturbance stage on $\alpha_{\text{sub-canopy}}$, however it was not explained by the vegetation variables directly. FHD and post-disturbance stage had a significant positive interaction effect on $\alpha_{\text{sub-canopy}}$, and leaf litter had a significant negative interaction effect, (Summary statistics of models in Table 3). The candidate model with FHD and leaf litter as predictor variables was the best performing with lowest AIC score (model (i), Table 4) and converged successfully. The dispersion value of the

candidate model was 0.87 with p-value = 0.56 indicating low signs of overdispersion.

Table 1: Summary statistics with standard error (S.E.) and degree of freedom (df) with pre-disturbance as a reference sampling stage where α_{rarefied} had a significant negative relationship with FHD. Significant values (P<0.05) are highlighted in **bold***

Response	Fixed effects	Estimate	S.E.	df	t-value	P
i) α_{rarefied}						
	Intercept	75.58	15.46	33.35	4.88	**<0.001***
	FHD	-28.59	8.47	33.74	-3.37	**<0.05***
	leaf litter	-0.24	0.19	31.82	-1.26	>0.05
	post-disturbance	5.20	17.15	32.43	-0.30	>0.05
	FHD * post disturbance	37.15	12.05	33.81	-3.08	**<0.05***
	leaf litter * post-disturbance	-0.77	0.23	32.02	3.25	**<0.05***
ii) α_{rarefied}						
	Intercept	205.68	76.02	30.51	2.70	**<0.05***
	FHD	-47.75	8.88	32.57	-5.37	**<0.001***
	canopy cover	-1.78	0.98	30/05	-1.80	>0.05
	post-disturbance	-119.69	94.24	30.58	-1.27	>0.05
	FHD * post-disturbance	61.69	12.99	33.03	4.74	**<0.001***
	canopy cover * post-disturbance	1.06	1.24	30.44	0.85	>0.05
iii) α_{rarefied}						
	Intercept	70.73	8.29	7.69	8.52	**<0.001***
	FHD	-52.79	8.55	33.91	-6.16	**<0.001***
	post-disturbance	-36.31	7.06	34.20	-5.14	**<0.001***
	FHD * post-disturbance	68.91	12.61	34.40	5.46	**<0.001***
iv) α_{rarefied}						
	Intercept	235.27	103.62	33.46	2.27	**<0.05***
	canopy cover	-2.49	1.33	33.37	-1.86	>0.05
	post-disturbance	-43.01	127.12	33.78	-0.33	>0.05
	canopy cover * post-disturbance	0.36	1.69	33.79	0.21	>0.05
v) α_{rarefied}						
	Intercept	63.19	16.79	35.34	3.76	**<0.001***
	leaf litter	-0.28	0.21	33.93	-1.30	>0.05
	post-disturbance	-43.01	127.12	33.78	-0.33	**<0.05***
	leaf litter * post-disturbance	0.36	1.69	33.79	0.21	**<0.001***

Table 2: Results of model performance for GLMMs using α_{rarefied} as a response variable (model with FHD and leaf litter as predictor variables was the best-performing and is highlighted in **bold**. All models performed better than the null model.

GLMMs	**AIC**	**Δ**AIC	**Weight**
(i) $\alpha_{\textbf{rarefied}} \sim$ FHD + **leaf litter cover** $*$ **sampling stage** + (1|**site**)	265.23	0.00	0.99
(ii) $\alpha_{\text{rarefied}} \sim$ FHD + canopy cover $*$ sampling stage + (1|site)	273.90	8.66	0.01
(iii) $\alpha_{\text{rarefied}} \sim$ FHD $*$ sampling stage + (1|site)	275.05	9.82	0.01
(iv) $\alpha_{\text{rarefied}} \sim$ leaf litter $*$ sampling stage + (1|site)	280.50	15.27	0.00
(v) $\alpha_{\text{rarefied}} \sim$ canopy cover $*$ sampling stage + (1|site)	298.87	33.64	0.00
$\alpha_{\text{rarefied}} \sim 1 +$ (1|site)	307.56	42.33	0.00

Table 3: Summary statistics with standard error (S.E.) with pre-disturbance as a reference sampling stage where $\alpha_{\text{sub-canopy}}$ had a significant negative relationship with FHD. Significant values (P<0.05) are highlighted in **bold***

