Biogeography, compositional turnover, morphology and vocal complexity of Genus *'Phylloscopus'*

by

Tushar P. Parab

10BB22A73006

A thesis submitted to the
Academy of Scientific & Innovative Research
for the award of the degree of

DOCTOR OF PHILOSOPHY
in
SCIENCE

Under the supervision of

Dr. Salvador Lyngdoh

and co-supervision of

Dr. Sandeep K. Gupta



भारतीय वन्यजीव संस्थान
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Sector 19, Kamla Nehru Nagar,
Ghaziabad, U.P. – 201 002, India

2026

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Year (2026)

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Azadi Ka Amrit Mahotsav

CERTIFICATE

This is to certify that the work incorporated in this Ph.D. thesis entitled, "Biogeography, Compositional Turnover, Morphology and Vocal complexity of Genus *Phylloscopus*", submitted by Tushar P. Parab to the Academy of Scientific and Innovative Research (AcSIR) in fulfillment of the requirements for the award of the Degree of Doctor of Philosophy, embodies original research work carried-out by the student. We, further certify that this work has not been submitted to any other University or Institution in part or full for the award of any degree or diploma. Research material(s) obtained from other source(s) and used in this research work has/have been duly acknowledged in the thesis. Image(s), illustration(s), figure(s), table(s) etc., used in the thesis from other source(s), have also been duly cited and acknowledged.

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PREFACE

Ornithology, the scientific study of birds, is one of the oldest organised scientific disciplines, and birds are among the best-studied groups. That being said, **why are we presenting another PhD on birds?** What we now recognise as a bird is the relatively small feathered surviving member of the dinosaur assemblage of reptiles. These warm-blooded vertebrates have evolved into tens of thousands of species, particularly in the past 65 million years. Species have become extinct as a result of this ongoing evolutionary process, both naturally and increasingly due to non-natural factors. Given this, and for a number of scientific reasons, it is essential to understand the characteristics of bird species, including their emergence, evolution, and adaptation.

The work of numerous researchers and scientists has long paved the way for our understanding of various bird groups by shedding light on our route through the decoding of genetic patterns, revised distribution models, and macro-ecological insights. As with all knowledge, what was previously innovative has now reached maturity, and the discipline encourages a more profound and comprehensive understanding. This drives me to a more elaborate synthesis—a union of form, sound, space, and time—rather than securing myself in strict thresholds of genetic difference or predetermined taxonomic measurements. Ancestral ranges, morphology, vocalisations, and species turnover patterns are not just datapoints; they are expressions of deeper unity among avian lineages. Accepting this plethora of evidence may not make the work easier, but it is consistent with the idea that completeness resides in integration.

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CHAPTER 1. GENERAL INTRODUCTION

1.1. BACKGROUND

From a scientific perspective, it is difficult to define a species, because species definition depends on a variety of features, and speciation and extinction are continuous evolutionary processes. The search for an avian tree of life went on hold for over 80 years after Furbringer in favour of revising classifications, the most significant of which were those of Wetmore (1930, 1934, 1940, 1960), Stresemann (1934), Mayr & Amadon (1951), and Storer (1960). What then happened to systematic ornithology between 1890 to 1970? It became apparent to characterise the phylogeny as unknown and unknowable. Additionally, the redefinition of systematics, which became more in line with "population thinking," overshadowed phylogeny. Stresemann remarked,

The construction of phylogenetic trees has opened
the door to a wave of uninhibited speculation.
Everybody may form his own opinion because,
as far as birds are concerned,
there is virtually no paleontological documentation.
Only lucky discoveries of fossils can help us...

In order to delimit species, even modern systematists made a continuing effort to consider as many characteristics as possible. Using the idea of evolutionary classification, which categorised the groups based solely on morphology, these criteria not only reflected relationships but also, in some ways, influenced the approach to avian phylogenetics. Consider it somewhat similar to combining two different colors of paint (yellow and blue) to create the ultimate color, green. Even though we are aware that green is composed of two fundamental constituent colors, it is neither of them. Additionally, varying shades of green will result from different proportions of blue and yellow. The same is true with systematics. Genomic sequences are currently the most widely used method, either used as a neutral marker or to identify the underlying causes of functional traits (Tietze 2018). Last

but not least, over the past three decades, researchers have been able to gather, store, and analyse ever-increasing volumes of data due to developments in fields of computation and bioinformatics hardware and software. So, in light of a century of research and our present knowledge, what is the best explanation for how these species evolved, and what were their ancestral biogeographic ranges? What do we know about their origins, past climatic events, and geological shifts that influenced their diversification and dispersal?

Ice ages have played a crucial role in forming life on Earth over the last five million years. As glaciers and ice ages progressed, they pushed dense forests southward, splintering ecosystems into more remote refuges like the Balkans, the Italian Peninsula, and the Iberian Peninsula. Numerous recent diversification episodes in Europe and beyond are often attributed to the recurring partitioning of refugia over multiple ice ages, a phenomenon that has been extensively studied. Every ice age is marked by habitat changes as well as a major event: a drop in global sea levels due to water freezing at the poles. This is especially apparent in Europe, as the North Sea dries out, forming a land bridge that joins Britain to the rest of the continent. In many parts of the world, the emergence of such land bridges has a significant impact on animal diversity. The Sunda Shelf in Southeast Asia is one region that best illustrates the consequences of shifting land distribution brought on by frequent ice age cycles. This area provides important routes for species migration and diversification by joining the Asian mainland with the large western Indonesian islands of Borneo, Sumatra, and Java. The links between various landmasses are seen in the dark green regions shown in Figure 1.1. This graphic may help us understand how various locations could be connected when land bridges appear during periods of low sea levels.

The global sea level fluctuation chart shows that the ice ages have cyclically and predictably recurred about 25 times during the past two million years. What is more noteworthy, however, is that their amplitude has been increasing and their strength has been rising with each appearance. As a result, the way we currently view Indonesia is only a snapshot in time. Eighty-five percent of the time over the last two million years, the western part of Indonesian Archipelago has been linked to Asia. We just happen to live in this strange episode when these landmasses are not connected. I hope it's obvious what this means for the species that resided on the Sunda Shelf or Sundaland. But how have the

cyclical changes in sea level during the Pleistocene ice ages affected the biogeography and speciation of organisms in the Indonesian archipelago?

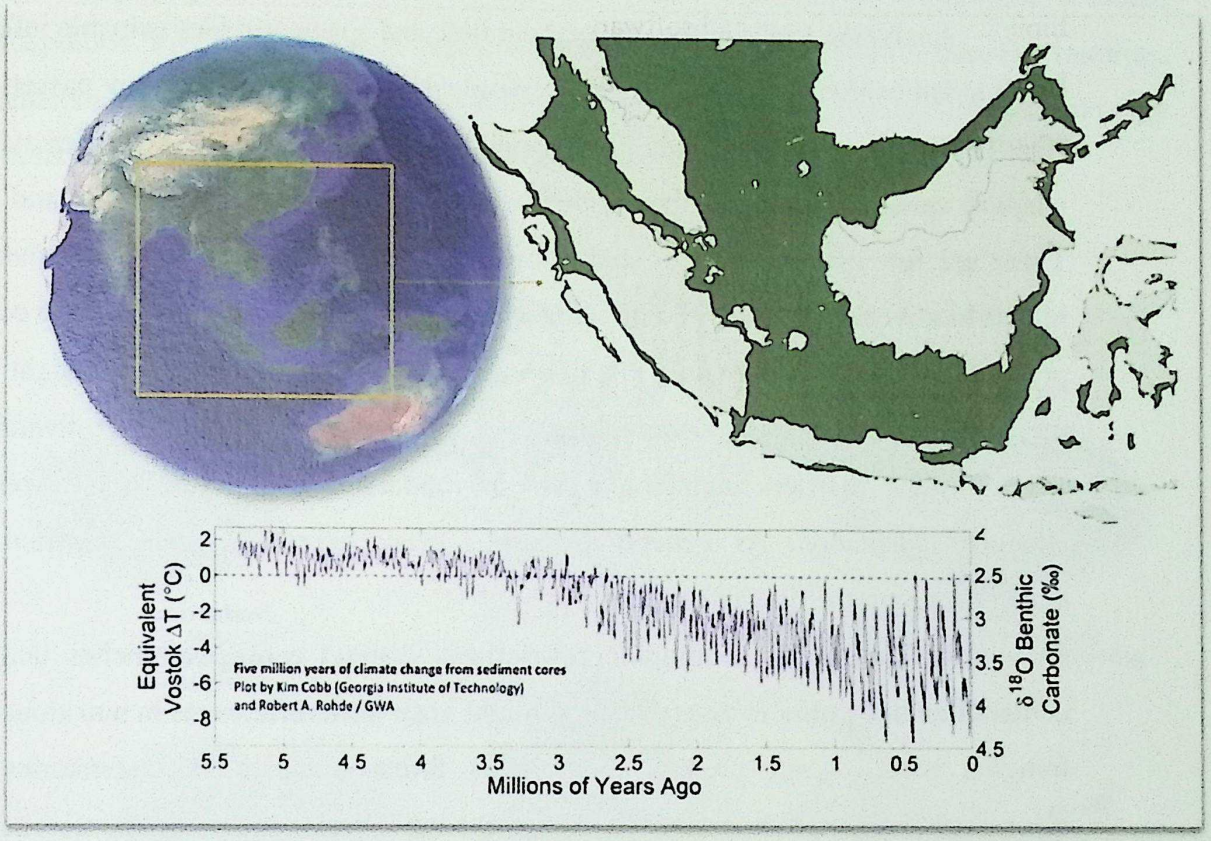

Figure 1.1. Southeast Asian land bridges and climatic oscillations over the past 5 million years.

The complex interactions among these bird populations reveal how geography and environmental changes shape their evolution. Earlier reviews of genetic introgression had already suggested that speciation with cyclical gene flow would have dominated diversification in Southeast Asia (Harrison & Larson, 2014; Het et. al 2019) and perhaps elsewhere prior to the introduction of next-generation sequencing (Rheindt & Edwards, 2011; Twyford & Ennos, 2012). Both expanding habitat belts and land bridges built during glacial phases might have enabled this. Leaf warblers are a prime example of a species which has experienced substantial divergence as a consequence to its natural environment. The number of recognized species has increased by 50% during the past three decades, with divergence times between sister species spanning 0.5 Mya to 6.1 Mya. Its radiation shows a monogeneric phylogeny, having the most recent common ancestor emerging 11.7 million years ago, and results in fewer taxonomic shifts than conventional classifications.

1.1.1. LEAF WARBLERS IN SPACE AND TIME

Analyzing leaf warblers throughout time and space provides valuable information about avian evolution, speciation, and ecological adaptability. These tiny passerine birds (family *Phylloscopidae*) provide a great model for understanding way species evolve and adapt to various settings because of their extensive range throughout Africa and Eurasia. There are few opportunities to study how speciation occurs and how the environment affects biodiversity because of their variances in morphology, vocalisations, and ecological preferences. One of the main goals of studying leaf warblers is to gain insight into the mechanisms of speciation. Geographical isolation is a major factor in their diversification since physical barriers including rivers or mountains that divide populations cause allopatric speciation. As genetic disparities grow over time, these isolated groups experience reproductive isolation.

In addition to geographic restrictions, distinct ecological niches that reduce competition and promote diversification might arise from differences in nutritional intake, foraging practices, or preferences towards forest canopies vs understories. Vocal divergence is another important consequence; song differences between species act as pre-mating barriers, sustaining reproductive isolation even in situations when species coexist geographically. Furthermore, temporal dynamics contribute to our understanding of leaf warblers' evolution. Molecular phylogenetics suggests that climatic changes such as glacial cycles were important in their development because they created new habitats and isolated populations. The narrative is made more challenging by hybridization occurrences. Closely related species can come into secondary contact after periods of seclusion, which may lead to gene flow, hybridization, or even a consolidation of formerly distinct species. Significant ecological restrictions or the colonization of new regions can occasionally result in fast speciation, demonstrating the dynamic nature of evolutionary processes.

Leaf warblers offer important biogeographical insights into their distribution patterns. Range expansions of these birds under favorable weather conditions and shrinking during unfavorable ones have an impact on their genetic diversity or population structure. Because co-occurring species often partition biological niches to reduce competition, numerous species can coexist in the same region. Furthermore, migration patterns play a

significant role in determining population connectivity and gene flow. By migrating over long distances between their breeding and wintering habitats—where environmental conditions play a role—many leaf warbler species demonstrate remarkable seasonal adaptation. Predicting changes in the climate depends significantly on this. For instance, understanding how leaf warblers respond to environmental changes can help predict range shifts and biodiversity loss due to global warming.

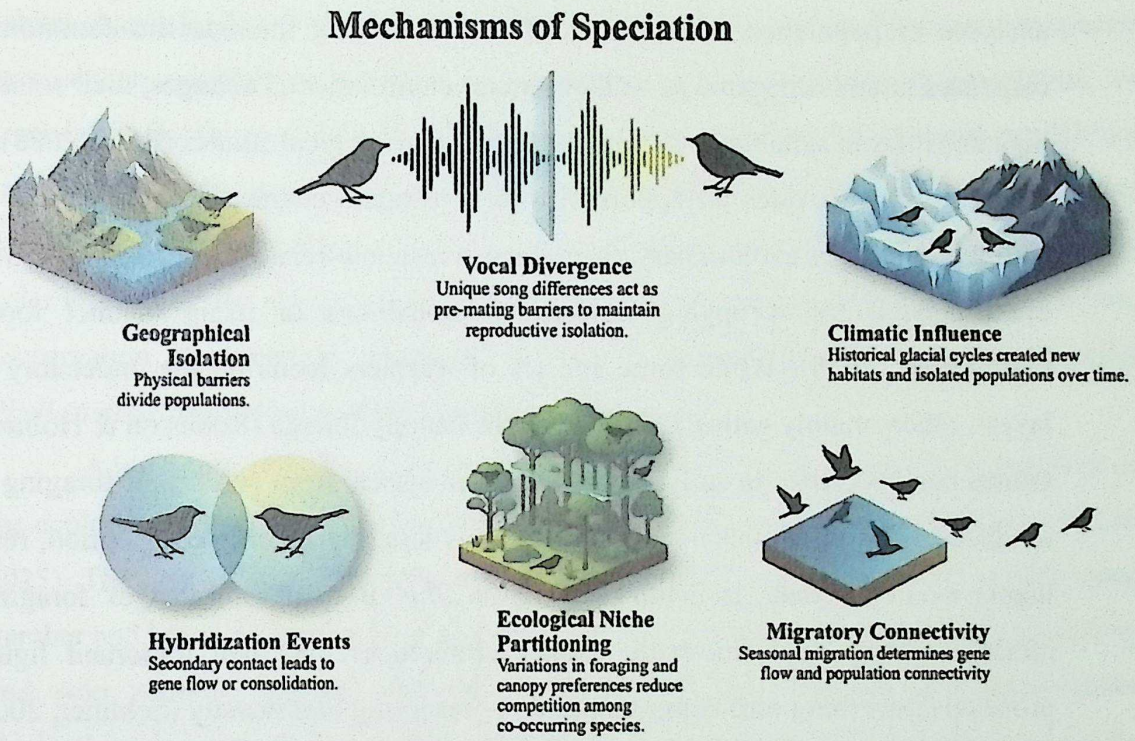

Figure 1.2. Mechanisms of Speciation

1.1.2. *PHYLLOSCOPUS* AS A MODEL

Genus *Phylloscopus* is renowned for its rich, well-documented natural history, wide range throughout Eurasia and Africa, and variety of ecological features. Because of their remarkable diversity in habitat use patterns, foraging techniques, migratory behaviors, and vocalisations, these small, predominantly insectivorous birds are essential for studying an extensive spectrum of ecological phenomena (Tietze, 2018). Furthermore, by in-depth analyses of population dynamics, relationships among interspecific communities, and responses to anthropogenic as well as natural environmental changes, their small size and high densities in suitable environments facilitate ecological studies (Price, 2008).

It also provides an opportunity to investigate character displacement, in which competition causes evolutionary divergence in resource-related features. Sympatric species often cohabit by occupying different microhabitats or using distinct food niches (MacArthur, 1958). While some species of warblers focus on the understory or shrub layers, others mainly gather insects from the canopy foliage (Robinson & Holmes, 1984). Others can specialize in sallying out to gather insects from perches or foraging from the air. Because of these niche variations, there is less interspecific competition, resulting in higher avian diversity. In-depth research on *Phylloscopus* assemblages' foraging habits, dietary makeup, and fine-scale habitat preferences has shed important light on the processes governing bird communities and preserving biodiversity (Schluter, 2000).

Another crucial area in which *Phylloscopus* is an outstanding model is avian migration. Numerous species in this genus migrate over great distances, often traveling thousands of kilometers between their breeding and wintering sites. A variety of environmental factors, like as climate, food availability, habitat quality, as well as prevailing wind patterns, influence the timing, routes, stopover locations, and overall strategies of these migrations (Alerstam & Hedenström, 1998). In order to carefully examine the migratory behaviors of *Phylloscopus* species, researchers are increasingly using sophisticated tracking technology like GPS loggers, geolocators, and sometimes stable isotope analyses. According to Liedvogel & Delmore (2018), these investigations have uncovered detailed migratory patterns, migratory connectedness, and the birds' reactions to environmental variables along the way. A further area of ecological

significance is the study of the physiological adaptations required for long-distance flying, such as fat storage and effective use of energy. Given the challenges posed by habitat loss, climate change, and other anthropogenic disruptions across their migratory pathways, an understanding of the migratory ecology in leaf warblers is therefore essential for effective conservation measures. Additionally, it provides unique opportunities to study how environmental change affects bird populations, which are useful bioindicators. They are useful for tracking the health of ecosystems because of their sensitivity to changes in habitat shape, food web dynamics, and climate factors. Numerous *Phylloscopus* species have shown population decreases as consequence of habitat loss, fragmentation, or degradation (Isaksson, 2018). The timing of migration, breeding, and resource availability are known to be disrupted by climate change, which may result in phenological mismatches that have a detrimental effect on survival and reproductive success (Trautmann, 2018). In order to evaluate the effects of environmental change on bird communities and to inform conservation management decisions, long-term monitoring studies which monitor *Phylloscopus* population provide important information.

Additionally, *Phylloscopus* species are being used more frequently in research on the ecology of avian diseases (Bensch et al. 2012; Hegemann et al. 2018; Weesner et al. 2025). They are possible hosts for a variety of parasites and diseases due to their great number and broad dispersion (LaPointe et al. 2012). In order to manage avian populations and stop zoonotic disease outbreaks, research on the incidence and transmission fluctuations in avian diseases within *Phylloscopus* populations provides insights into the variables influencing disease risk and dissemination. Furthermore, research on *Phylloscopus* immune function and disease resistance can help us better understand how environmental stresses impact bird health (Ishtiaq & Barve 2018). The study of bird vocalisations is another new field of ecological importance. Song is essential for attracting mates, defending territory, and identifying species. Changes in habitat, population size, and social milieu can all be reflected in variation in song structure (Catchpole & Slater, 2008). The evolution of bird communication, the function of sexual selection, and the consequences of noise pollution on avian vocalisations have all been better understood because of studies on *Phylloscopus* songs in the past. Gene flow and population structure can also be clarified by examining song dialects and their spatial variance.

1.2. OVERVIEW OF *PHYLLOSCOPUS* ECOLOGY AND DISTRIBUTION

Leaf warblers (genus *Phylloscopus*) are small insectivorous birds of the family *Phylloscopidae*, distributed widely across the Old World from Africa to Asia and Europe. The group has traditionally included the "typical" leaf warblers in genus *Phylloscopus* and the closely related "spectacled warblers" formerly placed in genus *Seicercus*. Leaf warblers are morphologically conservative but differ strongly in ecology, geographic range, vocalisations, and migratory behaviour, making them a useful system for studying biogeography and trait evolution. The marked taxonomic revision and expansion of this group over decades highlights the importance as a model lineage for investigating a plethora of concepts across the complex landscapes of Southeast Asia and Eurasia.

All the species in genus *Phylloscopus* can generally be categorized into complexes or groupings. The complexes or superspecies groups used in this study are: (1) *castaniceps* complex, (2) *davisoni* complex, (3) *cantator* superspecies group, (4) *borealis* superspecies group, (5) *tenellipes* superspecies group, (6) *collybita* superspecies group, (7) *fuscatus* superspecies group, (8) *burkii* complex, (9) *affinis* superspecies group, (10) *proregulus* superspecies group, and (11) *inornatus* complex. The distribution and habitat for the species are provided below.

***Phylloscopus castaniceps* complex**

There are now three species in this group, which have a reddish to chestnut colored head, undetectable coronal stripes placed laterally, and two prominent wing bars. Overall, these are mostly allopatric and are found from the center of the Himalayas to S China and throughout Southeast Asia to the Thai-Malay Peninsula, Sumatra, Borneo, Java, and Bali. *P. castaniceps* is distributed from the middle Himalayas to east & west Myanmar, south China, and as far east as the province of Fujian, where there are areas of subtropical to temperate montane forests (Martens 2010; also see Madge, 2020 for detailed distribution). *P. grammiceps* has a restricted range in the mountains of Sumatra (Madge et al., 2020), whereas *P. montis* is restricted to Borneo.

***Phylloscopus* (*davisoni*) superspecies group**

The *P. davisoni* species complex exhibits a classic Sino-Himalayan spread, extending from southwest and south China into Indochina and northward toward the Qinling region in Shaanxi. (Martens 2011). *P. hainanus* is endemic to China, and distribution is limited to Hainan Island, where it was widely dispersed in mountains surrounded by forest, although the area it can now grow in is extremely constrained (Martens 2010). *P. ogilviegranti* has a broad geographic range (mountains of NW Fujian and Guangxi, probably also N Guangdong) (del Hoyo et al. 2020) in East and Southeast Asia, and it represents the P. [*davisoni*] superspecies there (Martens 2010). *P. xanthoschistos* is a relatively common species distributed across the western Himalayas (northwest Pakistan to Kashmir, Nepal and southeast Tibet) (Madge 2020).

***Phylloscopus* (*cantator*) superspecies group**

Three taxa that appear to be closely related to one another are allotropically distributed in northern Indochina (*P. calciatilis*), large portions of China south of Qin Ling region, and disjunctly in northern Laos (*P. cantator*) and the eastern part of the Himalayan chain (Martens 2010). *P. cantator* is distributed east of the Arun Valley in eastern Nepal, are the southern foothills of the Himalayan range, as well as in Manipur and Myanmar (Martens 2010; also see Clement 2020 for detailed distribution). *P. calciatilis* inhabits limestone karst zones of North and Central Vietnam, North and Central Laos, as well as extreme South China (Guangxi) (Fjeldså 2020). The breeding distribution of *P. ricketii* is from south Gansu and Sichuan to Hubei and Fujian, south to Guizhou, north Guangxi, and east Guangdong, spanning central, south, and east China.

***Phylloscopus* (*borealis*) superspecies group**

Having among the largest breeding ranges of any *Phylloscopus* species, *P. borealis* can be found in northern Europe, the Siberian taiga region, Mongolia, all of Japan, as well as Alaska. A detailed distribution based on extensive work by Chrabryj et al. (1991) - Cramp (1992) as well as Lowther (2001) is presented in Alström et al. (2011). *P. borealis* and *P. examinandus* may meet at some point near central/northern Kamchatka. Currently known breeding distribution of *P. examinandus* extends from northeastern Russia, Sakhalin, the Kuril Islands, and Hokkaido in North Japan (del Hoyo et al. 2020). *P.*

xanthodryas is distributed across the main islands of Japan south of Kyushu, but at least excluding north Hokkaido.

***Phylloscopus* (*tenellipes*) superspecies group**

Distribution of *P. tenellipes* was known to be confined to the basins of the lower Amur & Ussuri Rivers in southeast Siberia, as indicated by Martens (2010). However, the breeding distribution known currently extends from southeast Russia to extreme northeast China and North Korea (Clement 2020). The distribution of *P. coronatus* is split into two disjunctive parts, with one along Amurland/Ussuriland (Martens 2010), the Korean peninsula, north-eastern China (to near Beijing), and the islands of Japan (Ornithological Society of Japan 2000). The other one spread across Sichuan (Cheng 1987) and Chongqing (Clement, 2020). *P. ijimae* is confined to Nakanoshima in the Tokara group, southwest of Kyushu, and eight kilometres from the Izu Islands of Japan (Ornithological Society of Japan 2000). (Martens 2010, Clement 2020). *P. magnirostris* is distributed from Pakistan and Kashmir into hilly SW China, where it was found in Yunnan, Sichuan, Gansu, Shaanxi, and Qinghai (Cheng 1987). The species was widely dispersed along the Himalayan chain (Ali & Ripley 1973; Bates & Lowther 1952; Roberts 1992). The distribution of *P. borealoides* is restricted to the southern region of Sakhalin, the major Japanese islands of Honshu, Hokkaido, and Shikoku, as well as the greater islands in the Kurils, of which the type locality is Kunashir.

***Phylloscopus* (*collybita*) superspecies group**

The superspecies comprises *P. collybita* sensu lato, extending over the Palearctic from the Canary Islands and nearly all of Europe and north Asia to east Siberia (Martens 2010). The range of nominate *P. sindianus* is the most remote and disjunct one of all Asian representatives of the *P.* [*collybita*] complex: the barren, high-altitude region north of the main Himalayan range and the Karakoram range (Ali & Ripley 1973, Roberts 1992, author's observation) is known to breed in semi-arid mountain valleys up to 4400 m and between 100 and 1200 m in the west Caucasus (Clement 2020). *P. neglectus* inhabits dry areas of West Asia, from the west Iranian Alborz mountains eastwards to NW Pakistan (Martens 2010), breeding between 2400 and 4200. (Clement & Kirwan, 2020).

***Phylloscopus* (*fuscatus*) superspecies group**

From distributional data, Martens et al. (2008) proposed that two central Asian taxa, namely *P. fuscatus* and *P. fuligiventer,* be united as a superspecies. These species breed mainly in high-altitude open and bushy habitats above the timberline of SE Tibet, the eastern Himalayas, and in W China and also within the upper forest belt (Martens 2010). The distribution of this complex is Sino-Himalayan, with a large, disjunct northern taiga part in Siberia in *P. fuscatus* but not in *P. fuligiventer*, which is exclusively Sino-Himalayan (Martens 2011).

***Phylloscopus burkii* complex**

Traditional polytypic *P. burkii* emerged as a group of closely related species which experienced a complicated evolutionary process, leading to both vicariance and regional sympatry across the Sino-Himalayan region (Alström and Olsson, 1999; Martens 1999; Packert 2004, 2016). Up to four (*P. tephrocephalus*, *P. soror*, *P. omeiensis* and *P. valentini*) of the eight (Alström et al. 2018 and references therein) currently recognised species of this complex are syntopic and almost entirely separated altitudinally (also evident from Alström 2006; Packert et al. 2004) with earlier references from middle and upper Chinese mountain belts.