Response	Fixed effects	Estimate	S.E.	z-value	P
i) $\alpha_{\text{sub-canopy}}$					
	Intercept	3.32	0.17	18.60	**<0.001***
	FHD	-0.08	0.07	-1.07	**<0.001***
	leaf litter	0.01	0.01	0.07	>0.05
	post-disturbance	1.81	0.20	8.92	**<0.001***
	FHD * post disturbance	37.15	12.05	-3.08	**<0.001***
	leaf litter * post-disturbance	-0.77	0.23	3.25	**<0.001***
ii) $\alpha_{\text{sub-canopy}}$					
	Intercept	3.31	1.10	3.00	**<0.001***
	FHD	-0.10	0.10	-1.02	>0.05
	canopy cover	0.01	0.01	0.12	>0.05
	post-disturbance	2.66	1.31	2.02	**<0.05***
	FHD * post-disturbance	0.41	0.12	3.24	**<0.001***
	canopy cover * post-disturbance	-0.01	0.01	-1.06	>0.05
iii) $\alpha_{\text{sub-canopy}}$					
	Intercept	3.45	0.06	53.54	**<0.001***
	FHD	-0.10	0.11	0.93	>0.05
	post-disturbance	1.33	0.07	17.32	**<0.001***
	FHD * post-disturbance	0.39	0.13	3.06	**<0.05***
iv) $\alpha_{\text{sub-canopy}}$					
	Intercept	3.17	1.19	3.10	**<0.05***
	canopy cover	-0.01	0.01	-0.26	>0.05
	post-disturbance	2.58	1.48	1.74	>0.05
	canopy cover * post-disturbance	-0.01	0.01	-0.76	>0.05
v) $\alpha_{\text{sub-canopy}}$					
	Intercept	3.23	0.12	13.94	**<0.001***
	leaf litter	0.01	0.01	0.69	>0.05
	post-disturbance	2.09	0.23	8.91	**<0.001***
	leaf litter * post-disturbance	-0.01	0.01	-3.06	**<0.05***

Table 4: Results of model performance for GLMMs using $\alpha_{\text{sub-canopy}}$ as a response variable (model with FHD and leaf litter as predictor variables was the best-performing and is highlighted in **bold**. All models performed better than the null model.

GLMMs	AIC	ΔAIC	Weight
(i) $\alpha_{\textbf{sub-canopy}} \sim$ FHD + **leaf litter cover** $*$ **sampling stage** + (1|**site**)	-57.84	0.00	0.95
(ii) $\alpha_{\text{sub-canopy}} \sim$ FHD + canopy cover $*$ sampling stage + (1|site)	-50.51	7.33	0.02
(iii) $\alpha_{\text{sub-canopy}} \sim$ FHD $*$ sampling stage + (1|site)	-50.28	7.56	0.02
(iv) $\alpha_{\text{sub-canopy}} \sim$ leaf litter $*$ sampling stage + (1|site)	-46.82	11.01	0.00
(v) $\alpha_{\text{sub-canopy}} \sim$ canopy cover $*$ sampling stage + (1|site)	-42.14	15.69	0.00
$\alpha_{\text{sub-canopy}} \sim 1 + (1\|\text{site})$	100.87	158.71	0.00

4. DISCUSSION

In our temporal comparison of bird community richness and composition before and after the onset of patchy, small-scale disturbances in eastern Indian Himalayan forests, we documented changes in community composition that may forecast a trajectory of species filtering determined by vulnerable or advantageous traits. While commonly described metrics such as alpha and beta diversity are relatively stable under patchy and small-scale disturbance regimes, community shifts are evidenced by a) a tendency for loss of large-bodied species, b) change in bioindicator species detected, c) subtle but potentially important shifts in the representation of different species with an increased presence of sub-canopy invertivores, and d) nuanced effects of vegetation on α-diversity.

Larger-bodied bird canopy species are generally expected to be more vulnerable to forest disturbances in the tropics owing to lower population densities (review in Sodhi et al., 2004). Additionally, smaller-bodied understorey birds are also at high risk to habitat disturbances due to lower physiological tolerances to microclimatic changes (Visco et al., 2015). While we did not find any significant differences in body mass distributions in pre- and post-disturbance stages, a shift was observed. A loss of large body sizes and an increase in smaller body sizes is consistent with the direction of change observed in other systems (e.g., in the Indonesian archipelago (Martin and Blackburn), 2010; in Southwest China (Chang et al., 2013)). If the disturbance persist or expand, the shift in body size distribution may amplify.