There are additional references that indicate that during the breeding season, at least three have been observed in a single forested edge and deteriorated secondary forest (see Martens 2003, 2011). In contrast, *P. whistleri* inhabits a consistent mountain belt in the Himalayas at the same altitudinal range between 2300 and 3800 m (Packert et al., 2004). The nominate *P. intermedius* is distributed along the mountains of southern China (NW Fujian) and is said to winter in southwest China and Indochina (Alström, 2020). The current distribution of *P. poliogenys* extends from the eastern Himalayas, from central Nepal to northeast India and neighbouring parts of north Myanmar and south China (south Yunnan); also, south Nagaland to Mizoram and Meghalaya with north Thailand, Laos, and Vietnam (Alström 2020). *P. burkii* breeds in the Himalayas, with its range extending from east Himachal Pradesh to south China (southeast Xizang) (Alström 2020).

***Phylloscopus* (*affinis*) superspecies group**

The area of *P. affinis* sensu lato stretches all over the Himalayas and the mountainous areas of southwest China, including parts of east Qinghai, but the high-altitude Tibetan plateau is uninhabited (Vietinghoff-Scheel 1986). Throughout its area, the members of the affinis complex live in mountainous open bush and forest edges at high altitudes, and this also holds for *P. griseolus* in Central Asia. All taxa of this group are mainly allopatric, but *P. griseolus* is believed to overlap with *P. affinis* in the westernmost parts of the Himalayas and the Karakoram (Roberts 1992). Their areas embrace the Tibetan plateau, including *P. griseolus*, which also thrives as far as southwest Siberia (Loskot and Vietinghoff-Scheel 1991). The whole complex thus, may have undergone the same north Palearctic–Sino-Himalayan diversification pattern as the truly arboreal species (Martens 2011). The breeding distribution of *P. subaffinis* extends throughout central, south & southeast China (southeast Qinghai east to south Shaanxi, Jiangxi, and Fujian; south to north & east Yunnan; south Guangxi; and north & east Guangdong) and north Vietnam (west Tonkin) (Clement 2020). *P. armandii* inhabits the regions of southeastern Mongolia and southwestern Jilin, south to east Qinghai, east Xizang, and west Sichuan in central and northeast China (Clement 2020). *P. pulcher* inhabits a relatively large area stretched from Nepal to Tibet, southwest China and north Myanmar (Martens 2010) and *P. maculipennis* can be found along the Himalayan range, except the westernmost portion, before moving north to Yunnan and Sichuan (Cheng 1987) and south to Indochina (Martens 2010).

***Phylloscopus* (*proregulus*) superspecies group**

This superspecies has a typical Sino-Himalayan distribution, with an eastward extension into the Qinling range; the distribution has a large, disjunct northern Siberian part (Martens 2011). *P. proregulus* is restricted to the taiga zone from the Urals to NE China (Cheng 1987; Sokolow & Vietinghoff-Scheel 1988; Duckworth 2009; Duckworth & Moores, 2008) and Korea, while *P. kansuensis* has a restricted range in central China (northeast Qinghai, southwest Gansu) (Alström 2020). *P. forresti* is possibly distributed across west and north Myanmar as well as south-central China (east Xizang east to south Shaanxi, south to Yunnan, and west Sichuan) (del Hoyo, 2020). The breeding range of *P. chloronotus* extends throughout the central and eastern Himalayas (Alström & Christie, 2020). The distribution of *P. yunnanensis* extends over a sizable area through Sichuan,

Gansu, Shaanxi, Shanxi, and Hebei provinces (in part) (Alström et al. 1992, Martens 2000a), while *P. subviridis* occupies only a little portion of the Himalayas in the west and a few distant mountains in Afghanistan (Paludan 1959), which constitute the entire region (Martens 2010).

***Phylloscopus inornatus* complex**

P. inornatus breeds throughout northern Russia from the middle and upper right Pechora and Urals east to East Siberia (right Anadyr area and Sea of Okhotsk), south to northeast Altai, north to north Mongolia, the Baikal Mountains, northeast to northeast China, and potentially north to north Korea (Clement 2020). *P. humei* is distributed throughout south central Russia, northwest China and Tien Shan to northeast Afghanistan and Kashmir, extending east through the Himalayas to south Bhutan and northeast India (Clement 2020).

***Phylloscopus trochiloides* complex**

P. trochiloides is distributed overall trans-Palearctic, extending from central Europe eastward through the taiga belt to central Siberia, until it coincides with *P. plumbeitarsus*, and then completely encircling the Tibetan plateau except for a break in northern China brought on by local deserts (Martens 2010). *P. plumbeitarsus* reaches the Pacific coast via East Siberia's Sayan Mountains, the taiga area, N Mongolia, and Heilongjiang province in far northeast China (Cheng 1987). *P. nitidus* is common throughout northern Turkey, north Iran (Elburz Mountains), northern Georgia, the northern Caucasus, and perhaps northwestern & central Afghanistan and southwest Pakistan (Baluchistan) (Clement & Sharpe, 2020).

1.3. INTEGRATING BIOGEOGRAPHY, SPECIES TURNOVER MORPHOLOGY, AND VOCALISATION

Four complementary viewpoints are integrated in this work. Different questions that each chapter addresses come together to form a cohesive story that links evolutionary history, contemporary compositions, and behavioral divergence. Time is the initial layer of our research. The genus *Phylloscopus*, which is distributed throughout greater Eurasia and Africa, is used as a starting point with deep evolutionary eras. Their journeys are influenced by glacial cycles, land bridges, constantly shifting resources, and geography. It allows one to identify patterns of migration or residency across the clade by reconstructing the ancestral ranges. Migratory and sedentary states are unlikely to be distributed randomly across lineages, but it may reflect phylogenetic history, environmental filtering, and ecological opportunity. Morphology or breeding biology were examples of factors that operated as levers, pushing species to make choices. In this research, our primary objective was to determine the origins of warblers and the characteristics they inherited. We apply this historical viewpoint to the present day through examining community structures with compositional turnover patterns and their respective drivers. The second objective therefore focuses on understanding how breeding-ground communities are structured across space. It tests whether compositional turnover among *Phylloscopus* assemblages reflect ecological dynamics within breeding grounds and whether co-occurrence is constrained by any environmental factors. The framework helps identify the historical, ecological and environmental factors which structure spatial overlap among species across heterogeneous landscapes. While some groups/complexes split into more specific endemics, others share a core of widespread species while accepting regional specialties. Snow cover, soil moisture, and terrain all function as quiet levers that determine which species persist therein. Anthropogenic factors, such as night lights or aerosols, create unique flair to this, yet the communities still assemble and dissolve. Where morphological species occur in sympatry or secondary contact, divergent acoustic signals may facilitate species recognition and reduce reproductive interference. In order to understand signal transmission, we pick one such set of sibling species and investigate whether song divergence is an evolutionary process or an acoustic adaptation to habitats. Thus, acoustic

signal structure is shaped not only by physical constraints on production of sound and its transmission, but also by selection on species recognition. In order to preserve reproductive isolation, sympatric species typically modify their songs in a variety of ways. Lastly, the human eye finds it just as difficult to distinguish between birds as it is for them to keep their identities. Eventually, these misidentifications find their way into public domains, where the majority of current research is conducted. We constructed a deep learning model using YOLOv5 as a filter to distinguish cryptic species in order to reduce this misidentification bias.

1.4. RESEARCH OBJECTIVES AND HYPOTHESIS

(i) To reconstruct the ancestral ranges, and understand the evolution of migration and associated life history traits in *Phylloscopus* warblers.

Hypothesis: *Phylloscopus* originated in the Indian/Indo-Chinese region and diversified with frequent jump dispersal events. Migration evolved with shifts into temperate breeding grounds, with morphological and life-history traits jointly shaping the evolution.

(ii) To understand the patterns and drivers of compositional turnover

Hypothesis: Patterns of diversity, ζ-decay, and the retention rates reflect ecological dynamics within breeding grounds and constraints on co-occurrence of species. These co-occurrences are influenced by environmental factors that influence productivity.

(iii) To understand relative roles of ecological adaptation, and phylogenetic constraint in shaping song divergence among morphologically cryptic complexes.

Hypothesis: Sympatric species exhibit distinct song traits, and the structure varies predictably with habitat characteristics and elevation.

(iv) To develop and evaluate an automated image-based identification framework for reliably distinguishing cryptic *Phylloscopus* species.

Hypothesis: In-natural-setting photographs can yield statistically accurate identification of co-occurring, visually similar species.

CHAPTER 2. LITERATURE REVIEW

2.1. Biogeography of Leaf Warblers

Genus *Phylloscopus* (Old-World leaf warblers) provides us an exceptional opportunity to study diversification, community structure, vocal adaptations, and applied science like biodiversity monitoring. The genus contains nearly 77 to 78 species, spanning Asia, Europe, and Afrotropics, and have undergone serious taxonomic revisions over the past two decades (Alström et al. 2018). While exploration on radiation and speciation processes of the groups has been attempted, major gaps remain in our understanding of biogeographic histories, ecological drivers of current assemblages, and the role of habitats in modulations in vocalisations.

2.1.1. Key studies on Phylloscopus dispersal, speciation, and range shifts.

Studies of genus *Phylloscopus* have treated biogeography superficially, with more general descriptive narratives of distribution and dispersal patterns, and are restricted to fewer hotspots, e.g., the Himalayas (Johansson et al. 2007). These studies were based on limited data and methods. For instance, the standalone biogeographic study for this genus used a handful of mitochondrial and nuclear markers to reconstruct the phylogenetic relationships, applying dispersal-vicariance models to infer ancestral states. The resolution seems coarse, in part due to the limitations on data and geographic zones used. However, more recent probabilistic reconstructions explicitly map the roles of anagenetic events, as well as cladogenetic events (Matzke 2013). Can such models truly capture the details of montane dispersals in a genus that is so finely tuned to habitats and elevation?

Subsequent works have increasingly highlighted the roles of jump dispersals in maintaining diversity across various taxa (see Heads 2012). BioGeoBEARS (Matzke 2013) formalised this process, allowing us to test if jump dispersal explains the distribution more than vicariance. For genus *Phylloscopus*, models with jump dispersal parameters may outperform those without it, suggesting jump dispersal into new areas crossing geographical barriers, with substantially rapid speciation. This again raises a much deeper conceptual question. Are *Phylloscopus* warblers' serial colonisers, dispersing from their original cradle in Southeast Asia, or are they fragmented by constant waning and waxing

of Eurasian forests throughout cyclically occurring climatic oscillations? The answer may be either of these two, or both, depending on the timeline.

2.1.2. What can we make from ancestral ranges?

Reconstructing ancestral states for this genus is not merely an academic exercise. It also speaks of the most foundational debates, such as whether tropical Asia serves as a museum for preserving ancient lineages (Price 2010). The most recently constructed complete phylogeny (Alström et al. 2018) offers an unprecedented resolution, with two major clades: (i) radiating across temperate Eurasian regions and (ii) concentrated in Southeast Asia. However, the issue is that Southeast Asia can include the Himalayas as well as a few regions from the Siberian subregion, each with numerous geographical gradients and ecological barriers. It would not be correct to merely interpret that the ancestor of a particular species (say *trochiloides*) was Southeast Asian, especially when its present-day distributions are tied to narrow montane belts.

Not only the ranges, but these reconstructions always intersect with questions related to the evolution of migration. If these species began in the tropics, then the shifts towards temperate grounds (especially breeding warblers) could have been driven by repeated evolution of migration throughout the tree (Nagy & Tökölyi 2014). This can also be viewed with a contrasting perspective. If temperate origins are more likely, tropical residency should represent the loss of migration. There is multiple evidence available that suggests the former scenario (Winger 2012; Sheard et al. 2020). But are we too quick to assume and agree on this unidirectionality? It might also be the case that a few lineages lost migration capabilities and later re-evolved. However, these queries are not trivial because the answer can only shape our interpretations of dispersal and diversification in the past, as well as future responses to global change. Out of all this, the best picture that emerges is the one of repeated contraction and expansion of ranges, their dispersal histories based on these dynamics, and finally migratory adaptations layered atop dispersal. With *Phylloscopus*, as we refine our models, we might question what dispersal stories are remaining latent behind our reconstructed coarse polygons.

2.2. Compositional Turnover in Avian Communities

The diversification and historical dispersals, as reviewed above, highlight the evolutionary backdrop for the ground day compositions. However, the past cannot solely dictate the ecological role. Species compete, replace each other, co-occur, or vanish from local assemblages, moderated by environmental filtering. If jump dispersals or range shifts decide where species occur, what exactly determines which species persist/co-occur in the same community today?

2.2.1. Metrics (diversity indices), drivers (climate, habitat fragmentation).

Community ecology has been specifically attributed to quantifying how assemblages vary across space. Traditional metrics like Jaccard's or Sorensen's indices of β diversity capture pairwise dissimilarity but often conflate turnovers shaped by nestedness with turnovers highly driven by replacements (Baselga 2010). But in the genus, such as *Phylloscopus*, some species are narrowly restricted endemics, while others are widespread generalists. This distinction really matters, as we may raise a question: Is the Himalayan region species-poor simply because it loses taxa more quickly than in other regions? Or because an entire new set of species is present there?

To overcome these limitations of pairwise comparisons, zeta diversity was proposed (Hui and McGeoch, 2014) to measure the number of species shared within any number of sites. Unlike traditional metrics, zeta diversity offers multi-site analysis that distinguishes the contribution of rare vs. widespread species. This method was later extended to multi-site generalised dissimilarity modeling (MSGDM; Latombe et al. 2018), linking zeta diversity to a set of environmental gradients such as climatic, topographic, or anthropogenic factors. These tools take us to address another possibility: to argue if *Phylloscopus* communities are primarily structured due to climatic envelopes or much finer-scaled filters related to habitats. Empirical work mostly suggests both. Especially in the Himalayas, we have sharp elevational turnover, where lowland species drop rapidly and are replaced by mid-elevation specialists (Price et al. 2011). However, if we examine the continental trend, turnover mostly correlates with precipitation and temperature regimes (Sekercioglu et al. 2004). Fragmentation further adds another layer in Southeast Asian regions, leading to isolation and higher turnover rates.

2.2.2. The factor of compositional decay

It is crucial to interpret the patterns suggested by models with caution when speaking of global trends. If attributed to our study species, zeta diversity may exhibit a consistent pattern of composition decay relative to the number of sites we will use. As more sites are considered, the proportion of the species shared between them will obviously decrease, and sometimes precipitously (Hui and McGeoch, 2014). Practically, it means that range-restricted or rare taxa will exert a disproportionate influence on the pattern of turnover. For example, species like *soror* or *omeiensis* would contribute largely to the decay rates, whereas widespread generalists like *trochiloides* would not. There can be many asymmetries within a single group. Also, the drivers of this decay go beyond broad climatic categories in the present world. Aerosol content (Sanderfoot and Gardner 2021) associated with fire regimes (Engstrom 2010), and even geophysical factors like gravitational anomalies (Mills et al. 2019), have been suggested as understudied factors for community structure. Canopy and understory strongly influence the species composition (Martens et al. 2011), yet most analyses have often ignored these variables, instead relying on temperature and precipitation averages. But from an evolutionary perspective, the patterns of turnover may feed back into the diversification.

2.3. Bioacoustics and Evolutionary Ecology

The turnover patterns mentioned above highlight how species sort themselves, yet, this is not just environmental or habitat partitioning; they must also recognise themselves with overlapping ranges or shared habitats. Where the ranges overlap and the plumage is cryptic, acoustic signals become the flagbearers for reproductive isolation. If dispersal sets up the foundation and turnover define the pillars, then songs (plastic, learned, or phylogenetically constrained?) are the walls that determine if species remain different or diffuse into each other.

2.3.1. The learned language.

Song is generally a learned behaviour in most avian groups, either acquired by social interaction or predisposition of genes (Catchpole & Slater 2008). In species where visual cues are very subtle, songs function as species identifiers or mate attractants

(Martens et al. 2003). Two hypotheses go well with these traits. The acoustic adaptation hypothesis (AAH) posits habitat or environmental constraints select for signals that maximize the efficiency of transmission (Rothstein & Fleischer 1987). Contrastingly, the species recognition hypothesis (SRH) suggests that vocal divergence in sympatric species minimises the risk of hybridisation (Saetre et al. 1997). However, acoustic divergence may also be shaped by interspecific competition, particularly where closely related species overlap in space, use similar acoustic channels, or compete for territories, ecological resources, and mates. To understand this duality, we are focusing on species belonging to the *Phylloscopus burkii* complex. Rhus the AAH/SRH framework should not be treated as a strict two-way contrast as habitat filtering, competitive interactions and reproductive isolation can act simultaneously on different components of the same signal. Across elevational gradients, temporal characteristics of songs generally show phylogenetic conservatism, while spectral traits differ in response to habitats (Martens et al. 2011). We are still unsure if it implies the temporal characters account for species recognition in the form of phylogenetic signatures, or spectral characters offer ecological tuning. Competition provides the third possibility, where some songs converge or diverge depending on whether selection favours reduced acoustic interference, heterospecific aggression, or more effective territory signaling. If this is the case, we may begin to examine how the same signal can carry out both functions.

2.3.2. Genetic divergence, plasticity, and adaptation.

Plasticity allows species to modulate their songs in response to local factors (Slabbekoorn & Smith. 2002). This definitely enhances transmission but may also diffuse species boundaries. The balance between genetic divergence and acoustic plasticity is delicate, where too little divergence may lead to hybridisation, and too much variation may falter species communication. In *Phylloscopus*, the Himalayan contact zones reveal sharp vocal differences despite morphological similarity, yet regional dialects have emerged (Singh and Price 2024). Meta-analysis has also revealed mixed evidence for predictability in song divergence driven by habitat (Boncoraglio & Saino, 2007; Freitas 2025). However, an important lookout is not only that habitats always mediate acoustic properties but also that evolutionary history plays a part in clade-specific ways.

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2.3.3. Where to expect more divergence?

If the divergence is strong where species have overlapping ranges, then these sympatric zones must play a major role in acoustic evolution. Sympatry is common in *Phylloscopus*, where elevational overlap has often forced multiple congeners into acoustic contact, especially in the Sino-Himalayan ranges. In this region, divergence can also be predicted with syntax, as it can be predicted with frequency. Even the reinforcement theory has suggested the selection against hybridisation has sharpened the differences within these zones (Pfenning & Pfenning 2010). But we do not know how consistent this pattern is. Could some divergences (which we often attribute to reinforcement) simply reflect stochastic processes for learned traits? These questions will remain open, but they will always point to the value of integrating genomic measures to acoustic variability.

2.4. Machine Learning in Ornithology

The difficulty of distinguishing these closely related sympatric species by acoustic traits naturally extends to a methodological question. How can researchers, with these millions of observations from public domains, reliably understand true signals from misidentifications and background noise? These domains often rely on expert knowledge, but the surge of data points, especially from domains like eBird, has far outstripped the capacity of experts to validate these records. In light of this, machine learning (ML) has emerged as a technological novelty and a partner to challenge traditional expertise.

2.4.1. Applications of machine learning in avian studies.

Computer vision, deep learning, and particularly convolutional neural networks have significantly transformed the tasks for image classification. In ornithological research, the YOLO object detection model (Redmon et al. 2016) possesses the ability for real-time classification. The model processes the images while simultaneously considering class probabilities and predicting bounding boxes, allowing it to identify the species photographed in challenging field conditions. YOLO builds on these challenges by implementing the hyperparameter evolution and model ensembles, achieving robust performance (Tan et al. 2022).

The application of these models is diverse in the field of ecology and was earlier used in the classification of mammals (Tan et al. 2022), amphibians (Takaya et al. 2023), reptiles (Pandey et al. 2020), and also birds (Ou et al. 2020; Liao and Tian 2021). For *Phylloscopus*, where species are too difficult to identify by plumage alone, these models offer the possibility of accounting for subtle traits like supercilium length, wing bar thickness, eye rings, etc. that may elude trained observers too.

2.4.2. Have we sidelined avian ecology?

Despite such advances, the prominence of machine learning also prompts a reflection on the risk of sidelining ecological questions. Much of the literature relevant to machine learning has often celebrated performance metrics but has not addressed how these models inform the understanding of behaviour, community dynamics, or habitat use. For *Phylloscopus*, it is undoubtedly valuable, but what are the ecological insights that it provides? There can be many disagreements, and hence, integrating machine learning with ecological theory is of paramount importance. A promising avenue to do that is explainable AI, which highlights features such as morphological traits that drive the decisions for classification (Molnar 2020). After aligning the features with an evolutionary or ecological hypothesis, it can quickly be modified from a black box to a tool to test theory. Even this would trigger a philosophical debate, as the field of ornithology has long relied on human skills, which are honed by long observations. These debates, however, should not emphasise the replacement of field expertise but how both can complement each other. While this literature review attempts the synthesis of broad perspectives on biogeography, compositional turnover, vocalisations and morphology, a deeper engagement with each theme is developed and presented in the respective data chapters (Chapters 3,4,5 and 6) that follow.

CHAPTER 3. ANCESTRAL RANGES AND EVOLUTION OF MIGRATION

3.1. INTRODUCTION

Understanding how migratory behaviour, life history traits, and geographic ranges co-evolve is a central goal, as repeated losses or gains in migratory behaviour have played a major role in shaping global passerine diversity (Fjeldså 2013). Phylogenetic approaches, which integrate ancestral distribution ranges and allow us to determine shared or differentiated life history / behavioural traits, provide a powerful framework for studying passerine biogeography and evolution (Barker et al. 2015; Oliveros et al. 2019; Nagy 2020). Although species concepts (Alström 2004), and both speciation and adaptive radiation (Gaston 1974; Price et al. 1998; Martens et al. 2004; Olsson et al., 2005; Price 2010) have received considerable attention, their biogeographic history (Johansson et al. 2007), ecological divergence (Forstmeier et al. 2001), and the evolution of life history traits (Martens 2010) remain poorly understood. Most studies have either addressed the effect of these aspects on isolation or focused on a limited subset of species.

Old World leaf warblers (genus *Phylloscopus*) represent an exceptional model for examining these broader processes. The recently established complete species-level phylogeny of *Phylloscopus* (Alström et al. 2018) provides a unique opportunity to use this clade for testing general hypotheses about the evolutionary origin of migration and the biogeographic history of all passerines. The biogeographic history of *Phylloscopus* leaf warblers was investigated by Johansson et al. (2007) who examined the emergence of the Himalayan avifauna. Their study provided valuable insights, using multiple genes (cytochrome b, 12S ribosomal RNA, and nuclear myoglobin intron 2 sequences) for 55 species (Johansson et al. 2007), and applying anagenetic dispersal-vicariance (DIVA) model (Crisp et al. 2011) on well-defined biogeographic regions. Based on these foundations, a recent phylogeny available for more than 75 leaf warbler species (Alström et al. 2018), together with newly developed methods for modeling historical biogeographic patterns (Matzke 2013), including greater balance between dispersal and vicariance (De

Queiroz 2005) and consideration of cladogenetic events (Ree et al. 2005), allow us to more comprehensively study the genus. Furthermore, recent biogeographic regionalisations (Morrone & Ebach 2022) delineate spatial units at finer resolution and explicitly recognise transition zones between major biogeographic regions.

Within this framework, investigating correlated evolutionary changes between migratory strategy (sedentary vs. migratory) and latitudinal distribution (tropical vs. temperate) is also possible (Nagy & Tökölyi 2014). Such transitions often coincide with shifts in seasonality, which may further impose selection pressures on migratory behaviour. Pertinently, birds breeding in the temperate zone, which experiences greater seasonality than their tropical counterparts (Parab et al. 2025), have evolved migratory behaviour to track seasonal peaks in food availability, whilst tropical sedentary species experience relatively constant resources throughout the year (Şekercioğlu et al. 2012).

Multiple hypotheses have been proposed to explain the origin of migration, suggesting that it emerged either in tropical ancestors with subsequent poleward expansion (southern home hypothesis), or in temperate ancestors that later expanded their wintering ranges towards the tropics (northern home hypothesis) (Salewski & Bruderer, 2007; Somveille et al. 2018; Winger et al. 2019). An alternative model emphasized the role of climate-related changes in species distributions in the origin of migratory behaviour (Louchart 2008). Consequently, migration is undoubtedly an evolutionary flexible trait due to numerous examples of independent losses or gains of migratory behaviour in various avian families (Winger et al. 2012).

Phylloscopus leaf warblers contain some species that are sedentary and other species that are long-distance migrants and are, therefore, an appropriate group in which to examine the relationship between historical dispersal, and the gain or loss of migration. Considering *Phylloscopus*, while the exact ancestral latitudinal positions of breeding ranges remain uncertain, the widespread present-day breeding distributions across temperate and tropical regions, combined with their phylogenetic relationships, suggest that multiple latitudinal shifts have occurred during the evolution of the genus (Price et al. 1997). Bird species that migrate exhibit morphological adaptations, such as having pointed wings to improve their flight efficiency (Hickman et al. 2008; Sheard et al. 2020). Meanwhile, species occurring at higher elevations evade adverse weather conditions

during the winter months by migrating to lower elevations (Boyle 2017) or warmer regions of the planet (Winger et al. 2019) to inhabit areas with an abundant food supply. In addition, migratory distances between the breeding and wintering grounds are often negatively correlated with the length of the breeding season (Winger & Pegan, 2021), suggesting trade-offs between migratory investment and reproductive timing. However, the importance of life history versus ecological factors in explaining the evolution of migratory behaviour requires further research attention (Bitterlin & Buskirk, 2014).

Here, we examine the historical and ecological processes that have shaped migration in the *Phylloscopus* leaf warblers. Specifically, we examine: (i) where and how *Phylloscopus* leaf warblers originated, proposing that the initial diversification and dispersal from Southeast Asia has shaped their present distribution across Eurasia and the Afrotropics, (ii) if shifts in temperate and tropical regions are coupled to the gain or loss of migration, so species shifting to temperate breeding grounds are more likely to have evolved to migrate compared to their tropical counterparts; (iii) whether life history traits are closely linked to the evolution of migration, hypothesising a role of seasonality, elevation, morphology, and fecundity trade-offs; and (iv) whether migratory and resident species significantly differ in their present climatic niches. Finally, we ask whether partial and complete migrants occupy climatic conditions equivalent to those used by resident species, or whether migrants occupy a distinct subset of climate space.