We also report a change in bioindicator species detected from pre- to post-disturbance

stage. At the outset, these changes may appear idiosyncratic in nature, but linking their ecological traits with the changing environment can aid in assessing overall habitat health (Carvalho et al., 2020). The pre-disturbance stage had two bioindicator bird species; Pygmy Cupwing *(Pnoepyga pusilla)*, a small-bodied understorey invertivore, and Yellow-billed Blue Magpie *(Urocissa flavirostris)*, a large-bodied high-canopy omnivore. However, in the post-disturbance stage, there was only one bioindicator species, Black Bulbul *(Hypsipetes leucocephalus)*, a medium-sized high-canopy frugivore. The change in indicator species represents a prominent change in functional groups suggesting that the health of the forests has undergone a shift. Similar patterns were observed in Indonesia's Borneo forests where fewer species (all generalists) are bioindicators of depleted forests while a greater number of species (both common and rare) are bioindicators of primary forests (Simamora et al., 2021).

At the trophic group level, we found that the richness of sub-canopy invertivores had significantly increased. Prior studies in the tropics have indicated that while overall richness remains the same, species belonging to specific foraging guilds may benefit more from disturbances than the others. For instance, in New Guinea, the proportions of insectivores and frugivores increased while those of nectarivores decreased following small-scale disturbances along forest-agricultural gradients (Marsden and Symes, 2008). The increased presence of these birds provide evidence for the prevalence of edge effect in now-disturbed and relatively more open forests (Banks-Leite et al., 2010) due to an expansion of newly available, and unoccupied niches (Ausprey et al., 2022). It is thus important to assess foraging guild composition as species richness alone could be an incomplete metric of the effects of habitat disturbances on tropical bird communities (Maas et al., 2009).

Although the overall alpha diversity has overlapping curves for both the sampling stages, we observed nuances when exploring the effects of varying vegetation. Higher values of FHD indicates a heterogeneous environment with increasing complexity and varying microhabitats which promotes species richness in forests, although the effects

can be spatial-scale dependent (Bar-Massada and Wood, 2014). In our case, we found the opposite to be true, signifying that loss of heterogeneous structures favoured species richness. Species richness is expected to decline following forest disturbances in the longer-term, but may peak at the onset (Hagan et al., 1996). Similar causes could have also contributed to the overall stability in $\beta-$. Our finding about the maintenance of bird species richness in tropical forests undergoing varying types of small-scale disturbances is consistent with the previous work. For example, in Indonesia, species richness in young secondary forests was reported to be similar to primary forests following small-scale disturbances, although the number of endemic birds was significantly lower (Waltert et al., 2004).

The increase of diversity of sub-canopy invertivores, although not directly explained by the vegetation parameters, could possibly be due to indirect effects such as edge effect of increased insect abundance. Intact primary forests neighbouring the disturbed forests facilitates an increased movement of species from edge habitats to forest interiors resulting in positive edge responses (Magura, 2002). Moreover, small canopy gaps support an increase in insect fauna and thus food availability (Przepióra et al., 2020). Even though we could not test for edge effects and insect food availability, these the possibility of these indirect effects responsible for an increase in diversity of sub-canopy cannot be ruled out.

The bird communities appear resilient at the onset of disturbance, their persistence cannot be guaranteed over the years if the disturbance further intensifies and may eventually lead to biotic homogenization (Ibarra and Martin, 2015). The likelihood of species hitting a threshold cannot be ruled out as species are soon expected to compete for finite resources (Hagan et al., 1996). However, the threshold at which the species richness starts declining is difficult to ascertain (Burivalova et al., 2014). We encourage the continued monitoring of bird communities in these forests using multiple metrics which can offer insights into their tolerance thresholds.

In the tropics, secondary and disturbed forests play an important role in maintaining biodiversity to an extent especially when neighboured by old-growth forests (Dent and

Joseph Wright, 2009), and therefore, the preservation of these now-secondary forests along with the tracts of neighbouring primary forests in community lands through local efforts will be important. We found that the eastern Himalayan bird communities are tolerant to small-scale disturbances and to a somewhat traditional land-use system, at least for a transient stage, however the effects of large-scale disturbances owing to the construction of highways and hydroelectric dams in Dibang Valley remain unknown.

Author contributions

AD and SC formulated the idea and designed the study. AD acquired the field grants, secured the permits, liaised with the Idu-Mishmi community, conducted the field work, analysed the data, and wrote the original manuscript. SC provided feedback and edits on drafts.

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Supplementary

Table S1: Summary statistics (mean ± standard deviation) of vegetation variables in five sites across two sampling stages.

Sites	Pre-disturbance stage			Post-disturbance stage		
	Canopy cover	Leaf litter	FHD	Canopy cover	Leaf litter	FHD
F1	78.5 ± 1.80	69.25 ± 1.92	0.62 ± 0.04	71.25 ± 1.63	36.75 ± 8.28	0.93 ± 0.05
F2	76 ± 1.00	57.75 ± 2.27	0.52 ± 0.05	70.75 ± 0.43	33 ± 3.53	0.45 ± 0.03
F3	76.5 ± 2.06	74.50 ± 2.29	0.11 ± 0.09	71.75 ± 1.78	57 ± 2.0	0.69 ± 0.27
F4	78 ± 0.70	75.25 ± 1.47	0.86 ± 0.11	68.25 ± 1.08	38.75 ± 1.47	0.07 ± 0.07
F5	77.5 ± 0.5	83.75 ± 3.49	0.52 ± 0.03	69.50 ± 3.27	41.50 ± 3.5	0.53 ± 0.12

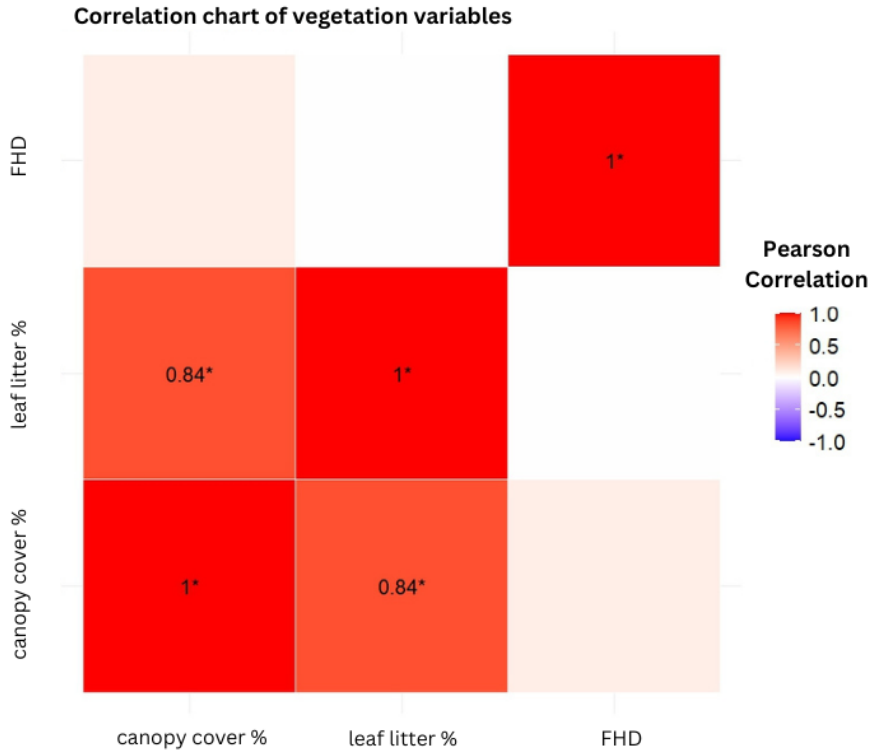

Figure S1: Correlation matrix of three vegetation variables, canopy cover %, leaf litter %, standardised foliage height diversity (FHD) using Pearson Correlation Test with darker colours (red) representing the higher strength of correlation. Canopy cover % and leaf litter % were highly correlated.