3.2. MATERIALS AND METHODS

3.2.1. Biogeographic Data and Classification

We obtained breeding range data from Birds of the World (*www.birdsoftheworld.org*) and BirdLife International (2023), and the most recent complete species-level phylogeny of 73 unique *Phylloscopus* leaf warbler species from Alström et al. (2018). While most of the taxa was treated at the species level, two operational taxonomic units (OTUs) were included as subspecies (*fuligiventer weigoldi* and *whistleri nemoralis*). Specifically, *fuligiventer fuligiventer* and *fuligiventer weigoldi* show a west-east geographic segregation across mountainous regions of Himalayas and south China, while *whistleri whistleri* and *whistleri nemoralis* are largely separated along latitudinal and elevational gradients across Himalayan regions. Following Morrone and Ebach (2022), each species was assigned to one of the following biogeographic regions: (A) the Afrotropics, (B) the Saharo-Arabian Transition Zone, (C) the Indo-Malayan Transition Zone, (D) the European Subregion, (E) the Siberian Subregion, (F) the Chinese Transition Zone, (G) the Indo-Chinese Subregion, (H) the Indian Subregion, and (I) the Mediterranean Subregion. Considering possible barriers (such as the Qinghai Tibet Plateau) and corridors (such as the Sino-Himalayan corridor) pertinent to biotic dispersal (Morrone 2024), transition zones were explicitly included to represent the regions where historical connectivity may have facilitated biotic exchange (Böhme et al. 2021; Wang et al. 2022; Markowska et al. 2025).

3.2.2. Ancestral Range Estimation

We modeled biogeographic processes and estimated ancestral ranges using the R package *BioGeoBEARS* (Matzke 2013). Dispersal Extinction Cladogenesis (DEC) (Ree et al. 2005, Ree & Smith 2008), Dispersal-Vicariance (DIVA) (Ronquist 1997), and the BayArea model (Landis et al. 2013), each in combination with a jump dispersal parameter *j*, were the six alternative models fitted to the data. The three fundamental models (DEC, DIVA, and BayArea) consider sympatric and vicariant speciation in distinct ways, though they all consider dispersal, extinction, sympatric speciation, and vicariance as mechanisms of range shifts. While vicariance is limited to narrow-scale events, the DEC-like model

allows narrow-scale and subset sympatric speciation. In addition, the DIVA-like model permits both narrow and widespread vicariance, as well as narrow-scale sympatry. In contrast, the BayArea model omits vicariance completely and focuses on sympatric speciation, over both restricted and widespread scales (Matzke 2013). These differences influence how each model reconstructs the biogeographical history of the *Phylloscopus* leaf warblers, thereby influencing perceptions of the relative frequency of new lineages arising from geographic division of ancestral ranges versus sympatry.

We used the Akaike Information Criterion corrected for small sample size (AICc) to assess model fit. A relative probability of each node, ranging from 0 to 1, was estimated to find the likelihood of that node being at a specified state. The higher likelihoods and node probabilities reflect stronger relative support for ancestral reconstructions (Matzke 2013). To evaluate the probability of cladogenetic and anagenetic events, such as dispersal, vicariance, and founder events, we conducted 50 biogeographical stochastic mappings for the best-supported model, following the approach used by Nagy et al. (2019). The relationship between maximum likelihood and stochastic mapping estimates was evaluated, and ancestral state probabilities at key nodes were compiled.

3.2.3. Evolution of Migration

The correlated evolution between migratory behaviour (resident vs. migratory) and breeding distribution (tropical vs. temperate) was investigated using the discrete module of *BayesTraits v4*. Each of these traits was binary coded (resident = 0, migratory = 1; tropical = 0, temperate = 1), which thereby offered four possible states for each species (resident + tropical, resident + temperate, migratory + tropical, and migratory + temperate). We built and compared two evolutionary models: (i) a dependent model (complex: with eight rate parameters), for testing correlated evolution, and (ii) an independent model (simple: with four rate parameters), assuming independent evolution of the two traits. As a complementary approach, we also used (iii) the multistate module to treat the binary trait combinations as one four-state character to estimate potentially asymmetric transition rates, providing a different perspective to the evolutionary pathway. All models used the same data, and five independent MCMC chains (22 million iterations) were run for each model, with a 10% burn-in, and samples being drawn every 1000 iterations.

Meanwhile, we applied an exponential prior, with a mean of 10, to all transition rate parameters. To ensure adequate mixing and assess convergence across MCMC chains, we examined the trace plots and verified effective sample sizes for rate parameters, which helped balance flexibility and informativeness of the prior in all runs. A likelihood-based approach was applied for testing correlations between binary traits on phylogenies (Pagel 1994), where support for correlated evolution is evaluated by joint models (dependent), if they fit significantly better than the independent models (Pagel & Meade, 2006). The log marginal likelihood for each model was estimated using stepping stone sampling (Xie et al., 2011), and the Bayes Factor ($2 \times \Delta$ logL) was calculated, and its magnitude was interpreted following Kass & Raftery (1995). The values of log Bayes Factors indicate support for models as follows: 0 to 2 = weak support for the dependent model, 2 to 5 = support for the dependent model, 5 to 10 = strong support for the dependent model, >10 = very strong support for the dependent model, -2 to 0 = weak support for the independent model, and <-2 = support for the independent model (Gilks et al. 1995).

3.2.4. Life History and Ecological Traits

We obtained life history and ecological trait data from published datasets and online resources (Tobias et al. 2022). Foraging niche and diet variables were recorded as binary categories, indicating which species use them (1) or not (0). To reduce dimensionality of such dichotomous traits, though, we (i) constructed foraging breadth and diet breadth indices, and (ii) computed phylogenetically independent contrasts (PICs) (Revell & Harmon, 2022) for all foraging niches (forest floor, shrubs, lower canopy, middle canopy, and upper canopy) and diet classes (insects, molluscs, berries, seeds, and nectar). Then, we performed canonical correlation analysis (CCA) and projected the first canonical covariate from each block to species scores to produce two continuous gradients (foraging niche axis and diet axis). These axes were used in all further models.

Prior to analysis, life history variables were z-transformed. To reduce redundancy, we retained a core set of variables, including clutch size, length of breeding season (LBS), hand-wing index (HWI), tarsus length, and body mass. To separate different hypothesized drivers of migratory behaviour, predictors were organized into three candidate blocks. Block A represented morphological and life-history traits and included clutch size, body

mass, hand-wing index, length of breeding season, and tarsus length. Block B represented ecological traits and included diet breadth, diet axis, foraging breadth, foraging niche axis and association with broadleaf deciduous forests. Block C represented a combined predictor set, incorporating selected variables from both the life-hitory and ecological blocks to test whether explanatory support improved when both trait classes were considered together. Migratory behaviour was analysed using a phylogenetic logistic regression (PGLM), implemented in the *phylolm* package (Ives & Garland, 2010). Finally, to evaluate the relative importance of each predictor, we constructed models with zero to four predictors for each block. After model fitting, we recorded the log-likelihood, AIC, ΔAIC, and weights for each model. Models with $\Delta AIC \leq 6$ constituted the top model set for the respective block (Garamszegi & Mundry, 2014), and we computed model-averaged parameters in a model selection procedure (Burnham and Anderson, 2002; Redondo et al. 2019).

3.2.5. Phylogenetic links between life-history traits and climate niche axes

Life histories may track the realised climatic niches more closely than coarse habitat proxies (Title & Burns, 2015), so we tested whether life history traits predict the position of species along the climate axes occupied by *Phylloscopus* leaf warblers following the phylogenetic generalised least squares (PGLS) approach. For each species, we summarised climatic niches by extracting WorldClim bioclimatic variables from Fick and Hijmans (2017) and elevation data from occurrence records from the Global Biodiversity Information Facility (GBIF, *www.gbif.org*) before performing a principal component analysis (PCA). Only recordings corresponding to the breeding season were retained, so that the extracted values represented breeding climatic niches rather than year-round/ migratory distributions. Breeding range polygons were used as spatial filters for occurrence records, which were further cleaned using the R package *CoordinateCleaner* (Zizka et al. 2019). To reduce spatial clustering and sampling bias, cleaned records were thinned to a 2 × 2 km grid. The first three PC axes were (i) PC1: contrasting warm, wet, low-elevation environments with cooler, more seasonal higher-elevation climates; PC2: capturing seasonal precipitation and growing-season temperature gradients; and (iii) PC3: capturing variation in elevation and precipitation of the wettest and driest quarters. As predictors, we selected five life history and ecological traits (body mass, length of breeding

season, clutch size, and broadleaf deciduous forest habitat) and standardised each trait before modeling. Phylogenetic dependence was modeled as Pagel's λ (Pagel 1999), implemented using functions from the *ape* (Paradis et al., 2004) and *caper* packages (Orme et al. 2013).

For each PC, we first estimated λ using the PGLS method from the full model (that included all five predictors). Further, we refitted the full model with λ and used this as a global model for subsequent multimodal inference. Model selection was performed using AIC and all other additive subsets of predictors. The PGLS models included fewer predictors than our block-wise migration analysis, so we applied a more conservative inclusion threshold ($\Delta AIC < 6$) to ensure that only well-supported models contributed to model averaging. Models within $\Delta AIC < 6$ of the best models were retained with coefficients and variable importance (Σmodel weights). Collinearity was assessed using variable-inflation factors (VIF < 1.5 for all predictors) and all models were fitted using maximum likelihood for both λ estimations and model selection.

Seasonal movements of birds are driven by the need to track favorable climatic conditions (Gordo 2007), so we further tested whether migratory and resident *Phylloscopus* leaf warblers are segregated within the multivariate climate space. To compare realised climatic niches, we used a PCA-based niche overlap framework, implemented in the R package *ecospat* (Di Cola et al. 2017). We merged species-level climatic data with a trait file containing three types of migratory strategies (resident = 0, partial migration = 1 and complete migration = 3) and retained all 75 species (19 residents, 15 partial migrants, and 41 complete migrants) in our dataset. Partial migration was defined as a migratory strategy in which only a subset of individuals, populations, or geographic populations within a species undertake regular seasonal movements (these include elevational movements), while other remain resident near or within the breeding range throughout the year (Jahn et al. 2010; Boyle 2017). We then performed a PCA on the scaled species-level climatic variables. Each *Phylloscopus* species was assigned a PCA score representing its mean position along those axes. Using those occurrences, we then quantified the climatic niches for all three categories of migration, further estimating niche overlaps using Schoener's D index (0 = no overlap, 1 = identical).

We implemented niche equivalency test and niche similarity tests in multivariate climate space (500 permutations). For the niche equivalency test, group labels were randomly reallocated across climatic space and the overlap observed was compared against the resulting null distribution. For niche similarity test, one group was randomly shifted within the available climate background while the other was fixed. Niche overlap was quantified using Schoener's D and Hellinger's I. We also calculated niche dynamics metrics including expansion, unfilling, and stability, to describe the proportions of climate space uniquely occupied by migrants, available to residents but unused by migrants, and shared between both groups, respectively.

3.3. RESULTS

3.3.1. Ancestral Range Estimation

Biogeographic model comparisons strongly supported the BayArea+J model (Table 3.1; Appendix 1-S1, File 1-3) indicating that range evolution was associated with high local extinction rates and non-negligible founder-event speciation, whilst gradual dispersal played a minor role in the biogeographic history of the *Phylloscopus* leaf warblers. Alternative models without founder-event speciation received substantially lower support. The deepest nodes suggest ancestral ranges spanning the Indian and Indo-Chinese subregions, often with Siberia. The common ancestor of all study species (Node 76 (root), 11.7 Mya) most likely occupied the Indo-Chinese region (probability = 0.65) (Table 3.2). Further, widespread ancestors were likely involved in diversification, subsequently expanding westwards into the Mediterranean region (Node 93) and northwards into Siberia (Node 87).

Two major clades are evident, potentially triggered by range contraction events 9.5 Mya (Node 104), before later radiating into the Indo-Malayan Region (Node 133), the Siberian Subregion (Node 146), and the Afrotropics (Node 114). Meanwhile, Himalayan species are scattered across the phylogeny and do not form a monophyletic group (Figure 3.1). Node summaries of anagenetic and cladogenetic events inferred from stochastic mapping are provided (Appendix 1-S1, File 4-6). Vicariance events were inferred at 12–17% of nodes, according to stochastic mapping, while dispersal and subset sympatry events were more common (Appendix 1-S1, File 7). The robustness of these estimates was validated by significant correlations between maximum likelihood and stochastic mapping probabilities ($R^2 = 0.98$; Appendix 1-S1, File 8-9).

Table 3.1. Model comparison of biogeographic scenarios using BioGeoBEARS shows the strongest support for BayArea+J, highlighting the role of jump dispersals in range evolution. LnL – log-likelihood of the model, AICc – Akaike's Information Criterion corrected for small sample size wt – weight for the model, d – dispersal (range expansion) rate, e – local extinction (range contraction) rate, j – founder-event (jump dispersal).

	LnL	d	e	j	AICc	wt
BAYAREA+J	-251.6	0.007	0.064	0.013	509.5	0.91
DEC	-255.6	0.018	0*	0	515.3	0.05
DEC+J	-254.9	0.017	0*	0.005	516.2	0.03
DIVALIKE	-257.7	0.021	0*	0	519.5	0.01
DIVALIKE+J	-257.4	0.020	0*	0.003	521	0*
BAYAREA	-265.9	0.010	0.120	0	535.9	0*

* very small values

Table 3.2. Node probabilities based on the best biogeographic model (BayArea+J)

Node	Node age	Ancestral state	Probability
76 (Root)	11.67	Siberian, Indo-Chinese, and Indian Subregions	0.65
81	7.93	Siberian, Indo-Chinese, and Indian Subregions	0.90
83	6.45	Siberian, Indo-Chinese, and Indian Subregions	0.90
87	2.36	Indo-Chinese and Indian Subregions	0.80
91	8.43	Siberian, Indo-Chinese, and Indian Subregions	0.66
95	2.39	Mediterranean Subregion	0.61
100	8.26	Siberian, Indo-Chinese, and Indian Subregions	0.79
106	8.39	Indo-Chinese and Indian Subregions	0.75
116	4.27	Afrotropical Subregion	0.99
126	7.30	Indo-Chinese and Indian Subregions	0.90
129	6.21	Indo-Chinese and Indian Subregions	0.89
141	7.89	Indo-Chinese and Indian Subregions	0.77
148	2.35	Siberian Subregion and Chinese Transition Zone	0.60

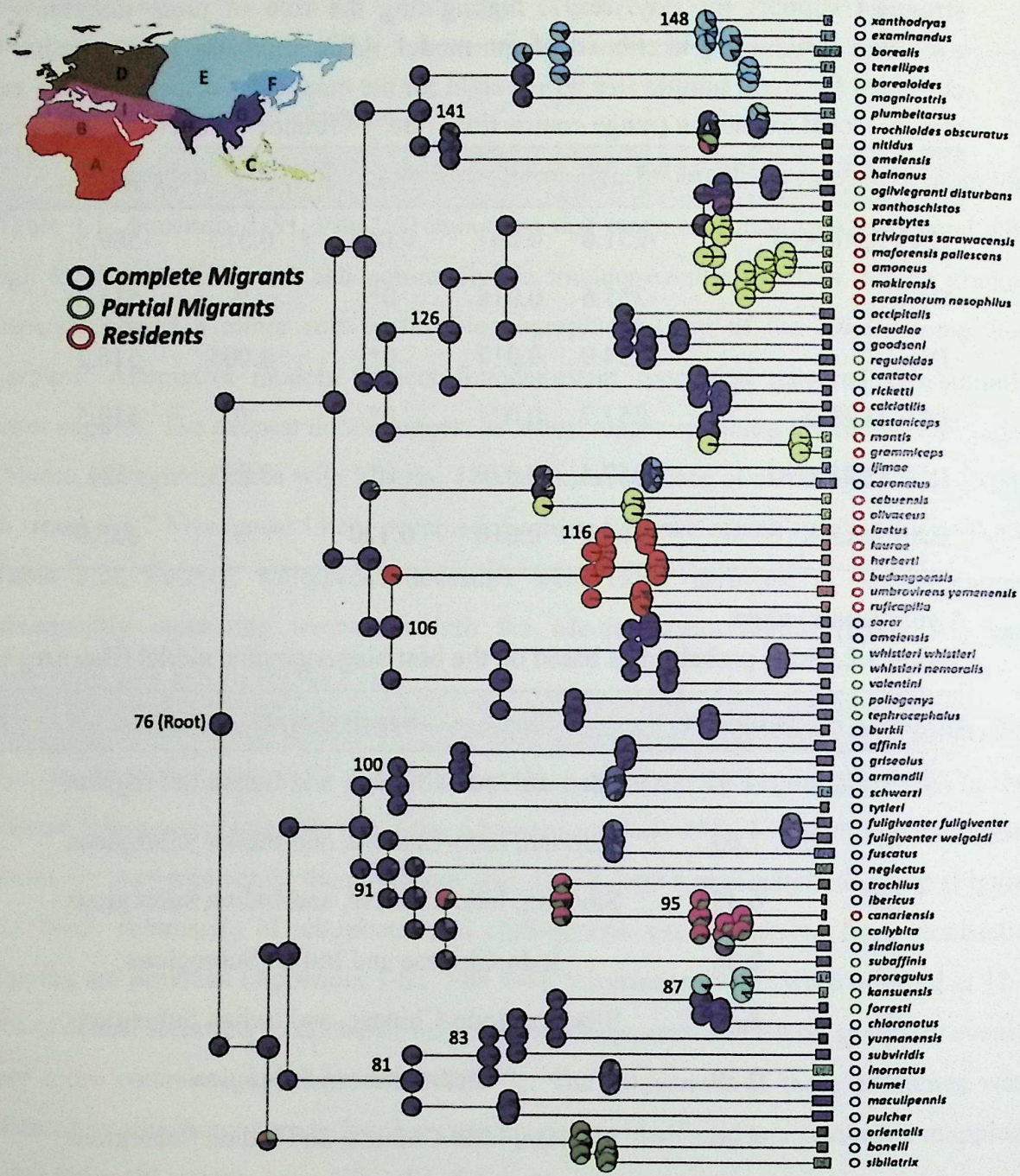


Figure 3.1. The results of the ancestral range estimation based on the best supported BayArea+J model. Pie charts at internal nodes illustrate the proportional probabilities of inferred ancestral ranges, while coloured boxes at the tips represent the current distribution areas of each species. The color scheme follows default BioGeoBEARS state-colour output corresponding to the area codes shown in the inset map. Coloured rings next to species names indicate migratory categories: complete migrants (blue), partial migrants (green), and residents (red).

3.3.2. Evolution of Migration

Across biogeographic regions, including the Siberian, Indo-Chinese, Indian, and Afrotropical subregions, migrant species of *Phylloscopus* leaf warblers primarily breed at higher northern latitudes and migrate southwards into tropical regions. The subtropic and montane regions, particularly South and Southeast Asia, are home to species undertaking partial migration, where movement is influenced by seasonality and elevational shifts. In contrast, residents are mainly limited to tropical and subtropical latitudes associated with more stable temperatures, particularly in the Afrotropical and Indo-Malayan subregions (Figure 3.2).

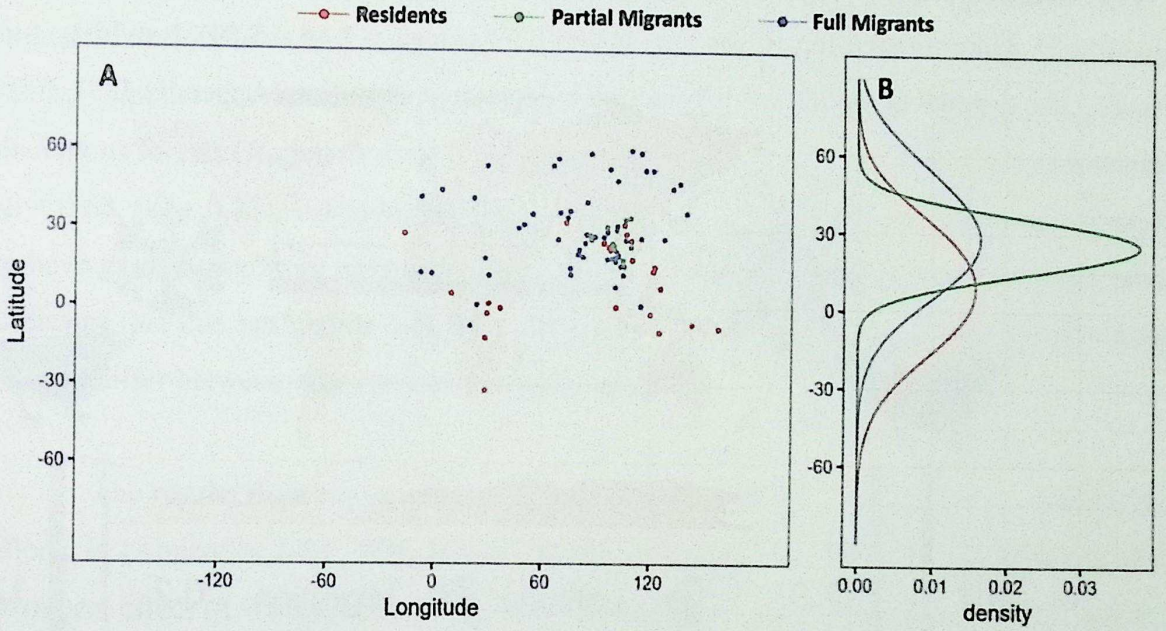


Figure 3.2. The distribution of *Phylloscopus* leaf warblers (A) in relation to their migratory behaviour (dots represent the centroids of breeding or year-round ranges), with (B) the density plot indicating that complete migrants live at higher latitudes than partial migrants who in turn live at higher latitudes than sedentary species.

In the dependent model, we estimated eight state transitions, that were defined by migratory behaviour and latitude (Figure 3.3). For shifts in migratory behaviour, the transition from being resident to becoming migratory was 7.99 in tropical lineages and 12.90 in temperate lineages. In contrast, migratory-to-resident transitions were 5.73 in tropical lineages and 0.23 in temperate lineages. For shifts in latitude, meanwhile, transitions from tropical to temperate regions were 0.08 in resident species and 1.48 in migratory species. Interestingly, the reverse shifts in transition rates from temperate to tropical regions were

11.84 for resident species and 0.20 for migratory species, indicating that temperate residents have frequently relocated to tropical regions during the evolution. Posterior root state probabilities for the dependent model were 0.20 (resident, tropical), 0.34 (resident, temperate), 0.21 (migratory, tropical), and 0.26 (migratory, temperate). The most probable ancestral state for *Phylloscopus* leaf warblers was likely resident in a temperate region, although alternative states have substantial support. Finally, the support for the correlated (dependent) model exhibits higher marginal likelihood values than the independent model. Across all five MCMC runs, the mean log marginal likelihood was -84.93 (± 0.69) for the dependent model, and -86.19 (± 0.26) for the independent model (Appendix 1-S2, File 1-2). The averaged log Bayes Factor was 2.53 (range = 1.15—5.89), providing support for the dependent model, while rejecting independent evolution (Appendix 1-S1, File 3-4).

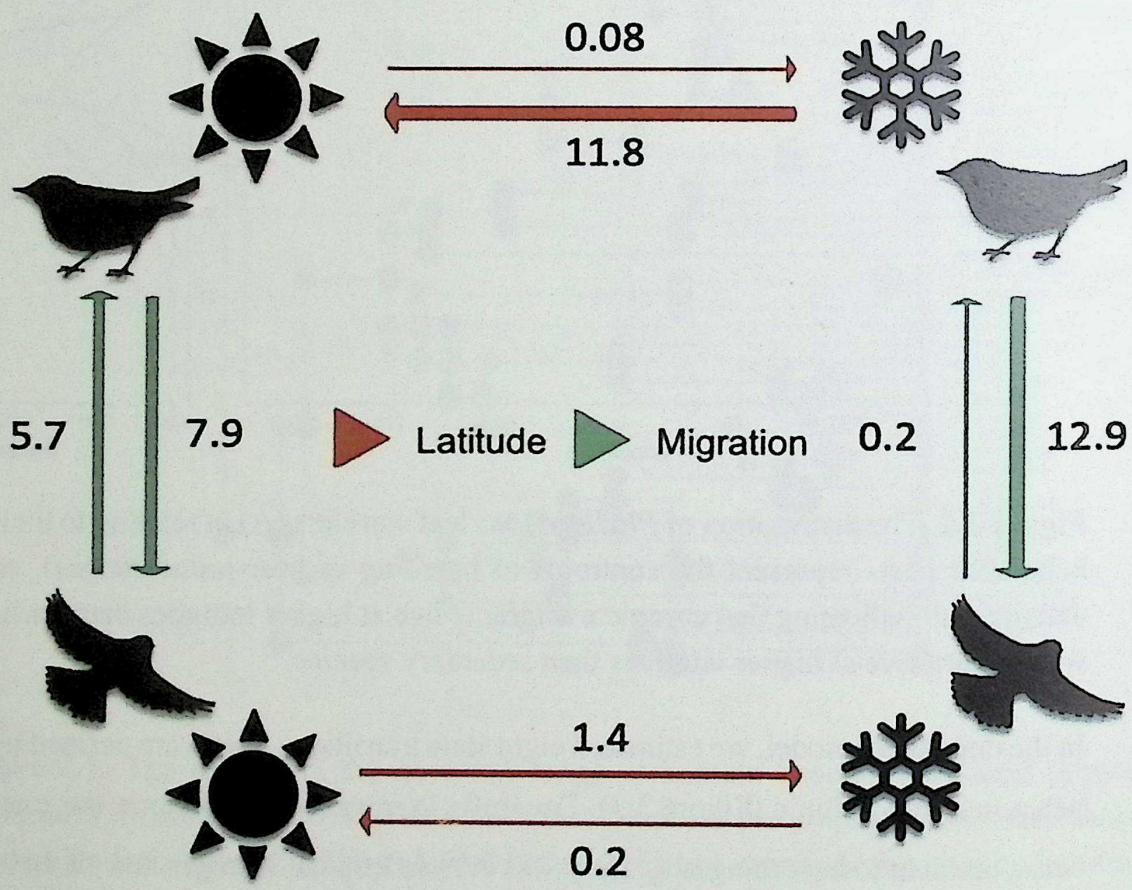


Figure 3.3. Mean transition rates between migratory state (resident vs. migratory) and latitude (tropical vs. temperate), as estimated by dependent evolutionary models across five MCMC runs.

3.3.3. Life History and Ecological Traits

Within the life history predictor set (Block A), model averaged estimates across the top-supported models identified hand-wing index (β = 1.4, SE = 0.63) as the strongest predictor of migratory behaviour, with species with more pointed wings being more likely to be migratory (Table 3.3). Other predictors like body mass, clutch size, tarsus length, and the length of the breeding season showed statistically non-significant effects, although they appeared in the top-ranked models (Appendix 1-S3, File 1a-1c).

Among the ecological predictors (Block B), meanwhile, habitat association (H3: broadleaf deciduous forest) showed strong positive effects (β = 3.03, SE = 0.78), indicating strong support for increased migratory propensity in species occupying broadleaf deciduous forests (Appendix 1-S3, File 2a-2c). Dietary axis showed a weak positive trend (β = 0.68, SE = 0.73), indicating that species with a greater reliance on insect prey tended to have greater migratory propensity, however, the wide confidence interval crossing zero indicates that this association was not consistently supported. Finally, foraging niche axis did not differ between migratory and resident species.

The results from the combined predictor block (Block C) were similar to those in Block B (Appendix 1-S1, File 3a-3c). Broadleaf deciduous forest habitat retained the strongest effect (β = 3.27, SE = 1.11), with occupants of that habitat being most likely to be migratory. Body mass showed a moderately negative effect (β = -1.15, SE = 0.61), providing a weak support (confidence interval crosses zero) for a tendency towards greater migratory propensity in small-bodied species. Meanwhile, the combined model set did not outperform the ecology set (Block B), indicating that migratory behaviour in *Phylloscopus* leaf warblers is primarily driven by habitat and elevation, rather than life history traits.

Table 3.3. Model-averaged coefficients from phylogenetic logistic regressions predicting migratory behaviour in *Phylloscopus* leaf warblers. Asterisk (*) indicates significant result based on the 95% confidence interval (CI).

Block	Predictors	β	SE	95% CI
A	Body mass	-0.83	0.66	-2.13 – 0.47
	Clutch size	0.82	0.68	-0.53 – 2.21
	Hand-wing index*	1.4	0.63	0.16 – 2.63
	Length of breeding season	-0.2	0.43	-1.03 – 0.64
	Tarsus length	-0.13	0.33	-0.77 – 0.52
B	Diet axis	0.68	0.73	-0.74 – 2.11
	Foraging niche axis	0.02	0.2	-0.40 – 0.46
	Broadleaf deciduous forest*	3.03	0.78	1.49 – 4.57
C	Body mass	-1.15	0.61	-2.36 – 0.04
	Clutch size	0.64	0.67	-0.68 – 1.96
	Diet axis	0.62	0.91	-1.16 – 2.41
	Broadleaf deciduous forest*	3.27	1.11	1.09 – 5.46
	Length of breeding season	-1.35	0.72	-2.77 – 0.06

3.3.4. Phylogenetic links between life-history traits and climate niche axes

Pagels λ estimates varied among the three climate PCs. For PC1, PC2 and PC3, λ estimates were intermediate (0. 34, 0.36 and 0.47, respectively), indicating moderate phylogenetic dependence in the residual variation of climatic niche positions when life history traits were included in the models.

Table 3.4. Conditional model-averaged coefficients ± SE calculated based on PGLS models of climatic niche axes (PC1–3). Asterisk (*) indicates significant result based on the 95% confidence interval (CI).

Response	Predictor	β ± SE	95% CI
PC1	Clutch size*	–1.40 ± 0.48	-2.37 – -0.44
	Body mass	0.52 ± 0.59	-0.65 – 1.70
	Broadleaf deciduous forest	–0.24 ± 0.38	-1.00 – 0.50
	Length of breeding season	0.04 ± 0.18	-0.33 – 0.42
PC2	Body mass	0.26 ± 0.31	-0.35 – 0.88
	Length of breeding season	0.09 ± 0.19	-0.28 – 0.48
	Clutch size	–0.08 ± 0.20	-0.48 – 0.31
	Broadleaf deciduous forest	–0.01 ± 0.11	-0.25 – 0.22
PC3	Length of breeding season	*0.17 ± 0.19*	-0.22 – 0.57
	Broadleaf deciduous forest	–0.12 ± 0.18	-0.49 – 0.25
	Body mass	0.05 ± 0.14	-0.23 – 0.35
	Clutch size	0.02 ± 0.10	-0.19 – 0.24

Across the primary climate gradient PC1, clutch size showed a strong negative association (β = -1.40, SE = 0.48; Table 3.4; Appendix 1-S4, File 1a) indicating that species laying larger clutches tend to occupy cooler and more seasonal high-elevation environments, whereas species with smaller clutches tend to be concentrated in warm and wet lowlands. Meanwhile, body mass exhibits a weaker, but not statistically significant positive trend, suggesting that heavier species possibly inhabit warm-wet climates. Other traits, like minimum breeding elevation and the length of the breeding season, received low statistical support on this axis.

Our results for the secondary climate axis PC2 indicated less consistent association between life history traits or habitat variables. This suggests that variation in seasonal precipitation or growing seasonal temperature does not strongly structure life history traits across the species in this clade (Appendix 1-S4, File 1b). Similarly, along our third axis

PC3, the length of the breeding season exhibited a non-significant trend towards a positive effect, indicating minimal evidence that species with longer breeding seasons occupy climates differing in elevation linked precipitation regimes (Appendix 1-S4, File 1c). Variable importance values that illustrate the relative contribution of predictors across model sets are provided in File 2 in Appendix 1-S4.

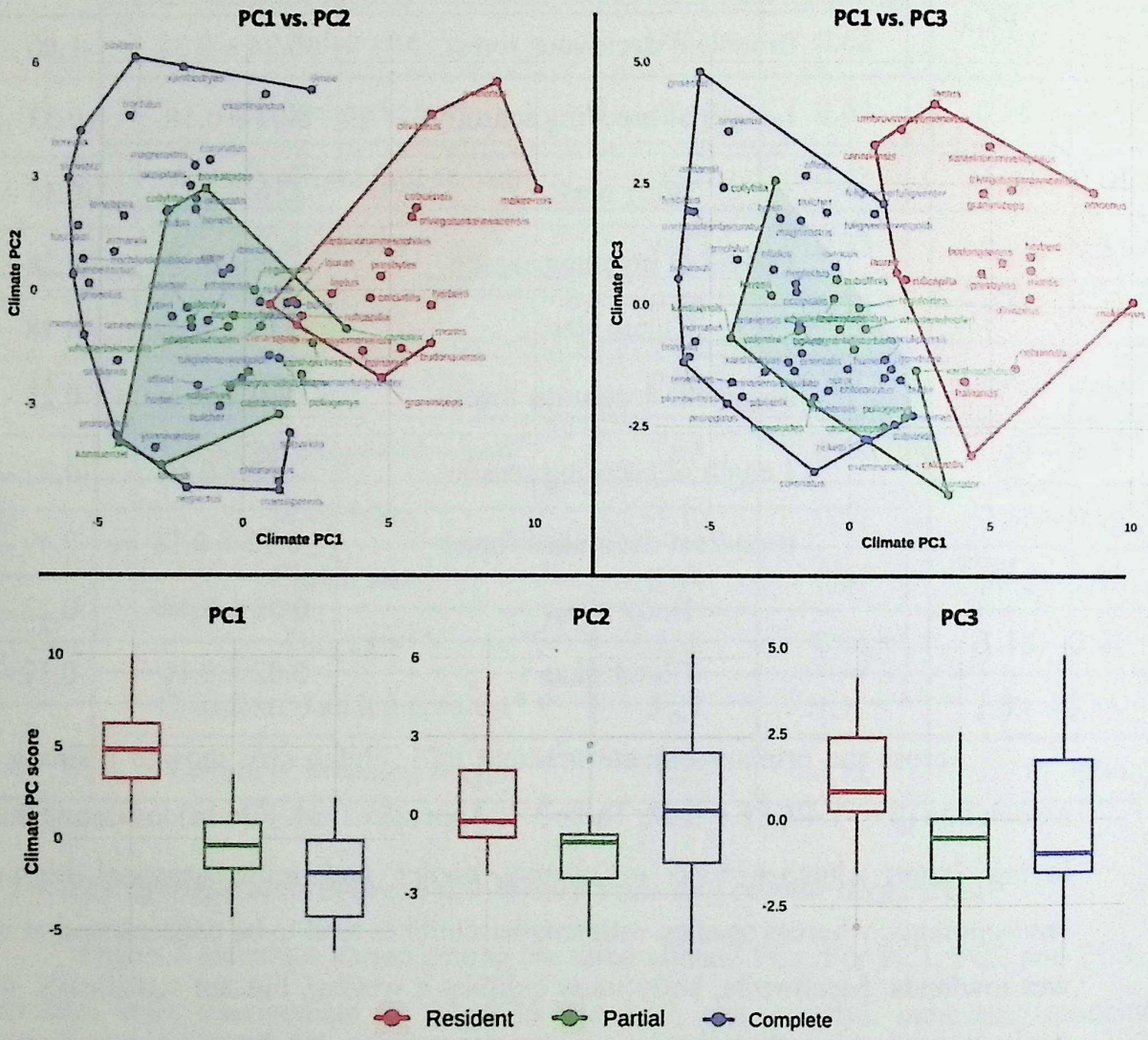


Figure 3.4. Climatic niche differentiation between resident, partial migrant and complete migrant *Phylloscopus* species in a PCA-derived climate space.

Migratory (complete and partial migrants) and resident species occupied broadly different regions of multivariate climate space, although a minimal amount of overlap was evident (Figure 3.4). All three migratory categories extended into distinct portions of climate space that were largely unique to either migrants (complete or partial) or residents. Consistent with this pattern, the niche overlap between both groups were low (Schoener's D = 0.11), indicating limited sharing of realised climatic niches. Niche dynamics analyses further suggest that less than half of the climatic space (stability = 0.45) was shared between the two categories, with a substantial proportion either uniquely occupied by complete and partial migrants (expansion = 0.54) or available to the residents but unused by migrants (unfilling = 0.48). Despite low overlap, niche similarity tests indicate that migratory and resident niches were more similar than expected within the available climatic background ($p = 0.61$ for Schoener's D).

3.4. DISCUSSION

The main findings of this study were that the diversification of the *Phylloscopus* leaf warblers across their distributional ranges was shaped by repeated dispersal and ecological differentiation events operating over deep time. It is likely that Southeast Asia acted as a primary center of origin and radiation for this genus, from which lineages expanded into novel regions where seasonality, elevation, and habitat structure imposed distinct selection pressures. Meanwhile, subsequent isolation, jump dispersals, and gradual diversification structured the present-day biogeographic patterns and composition. Within this broader historical framework, migratory behaviour, life history traits and occupancy across different climate niches emerge as being tightly interlinked components of this dynamic evolutionary system. This suggests that the current distribution and ecological diversity of this genus are an outcome of interacting historical colonisation processes and adaptive responses to temporal and spatial environmental heterogeneity.

3.4.1. Biogeographic history and radiation patterns

Our ancestral range estimation inferred a Southeast Asian origin for the *Phylloscopus* leaf warblers, with the BayArea + J model indicating multiple subsequent dispersal events across Eurasia. In particular, our reconstruction identified the Indo-Chinese and Indian subregions as important ancestral areas and suggested repeated colonization of northern Eurasia, western Europe, island systems, and the Afrotropical regions. These results are broadly consistent with previous phylogenetic and biogeographic studies showing that diversification in *Phylloscopus* began as early as 11-12 Mya, mainly occurring before the Pleistocene glaciations (Oliveros et al. 2019). Currently, the highest richness is observed in the eastern Himalayas and the forests in southern China (Johansson et al. 2007), and the expansions into North Siberia and West Europe were likely associated with available habitat use and ecological opportunities (Price et al. 1997).

Our model also inferred several colonization events involving migratory lineages. For example, the reconstruction suggests that some island taxa, such as *P. cebuensis* in the Philippines were derived from dispersing ancestors but are now sedentary. This result is consistent with broader evidence that island colonization by birds is often followed by reduced migratory behaviour or migratory loss over time (Dufour et al. 2024). Similarly,

our reconstructions placed the Afrotropical lineages as descendants of Indo-Chinese ancestors, suggesting long-distance colonization followed by subsequent isolation. This inference is compatible with the evidence that climatic fluctuations and humid phases may have facilitated faunal exchanges between Africa and Asia, although precise mechanisms and timings remain uncertain.

Our results provided limited evidence for in-situ diversification in the Himalayas. Instead, the Himalayan diversity appeared to be derived from lineages that colonized the region and subsequently diversified, which is in agreement with Johansson et al. (2007). The pattern may reflect a complex geological and climatic history of the Himalayas, where limited glacial advance during the Pleistocene (Owen & Benn 2005) and the shrinking of temperate forests during the dry and cold glacial periods (Ray & Adams 2001) could have influenced habitat availability for these insectivores. Together, our findings suggests that biogeographic history of *Phylloscopus* was shaped primarily by repeated colonization of new regions, followed by geographic isolation and further, allopatric divergence.

3.4.2. Ecological divergence among sister species

Closely related *Phylloscopus* species differ primarily along elevational and foraging gradients, but in ecologically predictable ways, supporting the view of adaptive radiation as an important driver of speciation (Price 2008). Our results revealed that most sister species-pairs of *Phylloscopus* leaf warblers occupy adjacent habitats (Martens 2010), in agreement with earlier studies (Richman & Price, 1992). Similar patterns have also been reported in other passerine groups, including e.g., *Turdus* thrushes, where shifts in habitats and elevational distribution have jointly shaped diversification (Nagy et al. 2019). This further indicates altitudinal and foraging niche segregation in the western Himalayan region, where the feeding strategies of extant species differ markedly from those of their ancestors (Surya & Keitt, 2019; Parab et al. 2023). This suggests that ecological differentiation among *Phylloscopus* sister lineages predominantly reflects gradual divergence along existing environmental gradients during periods of isolation, rather than rapid adaptive shifts into novel niches following secondary contact (DeCicco et al. 2024).

3.4.3. Evolution of Migratory Behaviour

The migratory behaviour of *Phylloscopus* leaf warblers differs across latitudes, with migrants breeding in temperate regions and spending the winter months in tropical regions, while year-round residents overwhelmingly occupy tropical/subtropical regions. Our phylogenetic comparative analysis demonstrated that migratory behaviour is evolutionarily conserved, because complete migration is concentrated in older, northern clades (e.g., *borealis* and *tenellipes* groups), while modern radiations in the tropics are mostly sedentary (Price 2008). Our findings are congruent with prior macroecological studies on birds, which emphasize latitudinal gradients and seasonal constraints being key drivers in the evolution of avian migratory behaviour (Somveille et al. 2013; Winger et al. 2019).

Partial migration is often considered as an intermediate evolutionary state between complete migration and sedentariness (Jahn et al. 2010), which corresponds with our observations that many *Phylloscopus* lineages exhibit partial movements within regions. The latitudinal distribution of *Phylloscopus* leaf warbler species confirms that partial migrants primarily occur in the region around the Tropic of Cancer, indicating that these species likely undertake elevational or regional migrations within subtropical regions (Martens 2010). According to our correlated evolutionary analysis, resident ancestors in temperate clades were more likely to acquire migration compared to tropical residents, whilst tropical species tended to lose their migratory behaviour more frequently than their temperate counterparts, though rarely reverting to migration. The predominance of evolutionary transitions to temperate migration supports a temperate origin (northern home) scenario, where migration evolved as an adaptation to seasonality (Salewski and Bruderer, 2007).

3.4.4. Morphological and life history correlates of migration

Our analyses show that ecological predictors, particularly habitat association, best explained the evolution of migration in the *Phylloscopus* leaf warblers (Bitterlin & van Buskirk, 2014). Those *Phylloscopus* leaf warblers occupying broadleaf deciduous forest habitats are most likely to be migratory, likely reflecting seasonal predictability of food resources in these habitats (Zhang et al. 2006; Ho et al. 2025). The length of the breeding

season displayed weak positive support, but this aligns well with the theory that breeding habitats at higher elevations impose stronger seasonal constraints, such as harsher winters than breeding habitats at lower elevations (Ashmole 1963). This, in turn, favours migration towards highly productive lower elevations during the non-breeding season.

Life history traits contributed moderately to the observed variation in migratory behaviour in the *Phylloscopus* leaf warblers. Species with more pointed wings were marginally more likely to be migratory, consistent with earlier studies (Mönkkönen et al. 1995; Sheard et al. 2020; Tobias et al. 2022). Other traits like clutch size and body mass showed differences between migratory and non-migratory species. Overall, we show that habitat type is the most important predictor of migratory behaviour in *Phylloscopus*, with elevation playing a secondary role.

3.4.5. Phylogenetic links between life-history traits and climate niche axes

Our analyses revealed two distinct ways in which life history traits align with climatic niches. First, clutch size predicts the position of species along the primary warm-wet vs. cool-seasonal elevation gradient. Species with larger clutch sizes tend to occupy cooler and more seasonal high-elevation environments, whereas species with smaller clutch sizes occupy warmer regions. This corroborates with the theory that harsh and more seasonal environments favour greater investment per breeding attempt (Lack 1954), whereas more predictable lowland climates allow for smaller clutches and potentially higher breeding frequency (Ricklefs 2000). Consequently, clutch size modulates the adaptation of birds along the primary temperature-precipitation-elevation axes, whereas the length of breeding season further fine-tunes species' positions along seasonal gradients. Migratory behaviour in *Phylloscopus* involves a shift in realised climatic niches for tracking favorable climatic conditions throughout the year (Graf et al. 2025). However, our analyses suggest that migratory and resident *Phylloscopus* species occupy only partially overlapping climatic niches. This suggests that migration primarily enables the occupation of temporally variable climates, rather than access to fundamentally novel climates.

CHAPTER 4. COMPOSITIONAL TURNOVER: PATTERNS AND DRIVERS

Building on the historical biogeography we established in Chapter 3, this chapter examines the present-day composition of Eurasian *Phylloscopus* warblers. Here, our goal is to quantify the spatial patterns of turnover within species groups using advanced occurrence metrics. In particular, we used zeta (ζ) diversity estimates and multisite generalised dissimilarity modeling (MSGDM) to evaluate how environmental factors shape the assemblages.

4.1. INTRODUCTION

Anthropogenic climate change has provided many unprecedented warnings (IPCC 2021), with multiple ecological impacts (Mendelson et al. 2000; Harley et al. 2006; Saunders et al. 2022). Birds are no longer exempt, as major shifts in land use and climate may alter their abundances and distributions (Saunders et al. 2022). Consequently, recent research follows on questions related to how environmental or climatic factors have influenced species richness and assemblage dynamics (Lindström et al. 2013). Computational resources, large-scale data availability (*www.gbif.org*), and high-resolution environmental raster's now facilitate research spanning continents. These advances are, in particular, valuable for taxa that is widespread, which need intensive data for robust analyses.

In this chapter, we focus on all the species analysed in Chapter 3, except the species from Afrotropics. The current distribution spans across the eastern Palearctic, Indo-Malayan, and Australasian regions (Martens 2010). The taxonomic revisions have greatly expanded the species counts in this genus, with recognised species rising from 52 in 1908 (Watson 1986) to about 77-78 by 2018 (Dickinson & Christidis 2014; del Hoyo & Collar 2016; Gill & Donsker 2017; Alström et al. 2018), with further new splits adding a few Indonesian species (Eaton et al. 2016). Within this genus, research to date has generally focused on systematics (Martens 2010; Alström et al. 2018), but other aspects, like adaptive radiations, too, have been studied (Price 2010). Vocalisations have been frequently studied

(Mahler & Gil 2009; Tietze et al. 2015; Wu et al. 2023), like breeding biology (Wesołowski & Maziarz 2009), assemblage structures (Richman 1996; Ghosh et al. 2014), and habitats (Tiainen et al. 1983; Forstmeier et al. 2001). Phylogeography (Johansson et al. 2007, Packert et al. 2012) and migration patterns (Norman 1987; Hedenström & Ptterson 1987, Ergen et al. 2017), too, have been well documented. However, all these studies have largely focused on the Himalayas (Price et al. 1997), East and South Asia (Zhang et al. 2021; Wu et al. 2023; Yang et al. 2023), and adjacent regions. Leaf warblers of wider Eurasia remain less explored due to gaps and limitations in data.

Most environmental factors that may influence community compositions have been established, but are seldom used. As examples, spatial layers for human impacts (burned area frequency or aerosols) are available (see Engstrom 2010; Sanderfoot & Gardner 2021; Sanderfoot et al. 2022), yet are less incorporated. On similar notes, atmospheric pressure (Richardson 1978, 1990; Chmura et al. 2020) and geophysical factors like anomaly in gravity (proxy for mountainous terrains) (Mills et al. 2019; Jones & Ward 2020) remain underutilised. Fine resolution of geospatial layers and wide distribution of leaf warblers offer an ideal system to test how geographic, climatic, and anthropogenic drivers jointly shape turnover of species. Traditional β-diversity estimation measures pairwise difference and emphasises more narrow range species, often overlooking the widespread taxa (Latombe et al. 2018). Zeta (ζ) diversity generalises β-diversity by measuring the number of species shared at multiple sites (Hui and McGeoch 2014; McGeoch et al. 2019). As we increase the number of sites, ζ typically declines as a low number of species are common across multiple sites, which is indicated by the decline rate. A gentle decline thus implies the dominance of widespread taxa, whereas a rapid decline implies the presence of more range-limited or rare species. By integrating these patterns with generalised dissimilarity models (GDM), we can quantify how environmental factors shape turnover in rarer vs more common species (Latombe et al. 2018; Alashi & Modak 2023).

In this chapter, we hypothesise that the community assembly in *Phylloscopus* warblers is governed by geographical range limits, habitat specificity and ecological constraints. In particular, (i) observed α diversity patterns and ζ retention/decline rates should reflect niche dynamics and co-occurrence limits within breeding areas; and (ii) variables associated with productivity (net primary productivity, soil moisture) and terrain

should modulate clade co-occurrence. For testing these ideas, we applied ζ diversity and MS-GDM using a detailed set of anthropogenic and environmental variables. This cross-continental study seeks to reveal global turnover drivers, elucidating both regional idiosyncrasies and shared patterns, to understand the response of leaf warblers to environmental shifts.

4.2. MATERIALS AND METHODS

4.2.1. Geographical extent of the study

Species composition unpredictably varies across time and space (Rosenzweig 1995; Sala et al. 2000); hence, we defined a broader region as our study area to capture the full *Phylloscopus* range. This area includes key biodiversity hotspots like the Caucasus, Caspian-Hyrcanian forests, Altai-Sayan, the Mediterranean basin, the Himalayas, and Southeast Asia. These regions favour multiple endemic species and cover breeding ranges of focal warbler species. We reviewed the published biogeographic analyses for *Phylloscopus* (Helbig et al. 1996; Irwin et al. 2001; Martens et al. 2004; Johansson et al. 2007; Peterson & Anamza 2017) and occasional migration studies (Stervander et al. 2017) to understand species ranges (Distribution of each species is provided in Appendix 2-ST1).

4.2.2. Species groups and occurrences

We grouped the study species according to the latest available species-level phylogeny of *Phylloscopus* warblers (Alström et al. 2018). Each group therefore represent phylogenetically related species. Further, the groups were organized into three broader sets represented by: (i) *P. castaniceps, P. cantator, P. borealis*; (ii) *P. burkii, P. affinis, P. proregulus*; and (iii) *P. davisoni, P. collybita, P. trochiloides, P. tenellipes*. These groupings allowed us to compare turnover within and among closely related lineages while maintaining consistency with the evolutionary structure of the genus. Geographic distributions were used as interpretive context when explaining clade-cpecific patterns of compositional turnover. We decided to exclude the species with extremely disjunct/ restricted ranges (eg, island endemics like *canariensis*) to avoid single taxa bias. Occurrence records for each species were later compiled from Global Biodiversity

Information Facility (*www.gbif.org*), focusing more on data during breeding seasons (Appendix 2- ST2). The records were limited to 2014-2023, aligning with the latest taxonomic revisions and ecological relevance. Rigorous data cleaning was applied later using the R package *CoordinateCleaner* (Zizka et al. 2019) to remove any spatial errors (which include records at country or institutional centroids, invalid coordinates). Data was thinned to a 2 x 2 km grid cell to minimise spatial clustering and sampling bias (Mair and Reute 2016).

4.2.3. Selection of Environmental Variables

To ensure ecological transparency in predictor selection, we compiled an expanded environmental-variable table summarising the description, data source, supporting references, and biological rationale for each variable used for modelling (Table 4.1). Predictors were selected to represent major ecological gradients expected to influence insectivorous birds, including terrain structure, moisture and temperature regimes, vegetation, resource availability, and human disturbance. Topographic variables such as elevation and gravity anomaly were included because they capture montane structure, elevational habitat partitioning, and dispersal constraints. Gravity anomaly was included as a coarse proxy for rugged terrain and potential montane barriers that may influence range continuity and species co-occurrence. Climatic and hydrological variables, including soil moisture, rainfall, NDWI, atmospheric temperature, snow cover, were included as they influence vegetation productivity, seasonal habitat suitability, and arthropod abundance. In particular, vegetation variables such as canopy height, canopy cover, NDVI and net primary productivity were retained for their representation of forest structure and potential prey-resource gradients. Anthropogenic and atmospheric predictors including distance to road, nightlights and settlement intensity, aerosol concentration, ozone etc. were included to capture habitat modification and disturbance. Aerosol was specifically included as an atmospheric disturbance predictor, as reduced air quality affects small insectivorous birds directly through physiological stress (Nehei et al. 2024) or indirectly through changes in vegetation and insect prey availability (Barton et al. 2023).

In total, we assembled 62 predictors considered biologically relevant to insectivorous forest birds. Native spatial resolutions varied among datasets, particularly between fine-scaled remotely sensed vegetation/topographic layers and coarser atmospheric products. Therefore, all the predictors were projected, clipped, aligned and resampled to a common 2 × 2 km analytical grid before extraction. Collinearity among these predictor variables was reduced by computing Spearman's pairwise correlations, which retained variables with $r < 0.7$ (Appendix 2-SF1-3). Subsets of these variables were then selected for each group separately (Table 4.2), based on ecological rationale. Spatial processing was performed using ArcGIS 10.5, and the analysis was performed using R (version 3.6.1; R Core Team 2019).

Table: 4.1. Environmental variables used in the MS-GDM analyses, including data sources, supporting references, and ecological rationale.

Variable Name	Description	Data Source	References	Ecological Rationale
Bare Soil Index	To assess the extent or presence of bare soil in a particular area	https://scihub.copernicus.eu/	Wentworth et al. 2010; Martinez et al. 2010; Schaub et al. 2010; Weisshaupt et al. 2011; Tagmann-Ioset et al. 2012	Bare soil may indicate open or sparsely vegetated microhabitats that influence ground foraging and arthropod availability.
Drainage Density	Quantification of the amount of stream channel length per unit area	Derived from Spatial Analyst tool	Iwata et al. 2010	Drainage density influences water availability, riparian habitat, and insect abundance
Elevation	Vertical distance above sea level	Earth explorer USGS	La Sorte & Jetz 2010; Maggini et al. 2011; Pernollet et al. 2015; Elsen & Tingley 2015; Rehnus et al. 2018	Changes in the elevational range can influence the habitats of birds.
Surface temperature	The temperature of the Earth's surface measured at ground level	https://scihub.copernicus.eu/	Fjeldså et al. 1999	Surface temperature influences the shaping of the micro-habitat.
NDSI- Snow Index	Extent of snow cover over a specific region	https://scihub.copernicus.eu/	Brambilla et al. 2018; Dickey et al. 2008; Liebezeit et al. 2014; Scridel et al. 2018; Wilson and Martin 2010; McKinnon et al. 2012	Changes in snow cover can alter the suitability of the habitat.
NDWI- Water Index	It is sensitive to changes in liquid water content of vegetation canopies. It is derived from the Near-IR band and a second IR band, ≈1.24μm when available and the nearest available IR band otherwise. It ranges in value from -1.0 to 1.0.	https://cmr.earthdata.nasa.gov/search/concepts/C1386204298-NSIDCV0.html	Serra Acacio 2021	The Normalized Difference Water Index (NDWI) makes use of reflected near-infrared radiation and visible green light to enhance the presence of such features while eliminating the presence of soil and terrestrial vegetation features.
Soil moisture	Water content present in soil, expressed as percentage of the soil's weight	https://scihub.copernicus.eu/	Zhao et al. 2021; Onrust et al. 2019	Soil moisture influences insect abundance, which may influence the forage quality.