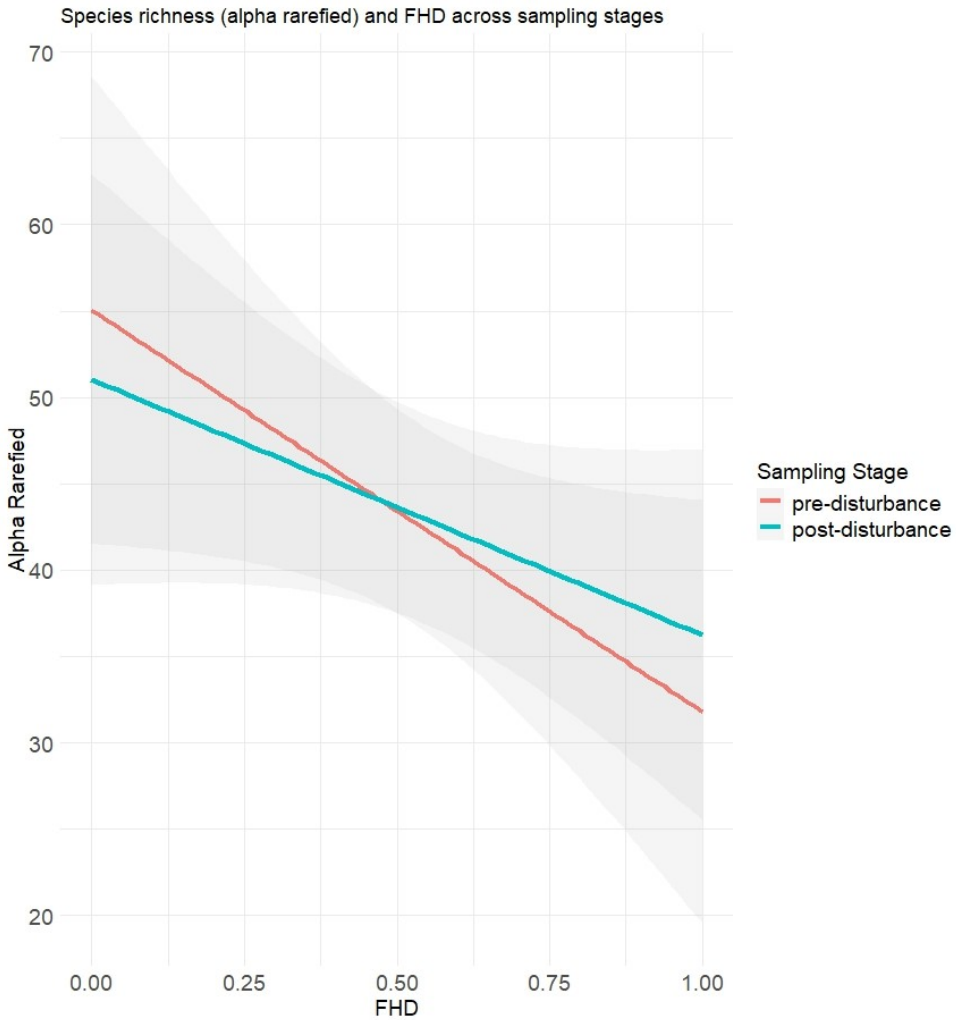

Figure S2: Relationship between α-rarefied and FHD was significantly negative.

Chapter 5

General Discussion

Climate change and land-use/ land-cover change in the tropical mountains can result in subtle or pronounced species and community patterns at varying spatial and temporal scales. In my thesis, each chapter presents unique community patterns characteristic to the abiotic conditions and habitat heterogeneity given the temporal and geographical scale that they were explored. Here, I summarise my findings, while asking further questions, and frequently reflecting on the principal question of the thesis- which traits contribute to resilience or vulnerability to change in tropical montane bird communities? Lastly, I discuss suggestions for conserving the landscape and potential future directions.

Scale effects

Do predictions of niches vary across scales? Several studies have repeatedly pointed towards the dominant role of temperature in shaping response to climate change and habitat alterations (Feeley and Silman, 2010; Frishkoff et al., 2015; Cuesta et al., 2020). However, the inaccuracies in estimating the role of water-related parameters in shaping species' niches, and as a result, their response to change, remain unclear. In **Chapter 2**, I demonstrate that under the present scenario, Muscicapidae species were highly sensitive to annual temperature, and to seasonal temperature of the wettest quarter, explaining the impacts of both temperature and water-related parameters on distributions. However, there were little to no traces of sensitivity to precipitation under the future climatic scenarios. In a smaller-scale assessment conducted in **Chapter 3**, I find strong evidence of bird communities responding to both temperature and humidity conditions, solidifying my assumption that eastern Himalayan bird communities seasonally track their thermal as well as hygric niches in each of the habitat types. It is noteworthy that several Muscicapidae birds studied in **Chapter 2** were part of the community analysis in **Chapter 3** as well, and showed responses to both variables at a smaller geographic scale. While species distribution modelling was performed at a broader scale encompassing climate data summarised over multiple years, a smaller-scale study allowed integration of finer details on seasonality in the assessment. This further evokes the question- how