Gravity Anomaly	Provides information on gravitational anomalies in a specific geographic area. May indicate variations in the density of the Earth's subsurface, helping identify potential geological features.	https://earth.esa.int/eogateway	Blaser et al. 2014	The gravitational field affects the energy required for birds to ascend or descend barriers like mountains, waterbodies, or other geographical features in the migration route.
Anthropogenic				
Distance to the nearest road	Derived Euclidean distance of a point from nearest road	Generated and extracted by Google earth engine	Chen et al. 2023	Anthropogenic activity may increase around the road and may influence species occurrence
Forest Fire	Provides information on forest fires, including their occurrence, intensity, and affected areas.	https://earth.esa.int/eogateway	Puig-Gironès et al. 2023; Barlow et al. 2002; Coelho et al. 2023	Forest fires may influence the vegetation structure and hence may influence species distribution
Global Settlements	Offers insights into global human settlements, providing information on population distribution, urbanization patterns, and land use changes.	https://earth.esa.int/eogateway	Jokimäki et al. 2021; MacGregor-Fors & Schondube, 2012	Different responses by birds to urbanisation can be observed
Mean Ozone	Provides information on the average ozone concentration in a specific region.	https://earth.esa.int/eogateway	Reif et al. 2023	A mechanistic negative relationship between bird population growth and O_3 concentrations is observed
Night Light	Captures the intensity of night time lights in a given area, providing insights into urbanization, economic activity, and energy consumption.	https://earth.esa.int/eogateway	Secondi et al. 2020' Korpach et al. 2022; Weisshaupt et al. 2022	Negative responses of birds have been observed towards night light.
Atmospheric				
Aerosol	Includes atmospheric aerosol concentrations, which can affect air quality, climate, and visibility.	https://earth.esa.int/eogateway	Engstrom 2010; Sanderfoot & Gardner, 2021	Exposure to aerosols has been linked to declines in spontaneous activity and may influence the species distributions negatively

Atmospheric Pressure	Provides information on atmospheric pressure levels in a specific region. Atmospheric pressure is a key meteorological parameter influencing weather patterns.	https://earth.esa.int/eogateway	Richardson 1978; Ramenofsky 1990; Chmura et al. 2020; Mitchell et al. 2012; Morganti et al. 2011; Åkesson et al. 2002	Atmospheric pressure influences bird arrivals in the process of migration.
Atmospheric Temperature	This file contains data on atmospheric temperatures, helping to understand temperature variations in a specific region and their impact on climate and weather.	https://earth.esa.int/eogateway	Liu et al. 2021; Manola et al. 2020; Griffith et al. 2021; Griffith et al. 2020; Churchill et al. 2023; Egwumah et al. 2022; Sebastianelli et al. 2022	Atmospheric temperature may influence resource availability, and changes in atmospheric temperature may also influence habitats.
Rainfall	Provides information on rainfall patterns, helping to assess precipitation levels in a specific area. It is crucial for studying climate, agriculture, and water resource management.	CHRS Data Portal	Chmura et al. 2020; Mitchell et al. 2012; Tsvey et al. 2007; Åkesson et al. 2001	The effect of rainfall has been consistent with several studies showing that departure probability increases on nights with little to no precipitation
Vegetation				
Canopy Cover	Measures the extent of canopy cover in a specific area, offering information on forest density and ecosystem health.	https://earth.esa.int/eogateway	Benitez et al. 2023; Zwarts et al. 2023	Canopy cover influences habitat quality, availability of resources, and protection from predators for smaller birds
Canopy height	Provides information on the height of the vegetation canopy in a specific region.	https://earth.esa.int/eogateway	Prado et al. 2022; Jara et al. 2020; Sinnott et al. 2021; Rajaonarivelo et al. 2020; Bakermans et al. 2012; Jones et al. 2020; Gallerani et al. 2023; Altamirano et al. 2019; Bale et al. 2020; Bakker et al. 2020; Amini et al. 2020; Anderle et al. 2023	Canopy height can explain the forest succession stage and so can influence the presence of species according to preference.
Net primary productivity	Provides information on net primary productivity, which represents the amount of carbon that plants convert into biomass through photosynthesis.	https://earth.esa.int/eogateway	Anderle et al. 2023; Kim et al. 2021; Murphy et al. 2020; Moudrý et al. 202; Ribeiro et al. 2019; Aloni et al. 2019; Fan et al. 2019; Barnagaud et al. 2019	Net primary productivity can influence the species richness of insects and other forages for the bird species.

NDVI	Values from -1 to +1 which reflect +1 is helathy vegetation and negative value reflects non vegetation areas.	https://scihub.copernicus.eu/	Iverson et al. 2023; Müller et al. 2023; Suarez-Rubio et al. 2023	Vegetation cover of the area may have an effect on bird assemblages because of the percentage greenes available in various land cover types.

4.2.4. Patterns of Compositional Turnover

The ζ diversity approach was used to investigate species turnover within the Phylloscopus complexes (Hui & Mcgeoch 2014; Latombe et al. 2017a, 2017b; Latombe et al. 2018). Zeta diversity was initially created to measure the species composition of communities; however, since the framework for assessing compositional turnover is still the same at this scale, it may also be used to compare species that are members of the same genus. The ζ diversity suggests the average number of species shared by i sites. When the number of sites (n) is taken into account as the ζ order, the ζ diversity values for lower orders reveal the turnover rate of narrow-range species (such as those shared between two sites), whereas values for higher orders show the turnover rate of the community's widespread species (Leihy, Duffy, & Chown 2018; Hui, Vermeulen, & Durrheim 2018). The ζ diversity at order n can be expressed as:

$$\zeta_n = \frac{1}{\binom{N}{n}} \sum_{i=1}^{\binom{N}{n}} \prod_{j=1}^{n} S_{ij}$$

where N is the total number of sites. Sij denotes whether species j is present at site I, n is the ζ diversity of order n, and (N/n) is the binomial coefficient that shows how many combinations of n sites from N there are. The retention rate indicates the pace at which species are retained with increasing orders, or the number of locations, as ζ diversity values decrease. Using the "*zeta.decline*" function in the "*zetadiv*" package (Latombe et al. 2017b) in R (R Core Team 2019), ζ diversity was determined independently for each species group. Additionally, we computed the spatial distance decay in turnover of ζ diversity using the distance decay function from the *zetadiv* package. The accuracy of ζ diversity estimations is increased by using ζ decay analysis, particularly for widely distributed taxa (Leihy, Duffy, & Chown 2018; Hui & Mcgeoch 2014).

4.2.5. Drivers of Compositional Turnover

We used the MS-GDM method, which combines ζ diversity and the generalized dissimilarity models (used in conjunction with beta diversity), to better understand how species composition changes as a result of environmental variables (Latombe et al. 2018). MS-GDM addresses the variations in species composition with various anthropogenic and

environmental causes by applying it to many orders of ζ (Alashi & Modak, 2023; Latombe et al. 2018). To ascertain the relationship, it also takes into account the distance that exists between sites. Since the Euclidean distance offers a simpler mathematical depiction of the shortest path between two points in a multidimensional space, we applied it to calculate the spatial distances. The monotonic fall in diversity along environmental gradients is addressed by MS-GDM using a generalised linear model in conjunction with i-spline functions. This approach helps understand the complexity of biodiversity's reaction to changing environments by producing a binomial dataset that enables nonlinear analysis (Alashi & Modak, 2023; Latombe et al. 2018; Ramsay 1988). For the model to be sufficiently efficient, 5000 random sites were combined. According to Latombe et al. (2018), the splines' inclination shows how the impact fluctuates across the range of values with respect to the explanatory variables. For example, the differences in snow within areas with considerable snowfall are indicated by a noticeable inclination at higher normalised difference snow index (NDSI) values. Similarly, a milder slope at lower NDSI values suggests that variations in NDSI within regions with less snowfall are less significant.

Table 4.2. List of variables used for each species for MSGDM's

P. castaniceps complex	*P. cantator superspecies*	*P. borealis superspecies*	*P. burkii complex*	*P. affinis superspecies*
Canopy Height	Aerosol	Canopy Height	Aerosol	Aerosol
Decay Disturbance Index	Canopy Height	Decay Disturbance Index	Canopy Height	Aridity Index
Distance to Drainage	Decay Disturbance Index	Elevation	Land Cover	Bare Soil Index
NDSI	Drainage Density	Gravity Anomaly	Gravity Anomaly	Decay Disturbance Index
NDVI	Gravity Anomaly	NDWI	NDSI	Drainage Density
NDWI	Night Lights	Night Lights	Night Lights	Land Cover
Net Primary Productivity	Net Primary Productivity			Gravity Anomaly
				NDWI
				Night Lights
				Mean Ozone

P. proregulus superspecies	*P. davisoni superspecies*	*P. collybita superspecies*	*P. trochiloides complex*	*P. tenellipes superspecies*
Aridity Index	Decay Disturbance Index	Aerosol	Aridity Index	Aridity Index
Atmospheric Pressure	Distance to Drainage	Canopy Height	Canopy Height	Bare Soil Index
Decay Disturbance Index	Gravity Anomaly	Elevation	Elevation	Canopy Height
Elevation	NDVI	Drainage Density	Distance to Settlement	Distance to Drainage
NDVI	Net Primary Productivity	Distance to Drainage	Net Primary Productivity	Gravity Anomaly
NDWI		Gravity Anomaly	Soil Moisture	NDWI

4.3. RESULTS

4.3.1. Patterns of Compositional Turnover

ζ diversity was used to estimate and interpret compositional turnover as an ecological signal. In each ζ diversity figure, panel A represents how shared species are lost as progressively larger sets of sites are compared. A gradual decline indicates that many species persist across multiple sites, reflecting wider distributions and broader ecological tolerance. In contrast, a steep decline indicates rapid replacement of species across space, suggesting restricted ranges, local endemism, or strong habitat filtering. Panel B shows retention ratios between successive ζ orders, which indicates how consistently shared species are retained when additional sites are added to the comparison. A high or slow declining ratio indicates that common or widespread species continues to structure the assemblage across space. A sharp decline indicates the shared component of the assemblage is lost quickly, suggesting the role of rare, localized, and endemic species.

4.3.1.1. The *castaniceps* complex and *cantator* and *borealis* groups

The richness of species within the site was quite low for the *borealis* group, whereas the *castaniceps* complex had the highest initial species richness (alpha diversity=1.18; Figure 4.1[A]), followed by the *cantator* group (alpha diversity=1.02). The slight increase in the ζ-ratio for each of these groupings indicates a slight overlap of all the commoner species. Additionally, the *borealis* group had the lowest ζ decay, indicating greater species loss with the growing number of species in ζ. This suggests that the *castaniceps* complex supports relatively more local co-occurrence, whereas the *borealis* group represents a simpler assemblage where only a few species are shared repeatedly across sites.

The retention rate decreased sharply for the *cantator* group, indicating rare/site-specific species influencing the turnover with the increasing number of sites, whereas the retention rate decreased gradually for the *borealis* group, indicating occupancy dominated by common species, even though the richness was lowest in that group (Figure 4.1[B]).

The diverse *castaniceps* complex drove turnover to decrease gradually until sharply declining after 300 sites, indicating that the groups' species composition was intermediate. The *castaniceps* complex, which has a sparse breeding range, had a gradually increasing regression slope (up to 10 orders) in the distance decay plot, indicating the impact of distance decay on the turnover of commoner species (Figure 4.1a). This suggests that the *castaniceps* complex is not simply composed of highly local species; rather, several species appear to persist across multiple sites before geographic distance starts eroding shared composition.

On the other hand, the slope showed a second-order downward tendency in the *cantator* and *borealis* groups and followed the same trend in the *cantator* group. Its longitudinal distribution indicates that distance decay has a significant impact on the turnover of rare species (Figure 4.1b). By the fifth order, however, the trend in the borealis group had slowed down and had negligible ζ decrease values (Figure 4.1c). Thhis indicates rarer species structure early turnover in the *cantator* group, while the *borealis* group is dominated by a small number of widespread species.

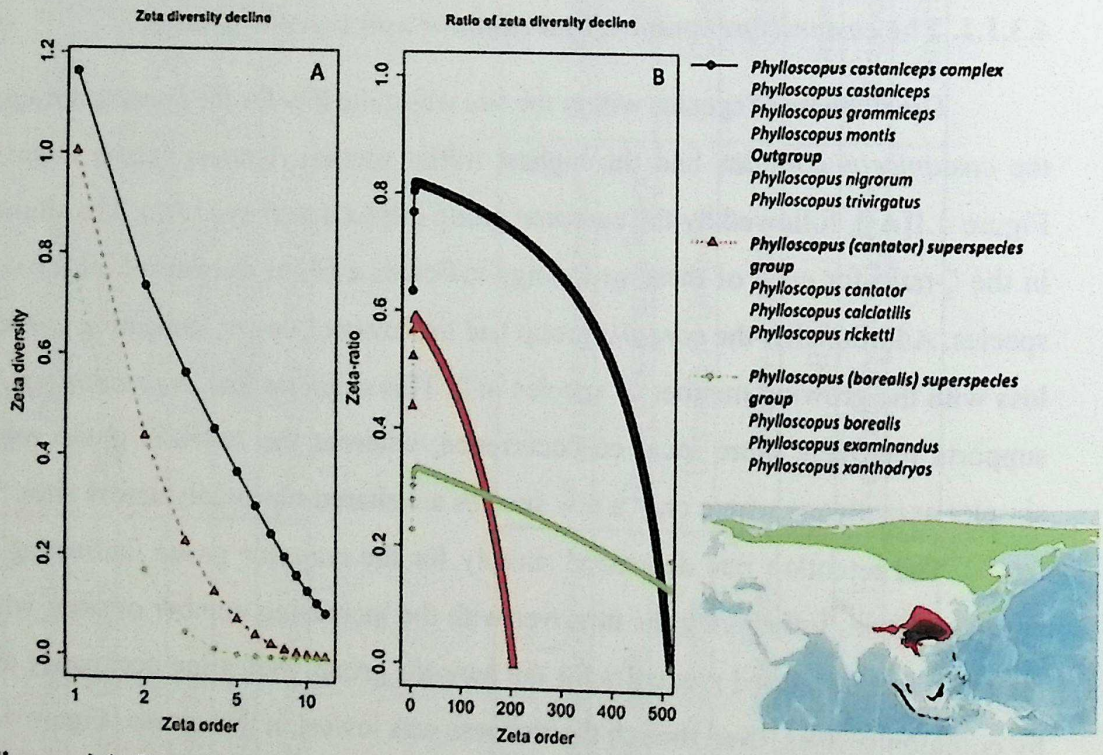


Figure 4.1. Zeta diversity of the species of the *P. castaniceps* complex, *P. cantator* group and *P. borealis* group. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these three groups is illustrated in the map.

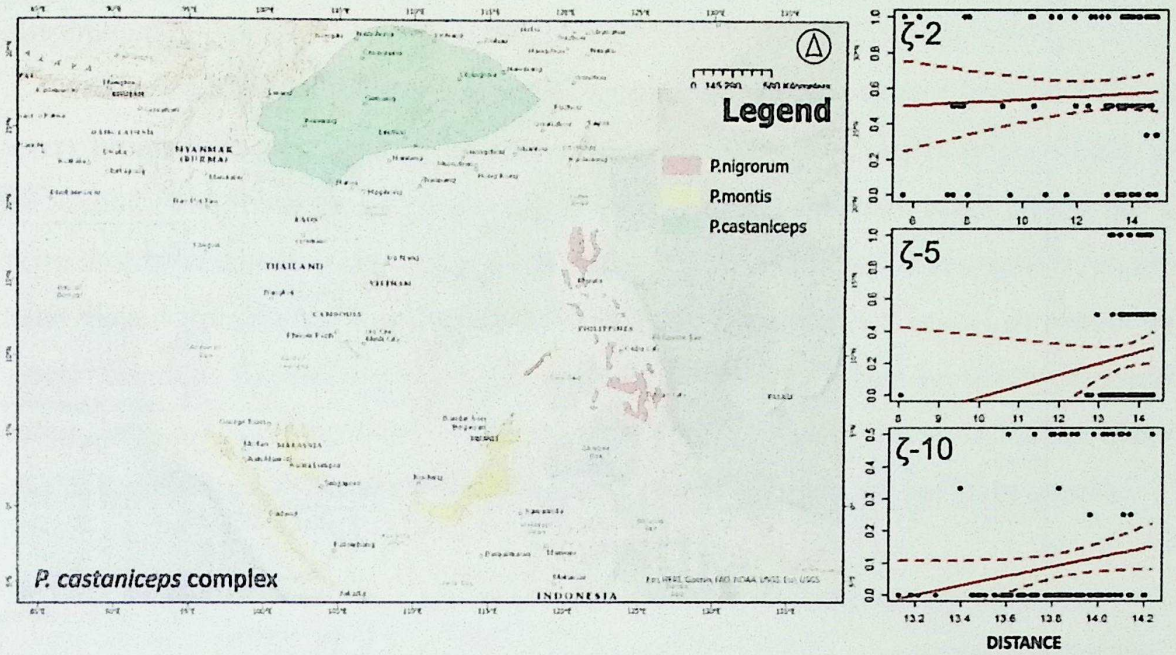


Figure 4.1a. Distribution of *P. castaniceps complex* and zeta diversity decay over space, for zeta orders 2 to 10, showing change in number of species shared with increasing distance between sites.

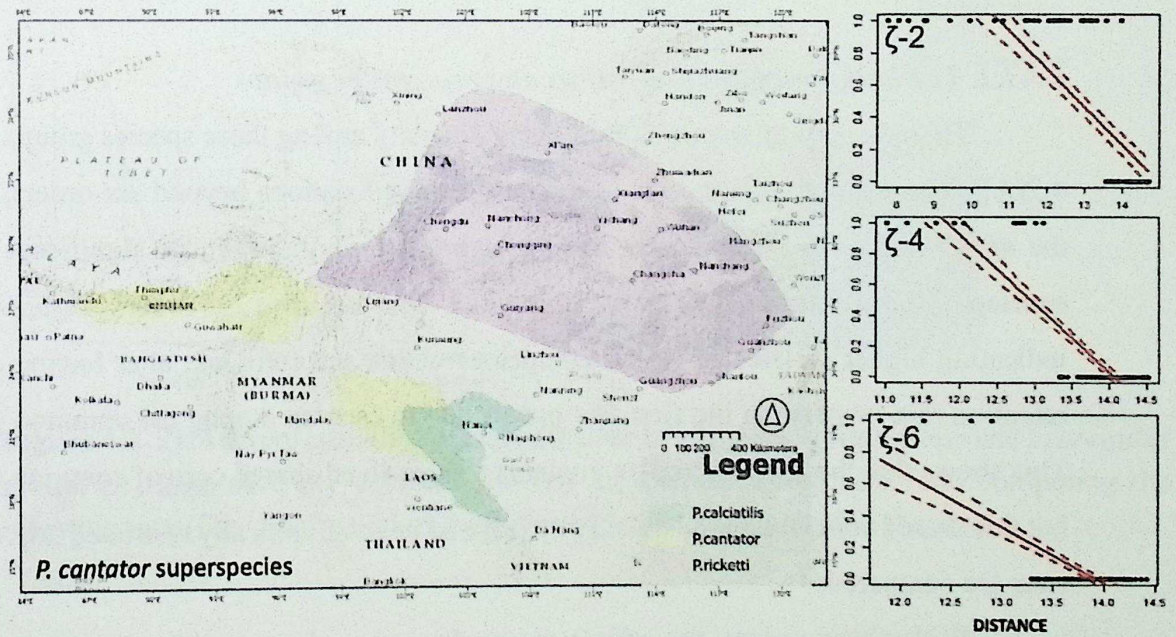


Figure 4.1b. Distribution of *P. cantator* group and zeta diversity decay over space, for zeta orders 2 to 6, showing change in number of species shared with increasing distance between sites.

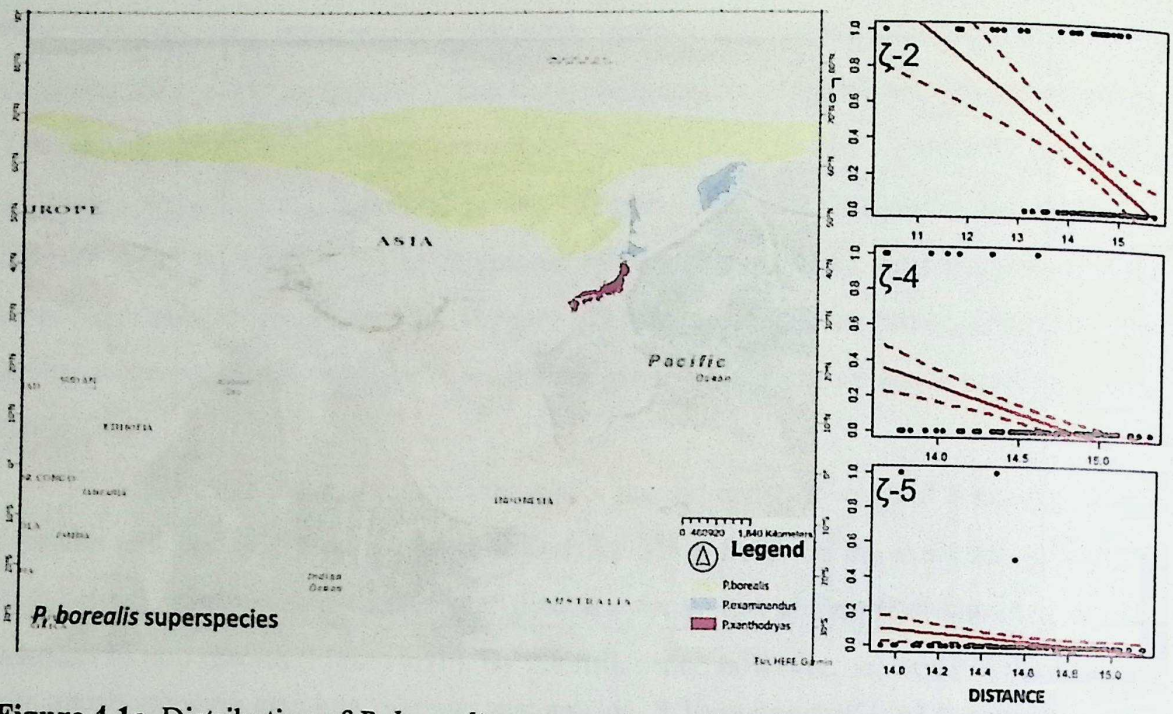


Figure 4.1c. Distribution of *P. borealis* group and zeta diversity decay over space, for zeta orders 2 to 5, showing change in number of species shared with increasing distance between sites.

4.3.1.2. The burkii complex and affinis and proregulus groups

There is very little variation in alpha diversity among these species groups (Figure 4.2[A]). Interestingly, no species is shared between locations beyond six orders, despite the *affinis* and *proregulus* groups having high ζ decays that indicate significant species overlap. The restricted *burkii* complex exhibits a rapid fall up to 200 orders (Figure 4.2[B]), indicating higher isolated or restricted species within the complex, after having a larger retention rate increase in the first few orders due to overlap among the common species. This shows that the *burkii* complex contains a short-lived shared core of common species, but this shared core is replaced quickly by isolated or geographically restricted taxa as more sites are compared.

With rising orders, the *affinis* group showed an intermediate drop, indicating a limited retention of the rarer species. In contrast, the *proregulus* group saw a slow, nearly linear decline, indicating a greater turnover of common species among sites. This can be the result of complex-related adaptive variables or species abundance. The *affinis* group is influenced by restricted species at intermediate scales, whereas, the *proregulus* turnover

may reflect gradual replacement among species with more continuous or broder distributions.

The longitudinally dispersed *burkii* complex, unlike the *cantator* group, exhibited a very progressive drop trend in the distance decay in the same ζ orders (Figure 4.2a). In the second order, both the geographically dispersed *affinis* and *proregulus* groups had a sharp drop with spatial decay (Figures 4.2b and 4.2c). Nonetheless, the *proregulus* group's trend dipped from the third order, indicating that site proximity had less of an impact on species turnover. It implies that geographic distance strongly divides rare species at lower orders, but once more localized species are lost, elevational or broader ecological filters may become critical components for the turnover, rather than simple spatial proximity.

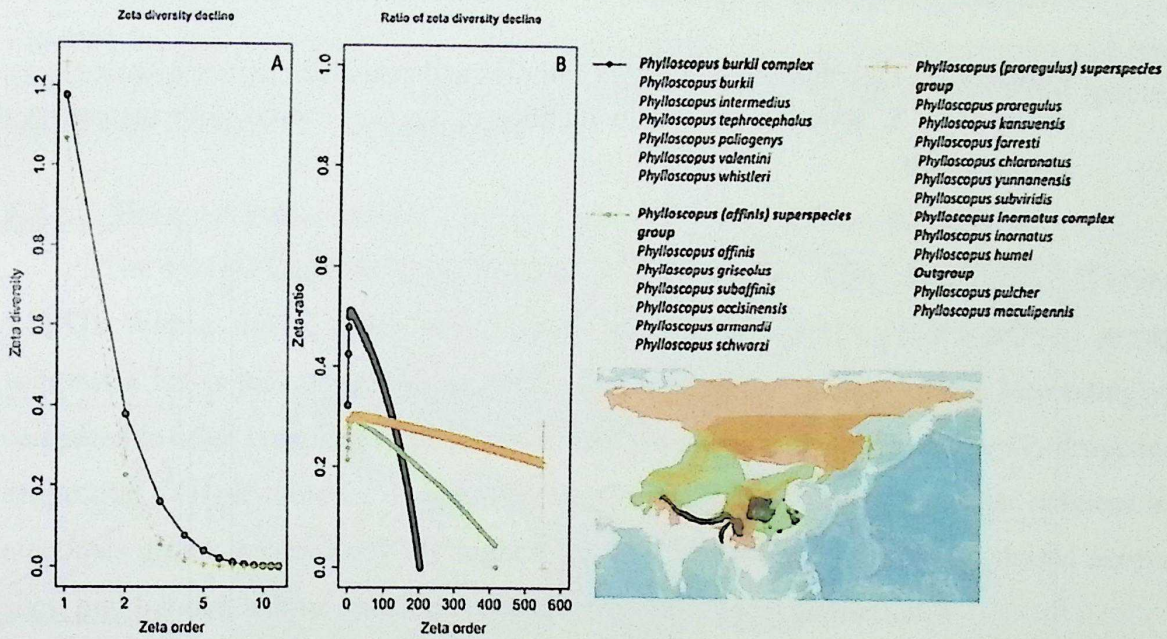


Figure 4.2. Zeta diversity of the species of the *burkii* complex, *affinis* group and *proregulus* group. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these three groups is illustrated in the map.

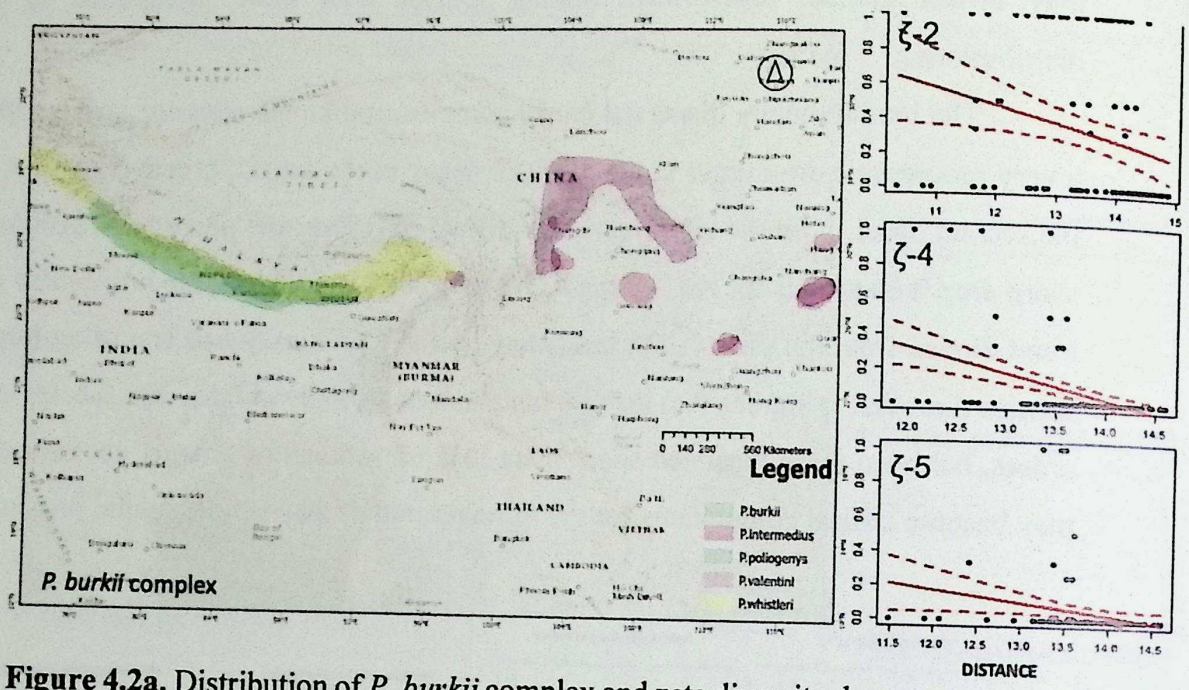


Figure 4.2a. Distribution of *P. burkii* complex and zeta diversity decay over space, for zeta orders 2 to 5, showing change in number of species shared with increasing distance between sites.

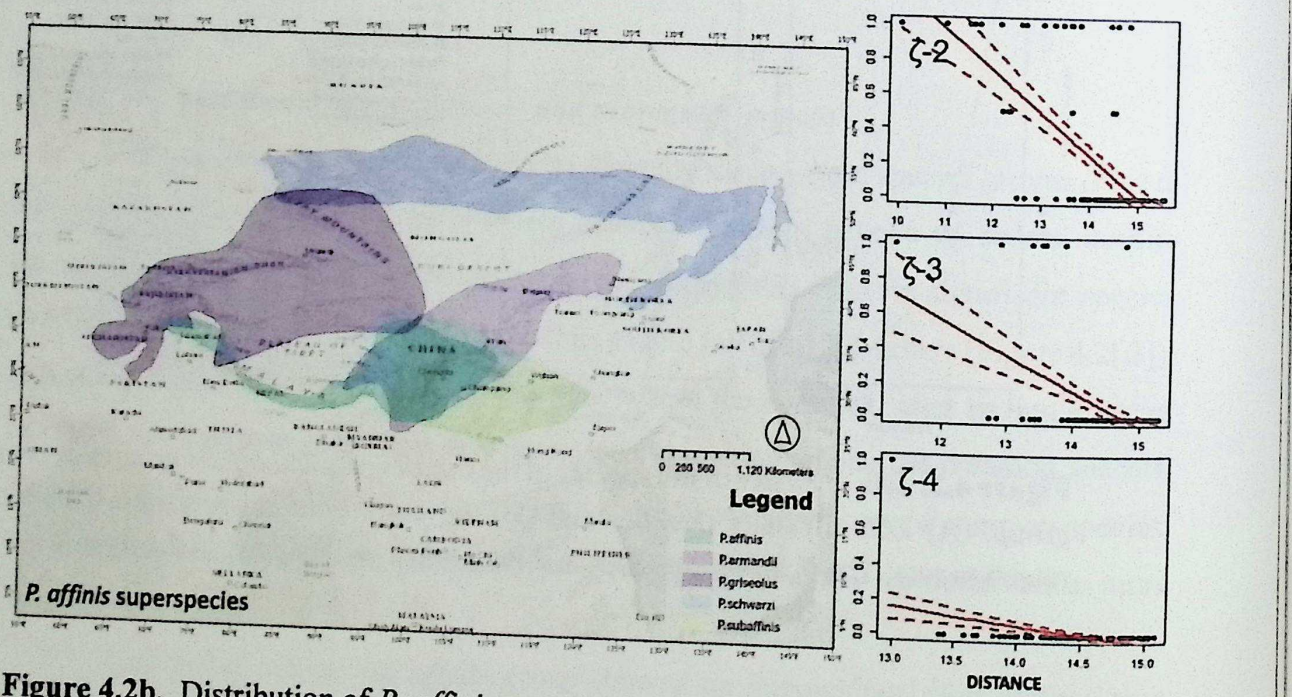


Figure 4.2b. Distribution of *P. affinis* group and zeta diversity decay over space, for zeta orders 2 to 4, showing change in number of species shared with increasing distance between sites.

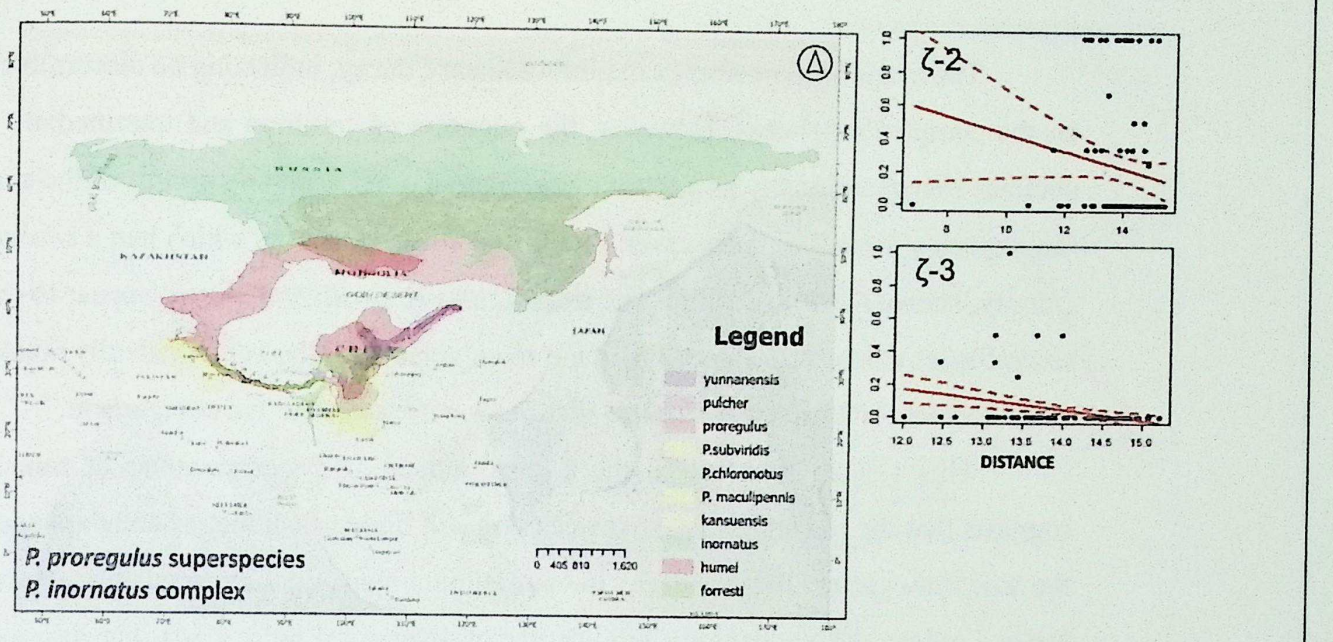


Figure 4.2c. Distribution of *P. proregulus* group along with *P. inornatus* complex and zeta diversity decay over space, for zeta orders 2 and 3, showing change in number of species shared with increasing distance between sites.

4.3.1.3. The trochiloides complex and davisoni, collybita and tenellipes groups

The species turnover in each complex was different in this combination (Figure 4.3[A]). With a slow ζ decay and a higher alpha diversity (1.1), the *tenellipes* group suggests a lesser loss of species as orders or groupings of sites increase. Interestingly, compared to other complexes, the retention rate was extremely low and abruptly dropped, suggesting a larger turnover of rarer species (Figure 4.3[B]). Although local richness in *tenellipes* group is comparatively higher, the species are not consistently shared across sites, highlighting habitat-specific occupancy or strong local restriction.

Similar trends were seen in the *davisoni* group's species richness, where common species only overlapped for a small number of orders. However, the retention rate gradually decreased for almost 3000 orders before decreasing, indicating that intermediate species had an impact on the complex's turnover. The *trochiloides* complex and the *davisoni* and *collybita* groups exhibit a progressive slope in all ζ orders of distance decay, indicating that they have an impact on the turnover of intermediate species (Figures 4.3a–4.3c). This suggests that both the groups are not dominated by only widespread species or by narrow local endemics, but by species with intermediate distributions that are progressively replaced across space.

The *trochiloides* complex exhibits a linear ζ decay, indicating no discernible impact on the complex's richness. However, the retention of common and intermediate species declines sharply, possibly as a result of substantial overlap among groups of the complex's rarer species. However, after seven orders, the *collybita* group, which had a similar linear ζ decay, showed a slow decline. The *trochiloides* and *collybita* groups appear to represent assemblages where shared composition is maintained initially, but it gradually breaks down when species with different regional distribution are added to the comparison.

This sudden decrease in the ζ-ratio, indicating faster turnover of rare species, suggests that the retention of rare species was still higher than that of common species. In the *tenellipes* group, distance decay has a minimal impact on the compositional turnover at lower ζ orders, despite having a high degree of diversity (Figure 4.3d). The decay exhibits a rising trend with the number of sites (up to the 63rd order, after which the predicted ζ values are negligible), confirming the rapid turnover of rarer species with site proximity. This highlights the sensitivity of the *tenellipes* group to local habitat conditions.

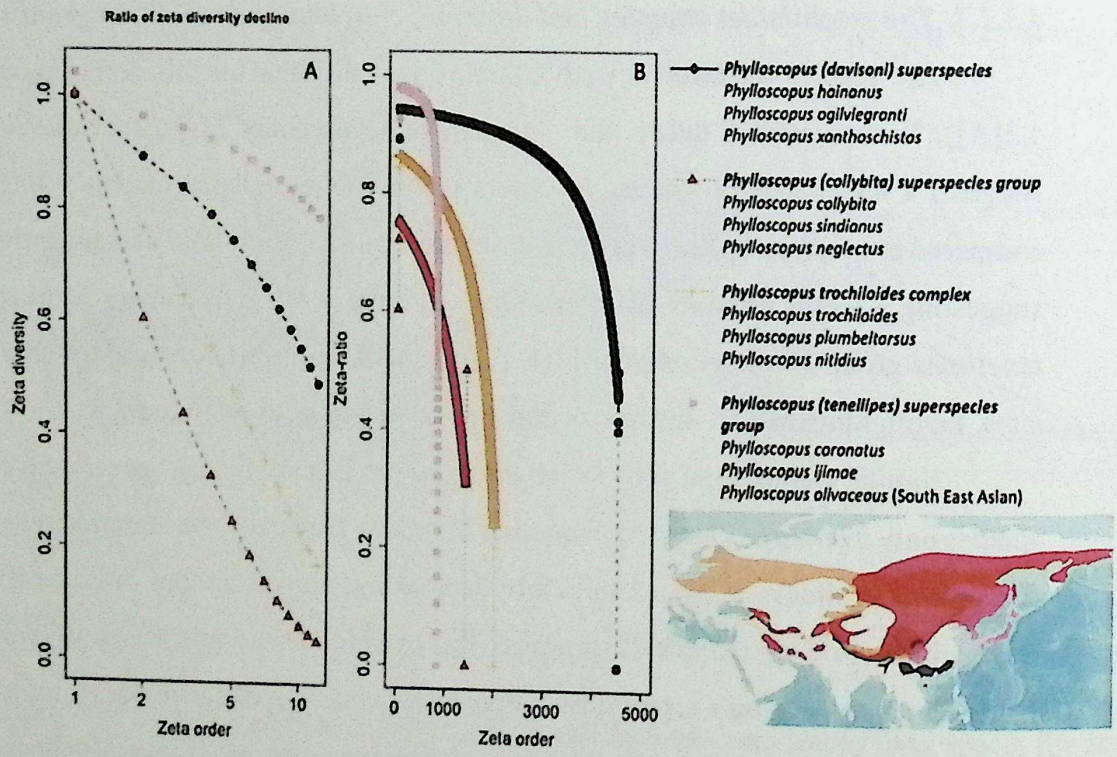


Figure 4.3. Zeta diversity of the species of the *davisoni*, *collybita* and *tenellipes* groups and the *trochiloides* complex. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these four groups is illustrated in the map.

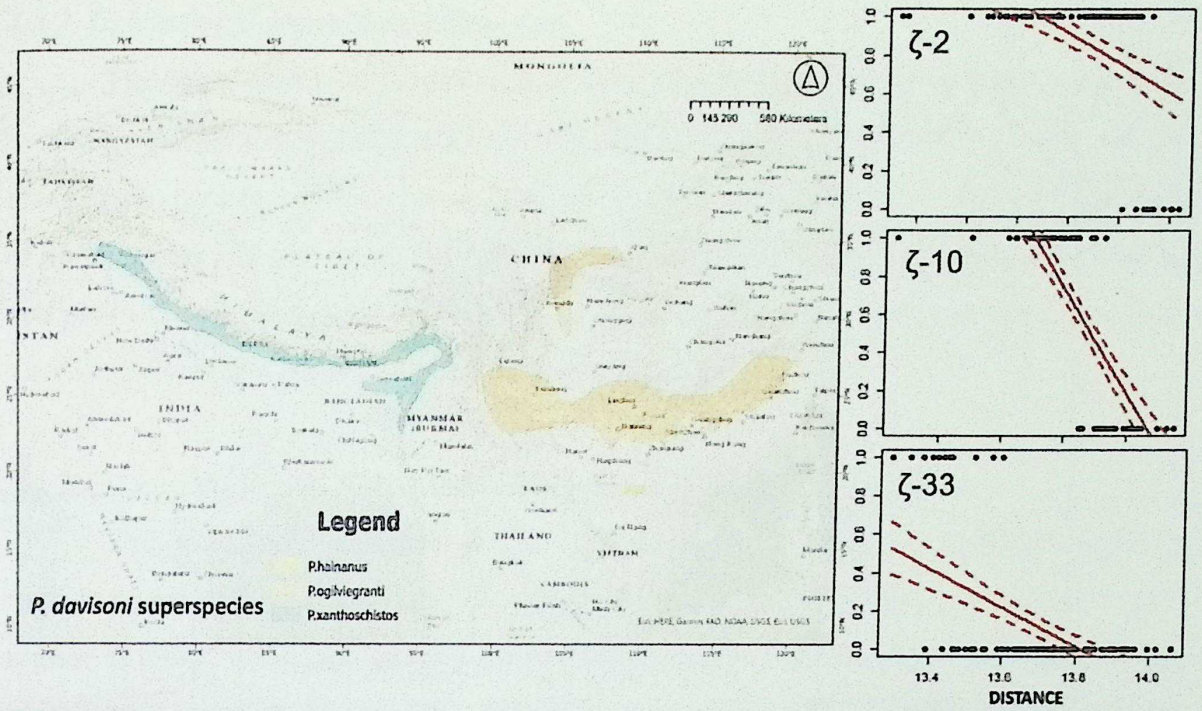


Figure 4.3a. Distribution of *P. davisoni* group and zeta diversity decay over space, for zeta orders 2 to 33, showing change in number of species shared with increasing distance between sites.

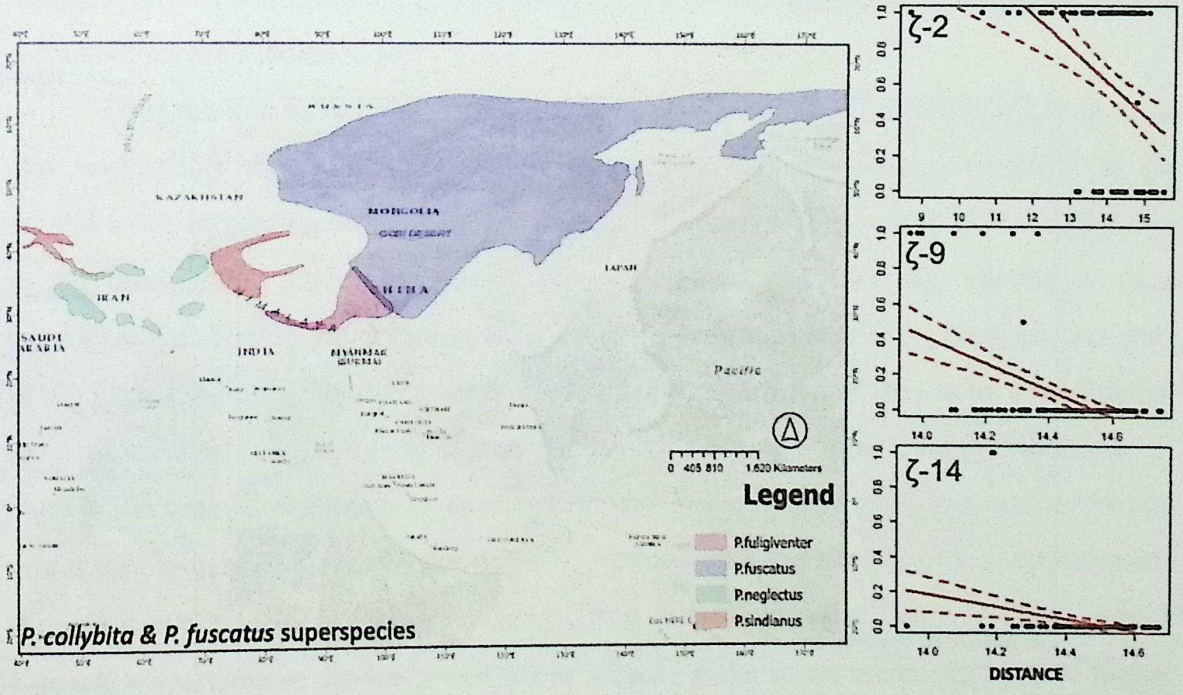


Figure 4.3b. Distribution of *P. fuscatus* group with *P. collybita* group and zeta diversity decay over space, for zeta orders 2 to 14, showing change in number of species shared with increasing distance between sites.

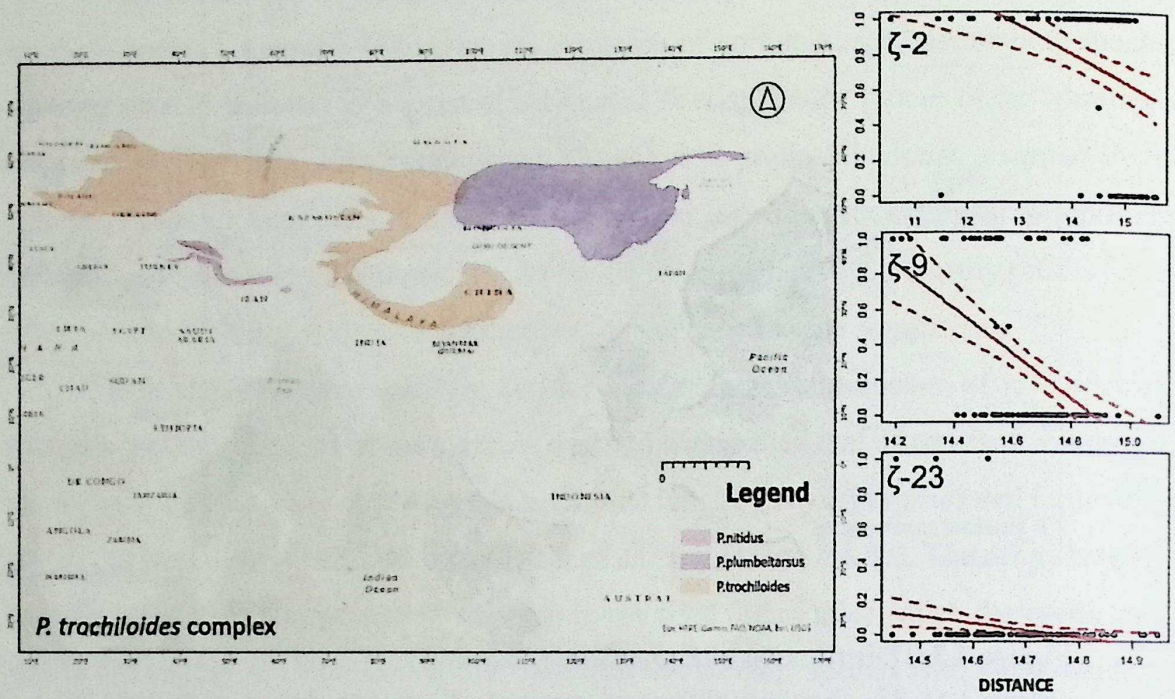


Figure 4.3c. Distribution of *P. trochiloides* complex and zeta diversity decay over space, for zeta orders 2 to 23, showing change in number of species shared with increasing distance between sites.

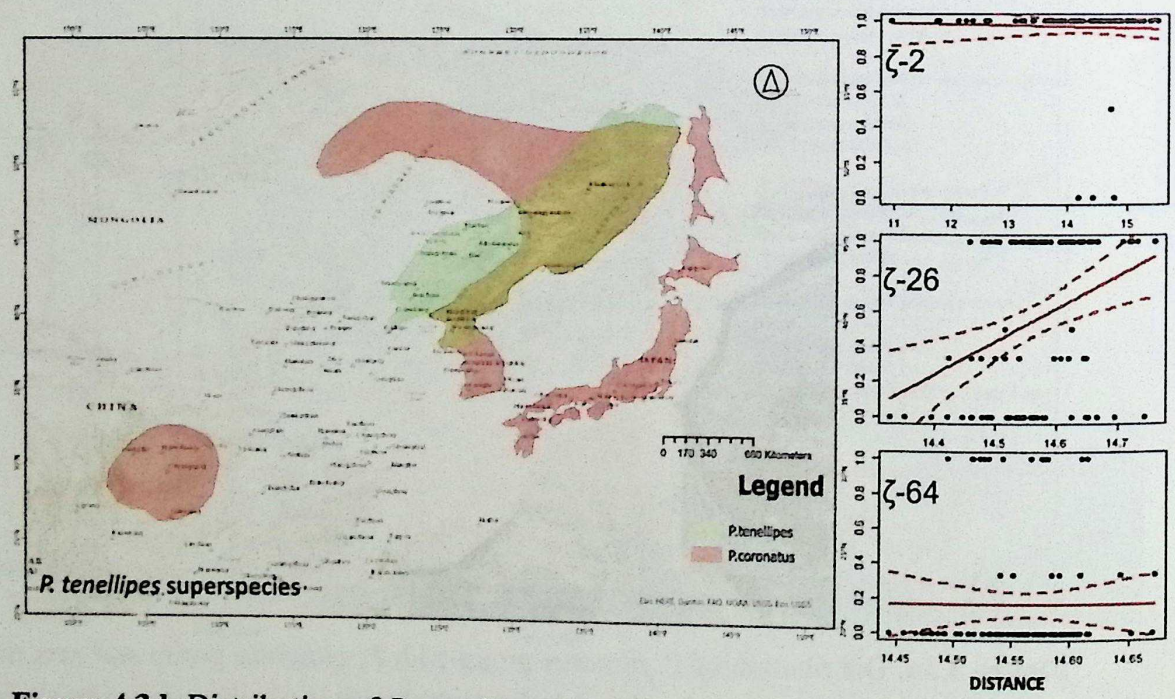


Figure 4.3d. Distribution of *P. tenellipes* group and zeta diversity decay over space, for zeta orders 2 to 64, showing change in number of species shared with increasing distance between sites.

4.3.2. Drivers of Compositional Turnover

The MS-GDM I-spline curve show how each environmental predictor contributes to compositional turnover across its observed range. The steep sections of a curve indicate environmental ranges where species turnover rapidly, whereas flatter sections indicate little or no turnover. The maximum height of the curve indicates relative strength of a predictor at a given ζ order, with lower ζ orders reflecting turnover among rarer species and higher ζ orders reflecting turnover among widespread species.

4.3.2.1. The castaniceps complex and cantator and borealis groups

The NDSI was found to be the most significant factor of the *castaniceps* complex's species turnover (Figure 4.4[A]). The group's turnover was impacted by the greater NDSI regime at lower orders, but as the ζ orders (group of sites) increased, the variable had less of an impact under the lower NDSI regime. This can be because generalist species migrate to regions with less snow or because their breeding range is not dependent on snow. This suggests that snow-associated habitats influence regional or local sorting in the *castaniceps* complex, but the widespread species are less tightly constrained by snow once broader site combinations are accounted for.