do differing seasonal or geographic sub-niches of tropical montane birds be assessed and categorised? I argue that the abiotic niche, which is a critical component of community structure organisation (Dunson and Travis, 1991), must be examined at multiple scales when investigating the effects of multi-scaled anthropogenic events.

What is the threshold of community tolerance to disturbances? Analysis of community reorganization due to anthropogenic changes remains a pivotal and fascinating question in ecological studies. In **Chapter 3**, I elucidate how taxonomic richness declined in human-mediated habitats, but in an even finer-scale study in **Chapter 4**, taxonomic richness was maintained, at least at the onset of disturbance. I observe that while a complete transformation of habitat will negatively affect species, the overall forest community in this case were tolerant at least at the onset of small-scale disturbance– further prompting if the relationship between the forest birds of Dibang Valley and disturbances is unimodal or not (intermediate disturbance hypothesis (IDH)) (Moi et al., 2020). These findings invite new avenues to test the applicability of IDH and assess community thresholds.

Resilient and vulnerable traits

Are trait-based responses in montane birds predictable? Community resilience or vulnerability to anthropogenic disturbances is often hidden in species' traits (Poff et al., 2010), but the predictions might not be as straightforward. I observed disparate patterns of traits in each chapter. In **Chapter 2**, I found that habitat generalists showed higher sensitivity to abiotic variables than habitat specialists- which deviated from the common assumption that habitat generalists are also climate specialists (Şekercioğlu et al., 2012). There was also little to no phylogenetic signal detected in sensitivity. These findings are paradoxical in nature- traits are the foundation of species interactions with the environment (and change), but the environment (and change) does not strongly predict trait variations- similar to that argued by Anderegg, 2023. It is likely that the climate change predictions in a large, multi-habitat environment with undetectable or no generalised patterns.

Relationships between disturbance species' traits can be more lucid at a relatively

smaller scale. In **Chapter 3**, I observed a congruent trend between species richness and phylogenetic traits, but not with functional traits. While phylogenetic richness can have a strong positive relationship with species richness (Tucker and Cadotte, 2013), functional richness has its relevance which is often not compensated for by maintenance of other metrics (Mazel et al., 2017). Additionally, jhum lands were found to have the heaviest birds which included some raptor species that use these open spaces as hunting grounds. It has earlier been conceptualised that the continued persistence of species in mosaic landscapes depends not only on their characteristic traits but also on the shifting land-use patterns which mediate movement patterns (Young, 2009).

Disturbance can result in a cause-and-consequence relationship. In **Chapter 4**, it was detected that heavier birds were starting to disappear from forests in the post-disturbance stage. These results may sound contradictory but are somewhat complementary when looked at from a landscape lens. Although, disturbance is said to negatively affect larger-sized birds (Cosset et al., 2020), these findings imply that the loss of body mass in forests is mitigated by jhum lands, and thus the overall body mass is maintained, at least locally. Moreover, in **Chapter 4**, I also note a rise in species richness of sub-canopy invertivores, implying they have "winning" traits required to benefit from forest disturbance- attributing them as habitat generalists. However, such a pattern is cyclical. While disturbance promotes species diversity of those with certain traits, their increased diversity contributes to the realised response of the community to disturbance. Such feedbacks often increase species richness, decrease variability, and influence relationships between diversity and disturbance (Hughes et al., 2007). However, this feedbacks can be even more complicated in a mosaic landscape as traits may be exchangeable amongst habitat patches.