Only the first three orders showed significant i-splines for the *cantator* group; after that, no variable showed any discernible impact on the compositional turnover. In the second level, increasing latitude had a significant impact on turnover (Figure 4.4[B]), but in the third order, the impact substantially decreased. Additionally, all orders were somewhat impacted by gravity anomalies, changing longitude (entire regime), and aerosols in the higher regimes. The turnover in *cantator* groupis primarily driven by low-order or local differences, suggesting region-specific habitat filtering or restricted distributions.

The main determinant of species turnover in the *borealis* group is the lower and moderate elevation regime (Figure 4.4[C]). Additionally, the second order and elevation showed a minor influence from the normalised difference water index (NDWI), which measures variations in the water content of leaves, in the lower water regime and higher latitudes. The *borealis* group is mainly structured by elevational partitioning, with latitude and moisture acting as secondary filters in determining where species overlap.

4.3.2.2. The burkii complex and affinis and proregulus groups

The *burkii* complex's species turnover was found to be influenced by increasing longitude, gravitational anomaly, and aerosol (Figure 4.5[A]). Beyond six orders, the gravity anomaly effect was more pronounced, while the effect of the other components decreased. Additionally, the species complex in the lower orders of ζ was marginally impacted by brighter night light. The broad montane structure becomes increasingly important for explaining shared composition across the *burkii* complex, while local effects are more relevant where only few species or sites are compared.

Only a few ζ orders exhibited substantial i-splines in the *affinis* group. The key determinant of species composition turnover in the higher regime was found to be the decay disturbance index (Figure 4.5[B]). Furthermore, the findings suggest that artificial night lights in the lower light regime and a gravity anomaly in the middle regime may have a minor impact on the group's species composition. The *affinis* group may be more sensitive to regional disturbance than to a single broad-scale environmental gradient.

After a few orders, the *proregulus* group's i-spline drops resemble those of the *affinis* group. Over the course of its reign, elevation remained the determining factor. In the second order, both the lower decay disturbance index regime and the lower NDWI regime significantly impacted the compositional turnover. The group turnover was also slightly impacted by increasing longitude in the third order (Figure 4.5[C]). The *proregulus* group is organized primarily along elevational gradients, but local moisture conditions at lower orders influences species replacement. The minor longitudinal effect suggests regional east-west distributional structure may contribute to turnover once immediate site-level overlap is considered.

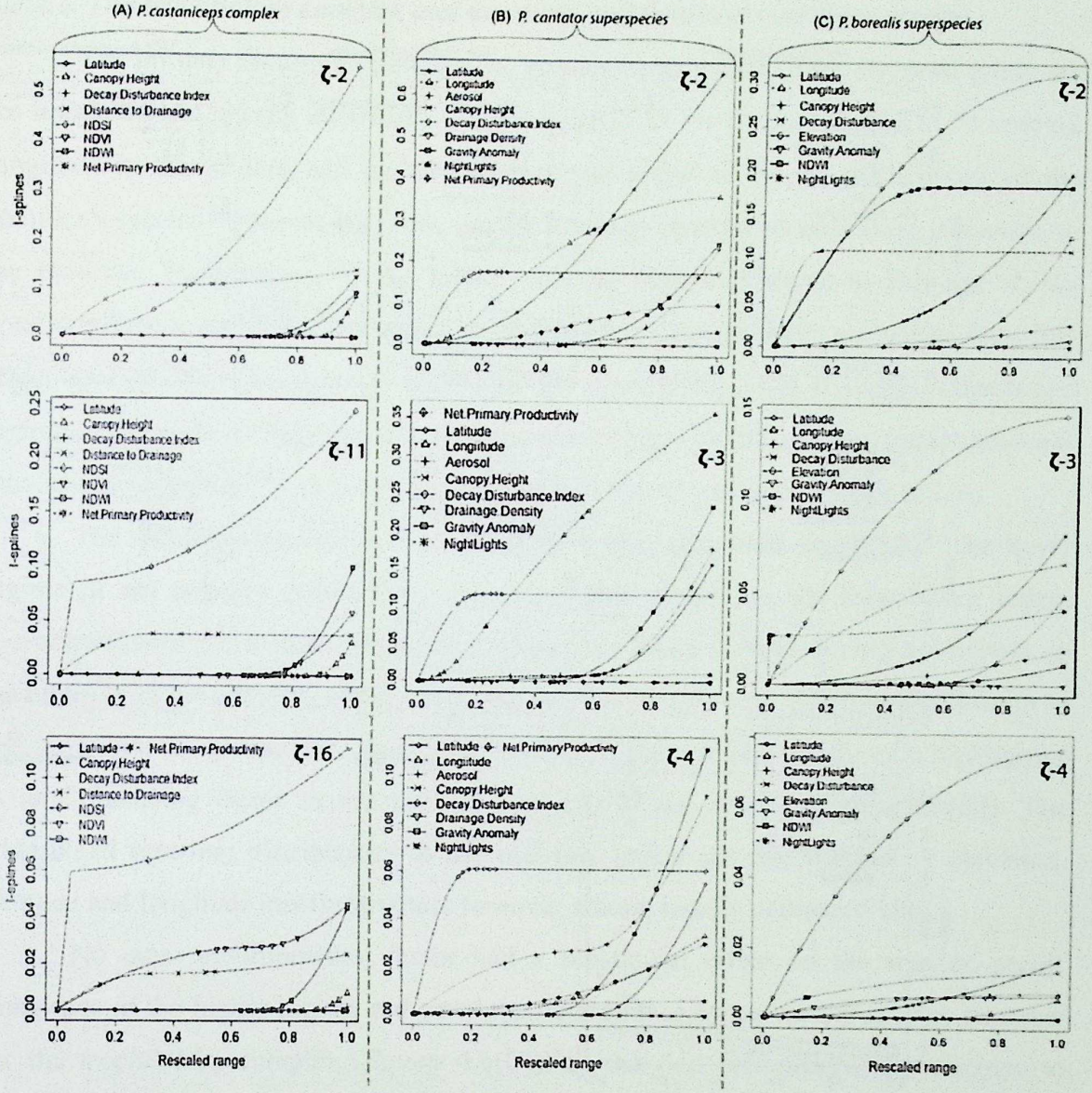


Figure 4.4. I-splines evaluated by multisite generalised dissimilarity modelling for the *castaniceps* complex (at ζ 2,11 and 16), *cantator* group (at ζ2,3 and 4) and *borealis* group (at ζ2,3 and 4), showing the contribution of environmental variables. The x-axis shows the rescaled range of each environmental predictor from low to high observed values, and the y-axis shows the fitted I-spline contribution to compositional turnover.

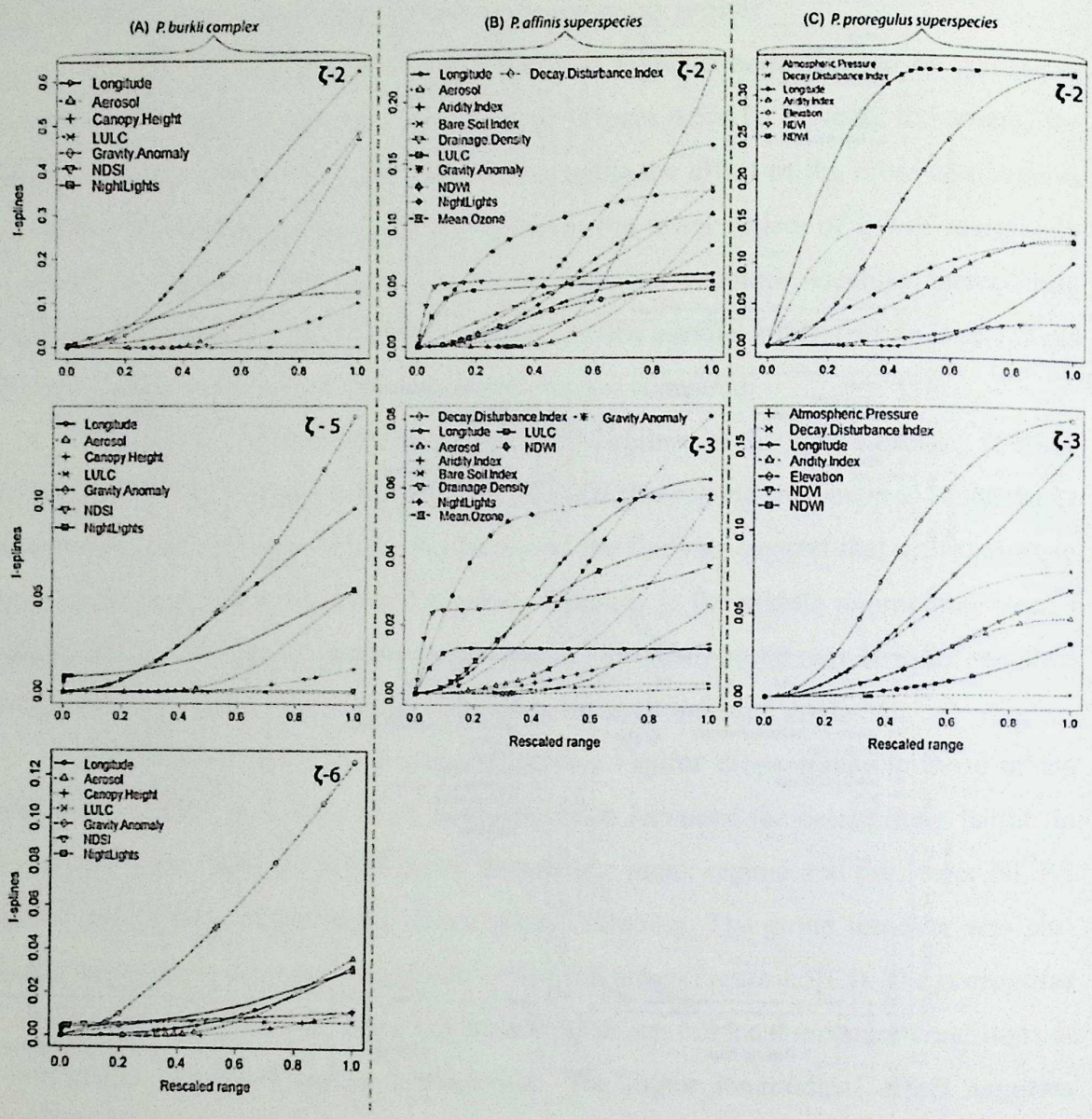


Figure 4.5. I-splines evaluated by multisite generalised dissimilarity modelling for the *burkii* complex (at ζ 2,5 and 6), *affinis* group (at ζ2 and 3) and *proregulus* group (at ζ2 and 3), showing the contribution of environmental variables. The x-axis shows the rescaled range of each environmental predictor from low to high observed values, and the y-axis shows the fitted I-spline contribution to compositional turnover.

4.3.2.3. The trochiloides complex and davisoni, collybita and tenellipes groups

The primary factors influencing the species composition of the *davisoni* group are the longitude and gravity anomalies (Figure 4.6[A]). In lower ζ orders (up to 24 orders), longitude in the middle and higher regimes was found to be the main driver of the complex's species turnover; after that, gravity anomaly showed an increasing influence on the turnover. Furthermore, in the higher distance regime, distance-to-drainage shows greater influence in the last few orders, even though we expected this element to have less effect because of the low i-spline value (i-spline at order 50: 0.13). It suggests that broad regional position first likely separate *davisoni* assemblages, while montane terrain becomes increasingly important in explaining persistence of shared species at higher orders.

The species composition of the complex is also marginally impacted by the lower regime of net primary productivity and the higher regime of the disturbance index. Elevation (lower and middle elevation regimes) was found to have the highest impact on the turnover of the *collybita* and *fuscatus* groups. Due of the wide breeding distribution of species within the groups, the lower longitude and higher latitude regimes are highlighted as an influencing factor in the lower orders (up to six orders) (Figure 4.6[B]). The widespread breeding distributions in the *collybita* group are still filtered by elevation. Latitude and longitude mostly structure turnover among locally compared sites.

No other environmental factor had a substantial effect on the species group. Longitude in the higher regime remained the determining factor for the species turnover for the *trochiloides* complex (Figure 4.6[C]). In the first few orders, the distance to settlement and higher soil moisture had limited effect. Large-scale geographic structure dominates *trochiloides* turnover, with local factors like disturbance and moisture exerts weaker pressure.

In the lower aridity index, the *tenellipes* group had a significant impact on aridity. On the other hand, the species turnover in this group was influenced by the bare soil index in the higher and lower regimes of the NDWI (Figure 4.6[D]). Finally, the higher orders were influenced by canopy height (in the lower height regime). The *tenellipes* assemblages are shaped by open, dry, and structurally low habitats, suggesting aridity or ground exposure are central for the ecological sorting of this group.

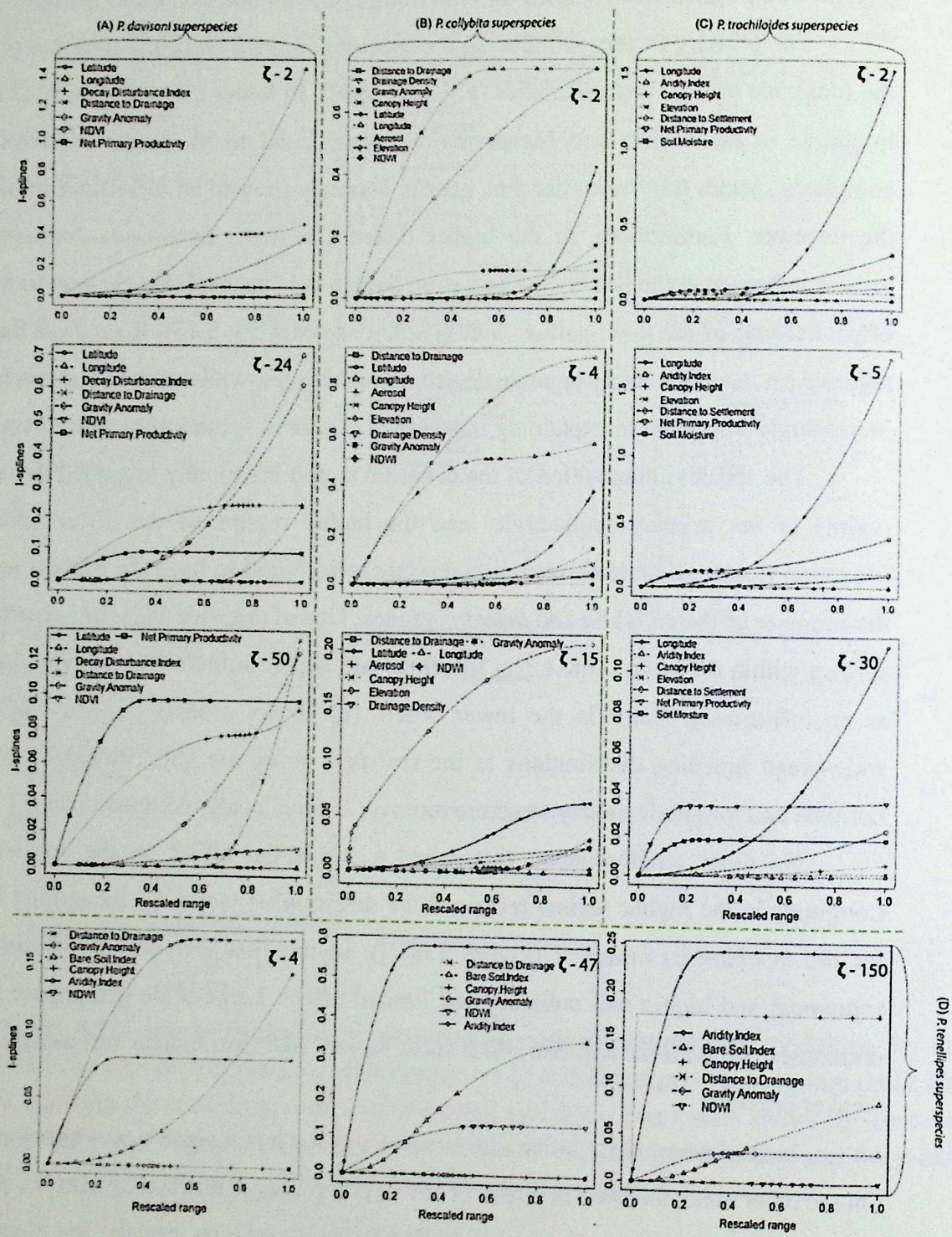


Figure 4.6. I-splines evaluated by multisite generalised dissimilarity modelling for the *davisoni* group (at ζ 2,24 and 50), *collybita* group (at ζ2,4 and 15), *trochiloides* complex (at ζ2,5 and 30) and *tenellipes* group (bottom, at ζ4,47 and 150), showing the contribution of environmental variables. The x-axis shows the rescaled range of each environmental predictor from low to high observed values, and the y-axis shows the fitted I-spline contribution to compositional turnover.

4.4.1. The castaniceps complex and cantator and borealis groups

The turnover of the *castaniceps* complex, which initially declined gradually followed by a steep drop, reveals the species composition of intermediate (*montis*) and uncommon (*grammiceps*) species within the group. Despite having somewhat distinct breeding sites, all three of these species are reported to cross paths in a fairly limited area in the Sumatran mountains (Martens 2010) (*https://birdsoftheworld.org*). Only the representative species (*castaniceps*) has a breeding range that is close to snowy areas; the other species are mostly found in Southeast Asia, which stretches as far as Indonesia and the Thai-Malay Peninsula. It explains why the complex initially retains shared species but eventually loses overlap, because species occupy partly different elevational and regional environments.

This could be the explanation for the findings, which point to NDSI as the primary cause of species turnover in this complex. Highlighting new sites and ranges from Nenjiang, northern China, where five months of snowfall are expected each year, is especially crucial (Li et al. 2012). Studies have indicated that species prefer an intermediate amount of snow cover, which is in line with their foraging tactics. Snow cover may simply not act as a climatic barrier, but may create foraging opportunities. Birds either use the melting borders of snowfields, where they can locate an abundance of larvae, one of their favorite and easiest-to-acquire prey items (Cramp, Perrins, & Brooks 1994), or they collect fallout from trapped invertebrate prey on the snow surface (Antor 1995).

The retention rate for the cantator group must have dropped drastically as a result of site-specific species (*calciatilis*) impacting turnover with an increasing number of locations. The impact of a positive gravity anomaly as a turnover driver at higher elevations is likely responsible for the patchy breeding distribution of *cantator* in the Himalayas and Southeast Asia. The *cantator* pattern clearly reflects a more fragmented assemblage in which terrain-associated range breaks and localized species dominate turnover.

Within the site, the *borealis* group has the lowest ζ decay with the least richness. A slight rise in the ζ-ratio indicates that the species (*examinandus*, *borealis*, and *xanthodryas*) have some overlap. Elevational preferences, which have also been identified as a major influencing factor for species turnover in this group, are contrasted by the relatively smaller range of *examinandus* and *xanthodryas* (see Saitoh et al. 2010) and the wide Palearctic

breeding distribution of *borealis* (one of the largest breeding distributions of all *Phylloscopus*). This, the *borealis* group appears to be structured by an imbalance between one widespread species and more elevationally restricted relatives.

4.4.2. The burkii complex and affinis and proregulus groups

Over the course of its complex evolutionary history, the *burkii* complex underwent vicariance as well as vertical and probably horizontal parapatry throughout the Sino-Himalayan region (Alström & Olsson 1999; Martens et al. 1999; Päckert et al. 2004). Most of the species in this complex occur at consistent elevations along continuous mountain belts (Päckert et al. 2004). Our findings show a higher retention rate in the first few orders due to the overlap in the breeding ranges of the common species (*burkii* and *whistleri*). This early retention reflects a shared montane component within the complex, where some species partially or narrowly overlap across neighbouring elevational belts.

The complex may contain more isolated species, though, as indicated by a steep fall. This is probably because the breeding ranges of several species (*soror*, *valentini*, and *omeiensis*) are dispersed across small, isolated mountaintops in China, and these species, along with *whistleri*, most likely evolved in northern refuge areas (Päckert et al. 2004). The results also show that the main cause of the compositional turnover in this complex is the positive gravity anomaly, which relates to elevation. The steep decline after initial retention suggests that the complex is a mosaic of shared isolated montane endemics and widespread species.

In regions with greater elevational gradients, gravity anomalies impact the energy needs of different bird species by acting as a geophysical barrier to their seasonal migration (Blaser et al. 2014). Remarkably, during the breeding season, Martens et al. (2003) and Martens, Tietze, & Päckert (2011) documented the presence of three species along a single forest edge. An intermediate retention of the rarer species with rising orders (likely *subaffinis* and *armandii* due to the scarcity of breeding sites) is indicated by an intermediate fall in the *affinis* group. Our MS-GDM results suggest that artificial night lights in the lower light regime and gravity anomalies in the middle elevational gradients may have a minor impact on the species composition of the group. Gravity anomaly should be treated cautiously, as it is treated as a coarse physiographic proxy for mountain structure, terrain

complexity, and potential dispersal barrier. This interpretation can be supported by the evidence that gravity anomalies can influence navigation and movement in pigeons (Blaser et al. 2014), however, its direct relevance for leaf warblers remains uncertain. Some *Phylloscopus* assemblages may be structured at fine spatial scales, where closely related species may occur near one another but can remain separated by microgeographic borders, habitats, or elevation.

Similar to the *burkii* complex, the *proregulus* group is another excellent example of diversity in the Sino-Himalayan region (Päckert et al. 2004). The majority of the species in this group are found in breeding distributions that are concentrated in areas where elevation most likely influenced the species' composition and ranges. The montane structure remains a dominant filter for Sino-Himalayan groups. The compositional turnover was significantly impacted by the NDWI in addition to the lower decay disturbance index regime of this group. Moisture availability and low disturbance habitats further refine species replacement within elevationally structured mountain assemblages.

4.4.3. The trochiloides complex and davisoni, collybita and tenellipes groups

This greenish warbler (*trochiloides*) complex exhibits a rapid drop in retention, indicating extensive overlap between geographical variants. The findings indicated that soil moisture was a contributing factor, which is explained by the fact that *P. trochiloides's* breeding distribution shows a gap in the arid, forested region of northern China (Martens 2010). While soil moisture mostly determines the vegetation composition of different regions, it also influences the region's primary productivity and insect abundance (Onrust et al. 2019). Soil moisture likely acts as a resource-linked filter, affecting both insect prey availability and vegetation structure.

These elements might be very important in habitat specialisation. A progressive slope in all ζ orders of distance decay is also seen in the *collybita* and *davisoni* groups, suggesting that it influences the turnover of intermediate species. Given the patchy breeding distribution ranges of *sindianus* and *neglectus* and the relatively wide-ranging *collybita*, elevation was found to be the main driver of species turnover for the *collybita* group. This shows that even groups containing widespread species can show strong turnover when tied to specific regional and elevational habitats.

Once more, it was found that the *davisoni* group, which is primarily found in the mountainous areas of China and the Himalayas, is primarily driven by species turnover due to gravity anomalies. The gravitational variance within mountain ranges may limit the movement of these species, just like it did for the *burkii* complex (Blaser et al. 2014). Notably, the reduced aridity index had a major impact on the *tenellipes* group, indicating that the arid regions of northeastern China might have impacted the composition. The *davisoni* group fits the broader montane-fragmentation pattern, while the *tenellipes* group reflects turnover driven by open, dry, and regionally distinct habitats.

Additionally, it turned out that the bare soil index in the higher regime had an ambiguous effect on the species turnover in this group. All things considered, variations in diversity, ζ decay, and retention rates reflect the ecological processes and interactions that take place within breeding zones. Furthermore, limits such as competition for resources, habitat specialisation and environmental conditions could limit the coexistence of species, which may influence the patterns of diversity that were observed. Together, the turnover in *Phylloscopus* is produced by various ecological routes: disturbance filtering in restricted and disjunct groups, and broad-scale elevational filtering in widespread montane groups.

This information supports our second hypothesis, which maintains that factors like soil moisture and gravity anomalies, which are connected to specific geological features and impact net primary productivity (more pronouncedly seen in the *burkii* and *trochiloides* complex), have an impact on co-occurrence patterns within the complexes. These variables may be taken into account in the future when conducting ecological research related to environmental factors. Overall, the ζ and the MS-GDM results indicate that the present day *Phylloscopus* assemblages are shaped by the interactions between environmental filtering, historical range structure, and local habitat constraints.

4.4.4. Conclusion

Understanding compositional turnover, which aids in identifying habitat preferences and species resistance to environmental change, enables targeted conservation efforts. By means of an in-depth examination and knowledge of the connections between leaf warbler distribution and environmental variables like elevation, precipitation, soil moisture, and gravity anomaly, this study provides a passive understanding of the effects of

anthropogenic and environmental factors that affect these bird populations. It improves our ability to recognise and evaluate how ecosystems and biodiversity are impacted by climate change. With this knowledge, more efficient management techniques can be used to preserve fragile species and ecosystems. In light of this, cross-disciplinary collaboration is essential to developing a thorough ecological understanding in relation to climate change.

CHAPTER 5. VOCALISATIONS: SONGS, ELEVATION AND SISTER SPECIES

The synthesis of Chapters 3 and 4 illustrates how closely related *Phylloscopus* species frequently move into sympatric zones due to historical range shifts and current climatic filters. Certain processes must restrict reproductive isolation in these interaction zones. These strategies are discussed in Chapter 5, with a focus on vocal traits that species have developed to prevent competition and/or preserve reproductive isolation. In this chapter, we concentrate more on analyzing how vocal divergences—which are influenced by both species recognition and environmental features—serve to strengthen species boundaries.

5.1. INTRODUCTION

Because of a shared common ancestor, closely related species often display similar anatomy and behavior. However, signals may diverge when they coexist in order to reduce hybridization and enhance species recognition (Simpson et al. 2021). Exaggerated ecological and behavioral features are frequently the result of this divergence, which is a common outcome of competitive interactions between sympatric, taxonomically identical species (Schluter 2000; Pfennig & Pfennig, 2010). The change in species-specific vocal traits is also noticeable during sympatry (Miller 1982). These characteristics can be observed in sympatric areas and at the parapatry intersections of vertically stacked range belts, where species prefer to live in close proximity to one another (Martens et al. 2010).

With six recognized species, the *Phylloscopus burkii* complex is a well-known case study for examining song divergence. Throughout the Sino-Himalayan region (Alström & Olsson, 1999; Martens et al. 1999), these sister species (only taxa name used further unless attributed to a complex) underwent a complex evolutionary history that resulted in vicariance, vertical as well as horizontal parapatry, and local sympatry (Packert et al. 2004). Even though earlier research on this complex looked at sympatry patterns (Martens et al., 2003, 2011) and showed how shared ancestry influences acoustic traits (Packert et al.