Role of indigenous people's lands in biodiversity conservation

Several species are expected to migrate as they track their suitable climatic niches, however, their movements can be constrained by the lack of corridors following fragmentation and

deforestation. Corridors in the tropics can maintain connectivity between populations and ensure high community, functional, and genetic diversity (de Almeida Vieira and de Carvalho, 2008; Gutiérrez-Chacón et al., 2020). Conventionally, the role of protected areas in holding important species' corridors in light of climate change has been emphasised (Fung et al., 2017), but indigenous people's lands are not yet widely acknowledged for the same. The Global Biodiversity Framework's 30 x 30 target which aims to protect 30% of global land by 2030 has been deemed unachievable for Asian countries given the population growth and the socioeconomic challenges (Farhadinia et al., 2022). However, the constant creation of protected areas in the tropics is deemed colonial in nature and sparks debate on its unjust "protectionist" practices which involve forced evictions and loss of ethnic identities of the indigenous people (Domínguez and Luoma, 2020). Moreover, several indigenous and community-conserved areas (ICCAs) and lands protected for cultural purposes (such as those mentioned in **Chapter 3**) are often not mapped or formally recognised by the governments to achieve national conservation goals (Robson and Berkes, 2010). It is thus crucial to investigate the role these lands play in providing climatic buffering at micro and macro scales and maintaining biological corridors.

In the tropics where forests are continuously modified with the changing economic and financial policies, and the human-environment interactions, maintenance of corridors is a challenge requiring a participatory and multidisciplinary approach (Chazdon et al., 2009a). For example, collective local perceptions and values of the people combined with spatial assessment of the forests are used to inform landscape management schemes to protect biodiversity in some parts of Africa and Asia (Pfund et al., 2011). Furthermore, an incentive-based approach can be efficient and self-sustaining in the long run, such as the recent establishment of a 70 square kilometre ancestor customary land as a community-conserved area in Dibang Valley.

In addition to corridors, maintenance of neighbouring habitat patches is crucial for the study region. While natural habitats are important for species, traditional agricultural lands (Giri et al., 2020) and fragments of secondary forests also play a pivotal role in

maintaining local biodiversity especially when neighboured by natural habitats in a mosaic landscape (Chazdon et al., 2009b), as seen in some of the community patterns in the previous chapters. In the large scheme of things, avian diversity in the community lands of Dibang Valley appears rather almost in a state of equilibrium with the local LULC changes.

Future directions

Tropical mountains are complex systems, and the assessment of anthropogenic impacts on their species requires both reliable data and on-ground knowledge. I studied the impacts of climate change and LULC change avian communities separately in **Chapter 2**, however, these events likely have synergistic and exacerbating impacts in the region. There are several pivotal examples of synergism in different taxa from other tropical mountains (e.g., mammals in Southeast Asia (Brodie, 2016); amphibians of Costa Rica (Nowakowski et al., 2017)). With improved satellite LULC imagery and growing citizen science data, it will be soon possible to make accurate predictions of the synergistic impacts on bird species and communities of the region.

Species in the tropics have high speciation rates and trait variations. Certain fast-adapting communities (and not individuals) may undergo plasticity under habitat alterations. For example, some avian communities in Southeastern China have rapidly adjusted foraging and perching heights following habitat changes (Zhang et al., 2016). Exploring such plastic functional traits with continued field monitoring can shed light on understanding the extent to which some of the generalist avian communities can go in the region to adapt to habitat modifications.

The importance of water-related parameters in driving community composition on an annual basis is seldom explored in the tropical mountains of the eastern Indian Himalaya. While I found that species communities generally had a positive relationship with relative humidity, conversations with some of the Idu-Mishmi people during fieldwork revealed that the bird species usually start disappearing from the study site in peak monsoon

season. Extreme rainfall is said to have a negative impact on bird species richness in tropical regions (Boyle et al., 2020), however identifying the exact threshold will reveal new insights into eastern Himalayan birds.

In the past decade, the field of ecology has witnessed a rise in cost-effective global and big data models, however, their generality of patterns cannot be assumed across all species and systems. It is thus imperative to conduct local-scale studies in the highly understudied tropical mountains to assess the effects of anthropogenic disturbances and fill data voids and knowledge gaps (Feeley and Silman, 2011). The eastern Indian Himalaya, although understudied, is also dominated by many human-modified landscapes, which raises several questions pertaining to the resilience and vulnerability of species. Investigating these patterns of responses will be crucial for sustaining species and their habitats as several anthropogenic events continue.

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