2004), little is known about how evolutionary histories or ecological factors interact to shape acoustic divergence. Habitats have a significant influence on sound transmission; attenuation and reverberation in denser canopies favor lower frequency signals, whereas more open habitats prefer higher frequencies and wider bandwidths to prevent masking (Morton 1975). Acoustic transmission is significantly influenced by the density of the canopy, the vertical stratification of the vegetation, and its structure. Specifically, there are no such records of systematic examinations of how environmental variables affect song qualities of many species across various habitats (Wiley 1991; Saunders & Slotow, 2004).

Furthermore, the lack of evidence for interspecific territoriality or habitat segregation among a few species within the same complex (*tephrocephalus*, *omeiensis*, and *valentini*; Opaev & Kolesnikova, 2019) raises the possibility that song similarities stem more from shared ancestry than from ecological divergence. Since elevation modifies atmospheric conditions like air density, temperature, and relative humidity, it can influence acoustic attenuation and the transmission distance of a signal (Wiley & Richards, 1978). Relative humidity and temperature are known to affect sound speed and atmospheric absorption (Snell-Rood 2012), while canopy structure and vegetation density can alter signal degradation through scattering or reverberation (Aylor 1972; Yip et al. 2017). Given the elevation, little is known about how signals are transmitted in these syntopic assemblages, particularly where acoustic adaptation may be driven by interspecific masking or interference (Martens et al. 2003). All of these unresolved questions point to the necessity for a comprehensive study of how the *Phylloscopus burkii* complex's acoustic traits are shaped by both ecological adaptations and evolutionary history.

Environmental factors including height, vegetation structure, and canopy density have a significant impact on the ability of birds to transmit songs. Songs experience greater attenuation and reverberation in dense environments, which frequently favor slower, lower-frequency (more stereotyped) songs to reduce acoustic degradation (Morton 1975; Wiley & Richards, 1978). The Acoustic Adaptation Hypothesis (henceforth AAH; Rothstein & Fleischer, 1987), which postulates that birds may modify their vocal features to maximize signal transmission, particularly under environmental constraints, is based on these ideas. Meta-analyses (Boncoraglio & Saino, 2007; Ey & Fischer, 2009) have generalized these sites across species, and they have been crucial to many studies on

data—along with environmental data—provide additional insight about whether variations in frequency have been noted. These findings suggest that while elevation offers a selection constraint for frequency modulation, other factors—possibly associated with habitat structure and species-specific vocal adaptations—likely contribute to the observed disparities, even within similar elevational bands. Additionally, low frequencies are usually less degraded than high ones since high frequencies are more vulnerable to absorption, dispersion, and reverberation by the environment and vegetation (Aylor 1972; Marten & Marler, 1977; Martens 1980). As a result, it was crucial to find out if this pattern holds true in different environments or if ecological traits have altered frequency modulation in other ways. Therefore, it was necessary to analyze the songs on the basis of habitats.

Our results demonstrated that habitat structure greatly affects song frequencies, even though the specific patterns vary between species and geographical regions. More precisely, a variety of latent factors, such as plant species richness, canopy cover, and canopy height within a certain geographic area, are probably responsible for this fluctuation. In the context of AAH, our results should therefore be interpreted as evidence that song traits vary along elevation-vegetation gradient, rather than as evidence for a direct effect of elevation alone. Even though a general trend could suggest that dense forests favor higher frequencies with simpler syntax and open habitats favor lower frequencies with more complex syntax, the truth is more complicated than the frequency variation. While *whistleri* exhibits a clear altitudinal pattern, using lower frequencies in high-elevation coniferous forests and gradually higher frequencies within lower-elevation deciduous broadleaf forests (possibly as a result of increased acoustic competition), *burkii*, one of the Himalayan study species, exhibits slight variations in F_{max} within its range. Another argument is that low-frequency bands are more vulnerable to degradation over high-frequency bands when transmitted via undergrowth because of greater interference between both direct and reflected pathways (Römer 1992). Thus, vegetation structure may partly confound the apparent elevational signal, and both variables should be interpreted jointly.

Similar findings were obtained when we took into account Chinese species, where there is a discernible habitat-dependent acoustic variation in *soror*, with larger F_{max} in lush undergrowth compared to secondary growth in evergreen broadleaf forests. With the

birdsongs because they connect the physical features of the songs to evolutionary divergence in vocalisations. Beyond changes in frequency, ecological forces shape song complexity by affecting repertory size and syntax. The requirement for taxon-specific assessments in dynamic habitats is highlighted by recent syntheses (Freitas et al., 2025) that indicate insufficient support for the consistent effect of vegetation on songs.

We used the *Phylloscopus burkii* complex as a model to study three questions in order to address this: (1) In order to maximize transmission, we examined the AAH by looking at whether the song components differ predictably over habitat gradients (altitude, canopy height, or canopy cover) (Simpson et al. 2021). We hypothesised that if acoustic adaptation plays a vital role, we expect lower maximum frequency at higher elevations and open canopies and higher maximum frequencies at lower/ more dense habitats (Cosens & Falls, 1984; but also see Brown & Hadford, 1996); and (2) we tested whether species recognition selects for distinct song structures between sympatric species to minimize hybridization (Saetre et al. 1997). If reinforcement operates, we expect sympatric species (Himalayan species such as *whistleri* and *burkii*) to show greater divergence in critical traits like frequency modulation and note length (Seddon 2005). While AAH predicts habitat/environment-driven divergence, the species recognition hypothesis (SRH) predicts the divergence, especially where closely related species occur in sympatry.

Finally, we evaluated whether environmental variables, such as elevation and canopy structure, influence song richness—a surrogate for vocal complexity. We hypothesised that dense canopies, which are essential for obligate insectivores like our study species, may favour rich vocal repertoires to navigate cluttered acoustic environments, while higher elevations may reduce acoustic competition, leading to lower song richness. In addition to that, we explored whether regional habitat variations (e.g., Himalayan vs. Southeast Asian landscapes) promote divergent song adaptations and whether genetic distance alone accounts for residual song divergence after controlling for habitat effects. These inquiries collectively clarify how ecological selection and evolutionary history have shaped song evolution in *Phylloscopus* warblers.

5.2. MATERIALS AND METHODS

5.2.1. Acoustic data collection

The *whistleri, burkii, tephrocephalus, soror, omeiensis,* and *valentini* are the six species that we focus on most in this study. Acoustic data for species was collected from the Jammu and Kashmir, Himachal Pradesh, Uttarakhand, Sikkim, and Arunachal Pradesh states of India and Nepal (Appendix 3, ST1). We used the TASCAM DR-40 (v 2.30) digital audio recorder and RODE NTG4+ shotgun microphone to record acoustic data systematically over three years (2021-2023). The recordings were sampled at 44.1kHz and 24-bit resolution (manually adjusted gain levels) to minimise background noise. In addition, to enhance the dataset, we also included recordings from Myanmar, Laos, Cambodia, Vietnam, Thailand, and Bhutan (through xeno-canto.org; Appendix 3, ST2), and China (xeno-canto.org and personal communication) (see Figure 5.1 for a full distribution, which is georeferenced using range data from *www.birdsoftheworld.org*). All the recordings used in the final acoustic analysis were in WAV format. MP3 or lossy-compressed files were excluded since it can alter acoustic measurements and automated acoustic indices.

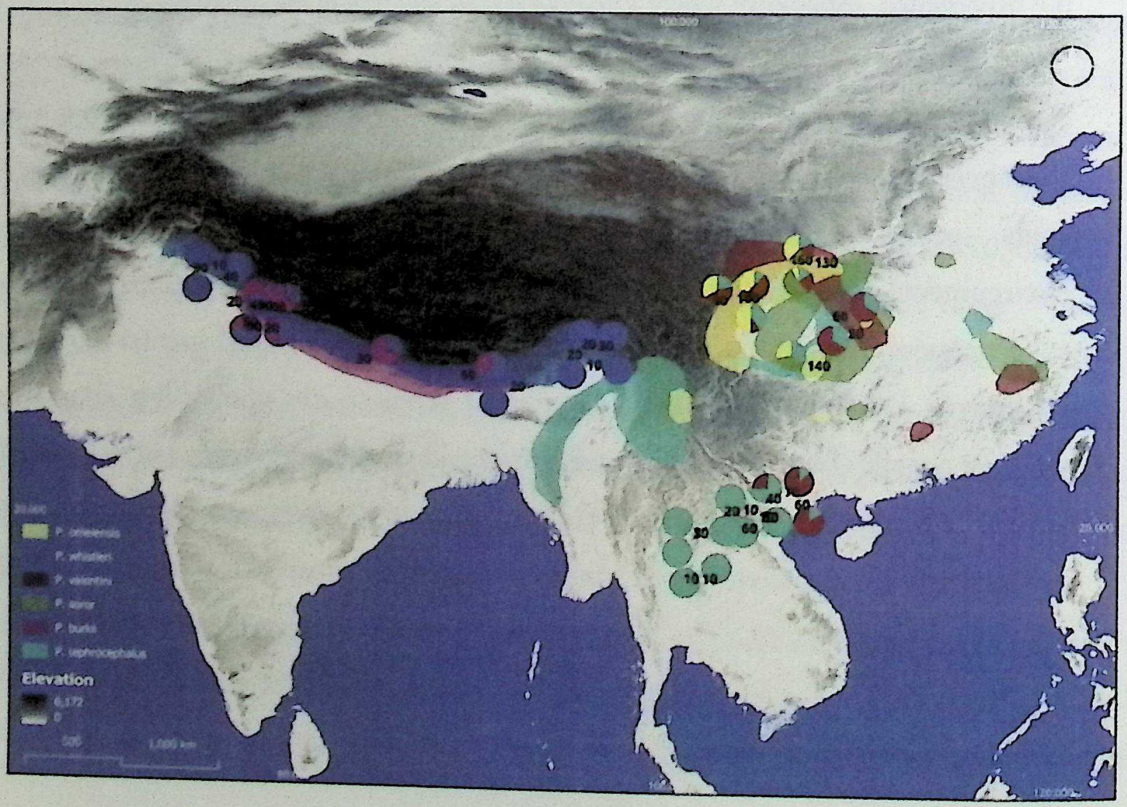


Figure 5.1. Distribution of *whistleri*, *burkii*, *valentini*, *omeiensis*, *soror*, and *tephrocephalus* as georeferenced from *https://birdsoftheworld.org/* along with recordings made.

5.2.2. Song annotation and extraction of parameters

We used Raven Pro (https://www.ravensoundsoftware.com) while strictly following manual annotation protocol for each audio file to ensure the accuracy and reliability of our results. Annotation followed a standardised protocol: (1) we only used recordings with high signal-to-noise ratio (> 20dB over ambient), (2) annotations were restricted to full songs only, and (3) notes were visually identified and labelled by duration, frequency contours and shape. An average of 30 songs per species were analysed, and sound segments from each file were labeled. Physical acoustic features were retrieved from labeled sound files after the annotation procedure as peak frequency (Hz), maximum and minimum frequency (Hz), bandwidth (Hz), and song duration (s). Additional metrics like the number of notes in a song- note count (N_C) and type of note within song- note type (N_T) in the form of selection tables, were used further to derive note diversity and song richness index. A representative sample of the examined songs is provided in Figure 5.2, which highlights the variations in song characteristics across the various regions within the distributional range of each species.

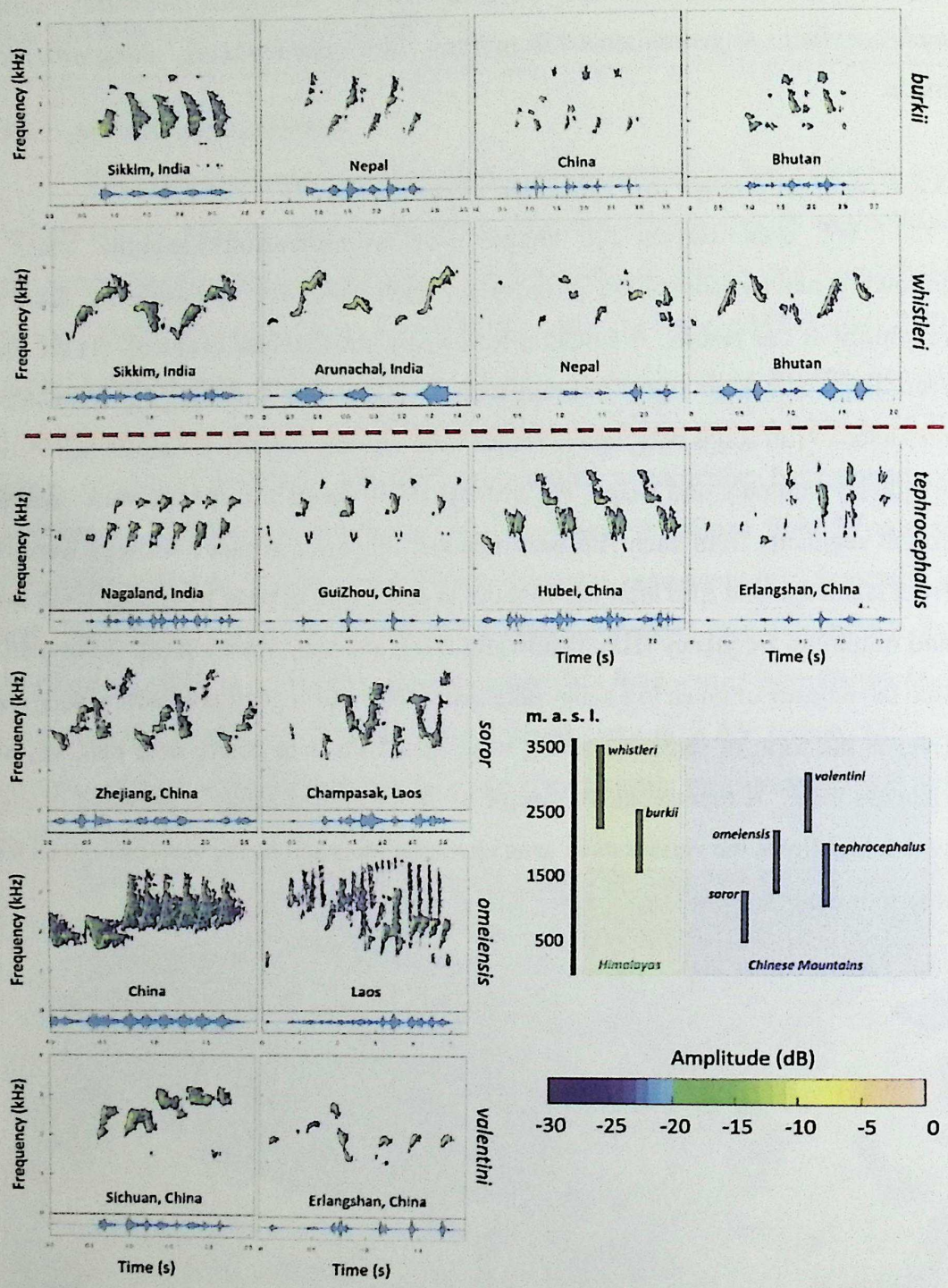


Figure 5.2. Representative regional sonograms of the songs highlighting the variations in song structure across different regions of the distribution range of each species. Sonograms were generated from recordings collected during this study and from archived recordings obtained through Xeno-canto and personal communication (source details including recordist names, catalogue numbers, altitude and locality are provided in Appendix 3, Supplementary Table ST2). Inset altitudinal panel are redrawn and simplified from species accounts and altitudinal information presented by *Alström & Olsson, 1999*.

5.2.3. Quantification of Acoustic Traits

The song structure for each species was deduced using the note types retrieved during parameter extraction. First, we used the non-parametric Kruskal- Wallis rank sum test (Patil 2021) and the *post hoc* Dunn test to examine maximum frequency (further F_{max}) for songs of study species. We estimated the song richness index using other extracted parameters, i.e., note count (further N_C) and note types (further N_T). Note types were characterized from spectrograms in Raven Pro using a visual classification protocol based on note shape, frequency tractor, bandwidth, duration, and its relative position within the song phrase. Notes with similar spectrographic contours and comparable frequency-time structure were assigned to the same note type, while clearly different contours were treated as separate. While the classification was visual, it was supported by quantitative acoustic measurements extracted for each annotated note. For a song with N_C number of notes and N_T note types, the Song Richness Index (further SRI) can be defined as:

$$SRI = \frac{N_T \sqrt{N_c^2 - \sum_{i=1}^{N_T} (M_i - 1)^2}}{N_C^2}$$

In this case, M_i denotes the frequency of each N_T occurrence, with $i \in (1, N_T)$. By penalizing any instance of an N_T repetition, SRI quantifies the song diversity based on the diversity and repetition of each N_T. After normalizing the numerator using N_C^2, which quantifies note repetition, the output values of SRI $\in (0,1)$ are obtained. Higher SRI values suggest high diversity and less repetition for songs with the same length (N_C), whereas lower values indicate greater repetition and less diversity (Sawant et al., 2021). Once every song element was extracted, we carried out thorough cross-habitat comparisons to find acoustic variations.

5.2.4. Habitat and Environmental Data

Rather than relying just on compositional variations, habitat complexity is inferred from vegetation structure and acoustic transmission characteristics associated with specific forest types. The division of forests into distinct categories (e.g., undergrowth vs. broadleaf) provides a stand-in for structural complexity, as species composition was not

directly examined. We tested if any latent variable influences frequency characteristic. To validate this, we examined the contributions of canopy height, canopy cover, plant phylogenetic richness, and plant species richness (considering study species being obligate insectivores and the correlation between plant and arthropod abundance). The elevation data was obtained from the CGIAR SRTM dataset (http://srtm.csi.cgiar.org/srtmdata), while the canopy height and canopy cover data were obtained from the NASA GEDI dataset (https://glad.umd.edu/dataset/gedi). All three variables were extracted at 30-meter spatial resolution for each recording locality. This resolution was considered appropriate for the scale of analysis as it captures forest structural heterogeneity relevant to acoustic transmission while remaining fine enough for representing the elevational and canopy gradients occupied by the study species.

5.2.5. Acoustic Data Analysis

As the patterns of habitat-specific song characteristics were established, we further used structural equation models (further SEM) to evaluate associations among habitat structure, elevation and song richness. Specifically, we examined whether habitat type, represented by canopy cover and canopy height, was associated with elevational gradients and whether the variables jointly explained the variation in transmission related traits. Since the study is observational, the SEM framework was used to test if proposed relationships were consistent with covariance structure of the data. We examined conditional associations between explanatory variables, including whether an intermediary variable could statistically mediate relationships (Bollen 1989a; Arhonditsis et al. 2016; Kline 2012)

Influence of elevation (Branch & Pravosudov, 2020; Huang et al. 2022), canopy height (Mejias & Wilson, 2023; Jablonszky et al. 2022), and canopy cover (Phillips et al. 2020; Arnberg et al., 2023) on SRI was examined to determine their respective contributions and extent of their impact using Structural equation models in *lavaan* R package (Rosseel 2012). Fisher's C statistic was used to determine if the proposed framework accurately represented the covariance structure among the variables in the dataset (Crino et al. 2022). All path coefficients were therefore interpreted as statistical relationships among measured variables and may covary in natural systems. In addition to

basic frequency modulation, to assess if acoustic adaptations encompass more complex factors like song diversity and richness, linear discriminant analysis was performed.

5.2.6. Linear Discriminant Analysis

Using sets of features (predictor variables) manually extracted from recordings, discriminant analysis has been extensively used to classify vocalizations (Lovell & Lein, 2004; Sharp & Hatchwell, 2005; Grava et al. 2008). We used linear discriminant analysis (further LDA) in *MASS* R package to perform a comprehensive analysis of the acoustic features, taking into consideration both the functional and structural elements of the songs. An additional parameter used in this analysis, *note diversity*, refers to the variety of notes and is quantified using the stationary probabilities of notes within a song. The features most important in differentiating between multiple song classes were found by examining the coefficients of the LD functions.

5.2.7. Phylogenetic and evolutionary context

We used time calibrated phylogeny of *Phylloscopus* warblers from Alström et al. (2018), to assess whether evolutionary divergence relates to ecological or acoustic divergence. To test if song traits reveal phylogenetic conservatism, we quantified the phylogenetic signal estimating Blomberg's K in *phytools* package (Revell 2012). The median values for peak frequency, bandwidth and note duration were calculated for each species. These traits were assembled with the phylogeny, for which we computed the observed K, permutations of trait values across tips and compared values against a Brownian null distribution (10000 simulations). Further, we performed LOO (leave-one-species-out) analysis, recalculating the K after dropping each species in sequence, to assess the stability. In Brownian motion framework, $K < 1$ indicate overdispersion and $K>1$ indicates strong resemblance among closely related species.

5.3. RESULTS

5.3.1. Acoustic Adaptation Hypothesis

5.3.1.1. Elevation and differences in F_{max}

From a total of 340 recordings (690 bouts) analysed comprising all species, the songs of all study species of the *P. burkii* complex differed significantly ($\chi 2$ (6) = 170.88 $P = 2.93e\text{-}^{34}$), according to the Kruskal-Wallis test. Six study species can be visualized in two groups based on their distribution. Two species, *whistleri* and *burkii*, each inhabiting a consistent mountain belt in the Himalayas, vary significantly in F_{max} [occurring at higher elevations (4688.79Hz) and at lower and mid elevations (6852.81Hz), respectively, $P = 2.21e\text{-}^{27}$], while the other four, *tephrocephalus, soror, omeiensis,* and *valentini,* inhabiting together in Chinese mountains, show significant variation in F_{max} (Figure 5.3). A significant difference in F_{max} was observed between the songs of *omeiensis* and *valentini* (7323.18 Hz and 3569.57 Hz, $P = 4.64e\text{-}^{08}$). The high $\chi 2$ value and extremely low *P*-value ($2.93e\text{-}^{34}$) indicate that the variability in song features is not a result of random events but rather indicates differences between species occurring at middle elevation zones (*omeiensis*) and at higher elevations (*valentini*). Across species, F_{max} was observed to be lower at higher elevations (*whistleri* and *valentini*), whereas low/mid elevation taxa exhibit higher F_{max} (*burkii* and *omeiensis*), supporting a negative F_{max} - elevation relationship.

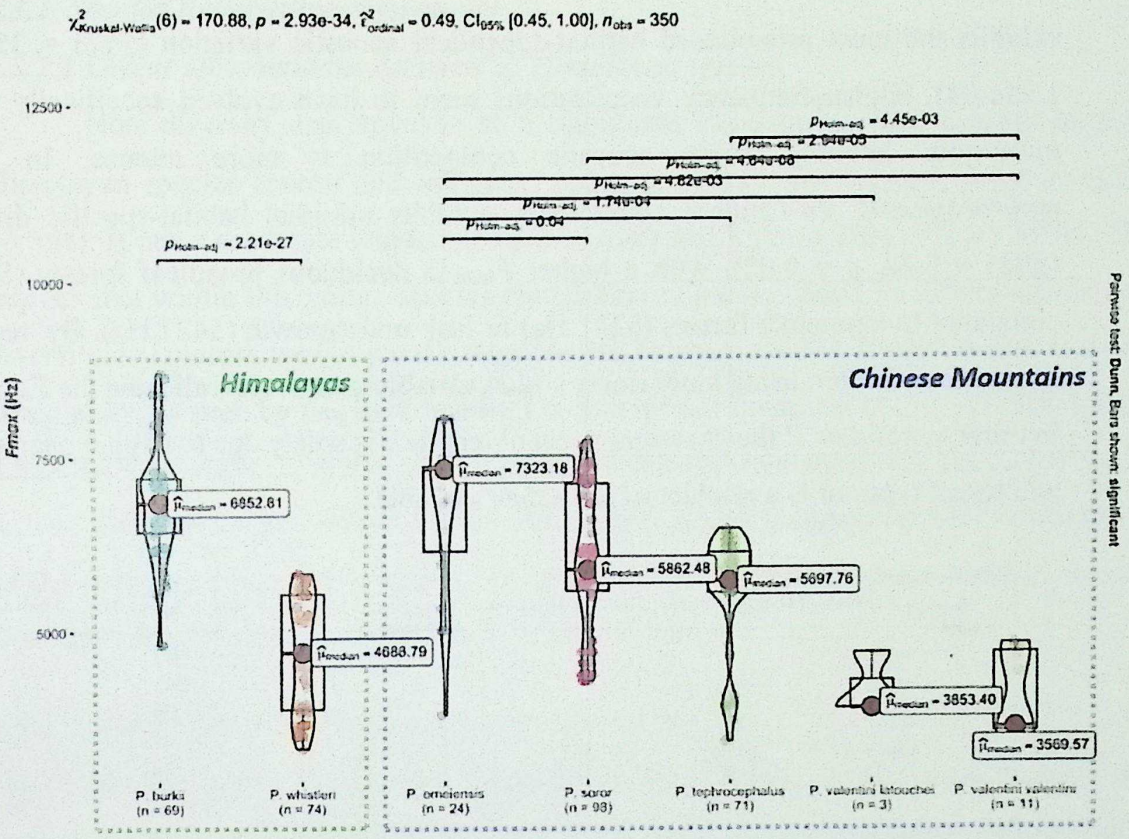


Figure 5.3. Graph representing differences between the F_{max} within the studied species, analyzed using the Kruskal-Wallis test and Dunn's pairwise comparison with Holm*adjustment* for multiple comparisons. The figure displays variations between groups, with statistical significance indicated by annotations. Pairwise comparisons highlight specific differences between species, providing a clear visual representation of the results.

5.3.1.2. Acoustic Adaptation and Drivers of Song Variability

Distinct acoustic adaptation mechanisms driven by habitat characteristics and geographical distribution were determined by comparing the song frequencies of *Phylloscopus* warblers (Figure 5.4). Different patterns were observed in the Himalayan species; *burkii*, for example, shows more subtle but statistically significant variations in F_{max} within its habitat range ($\chi^2(2) = 6.31$, $p = 0.04$). *whistleri*, on the other hand, exhibits an altitudinal pattern, with lower frequencies in coniferous forests at high elevations (4558 Hz) and progressively higher frequencies in deciduous broadleaf (5103 Hz) and temperate forests (5203 Hz) at lower elevations where acoustic competition is more intense. Similarly, with a significantly higher F_{max} in lush undergrowth (7109 Hz) compared to evergreen broadleaf forests (5509 Hz) and secondary growth (5677 Hz), the Chinese *soror*

exhibits the most pronounced habitat-dependent acoustic variation ($\chi^2(2) = 35.50$, p = 1.95e-08). Higher-frequency vocalizations seem to have evolved specifically in dense understory habitats where acoustic competition is more intense. In contrast, *tephrocephalus*, its Chinese counterpart, exhibits minimal habitat-specific differences ($\chi^2(2) = 8.28$, p = 0.02), with a higher F_{max} in deciduous broadleaf forests (5655 Hz) compared to temperate forests (5231 Hz) or lush undergrowth (5427 Hz). By teasing the forest types further, using more finely scaled variables, we cross-validated the F_{max} features in order to validate if the observed vocal divergence is solely due to habitat characteristics and forest types or is a product of any latent variable.

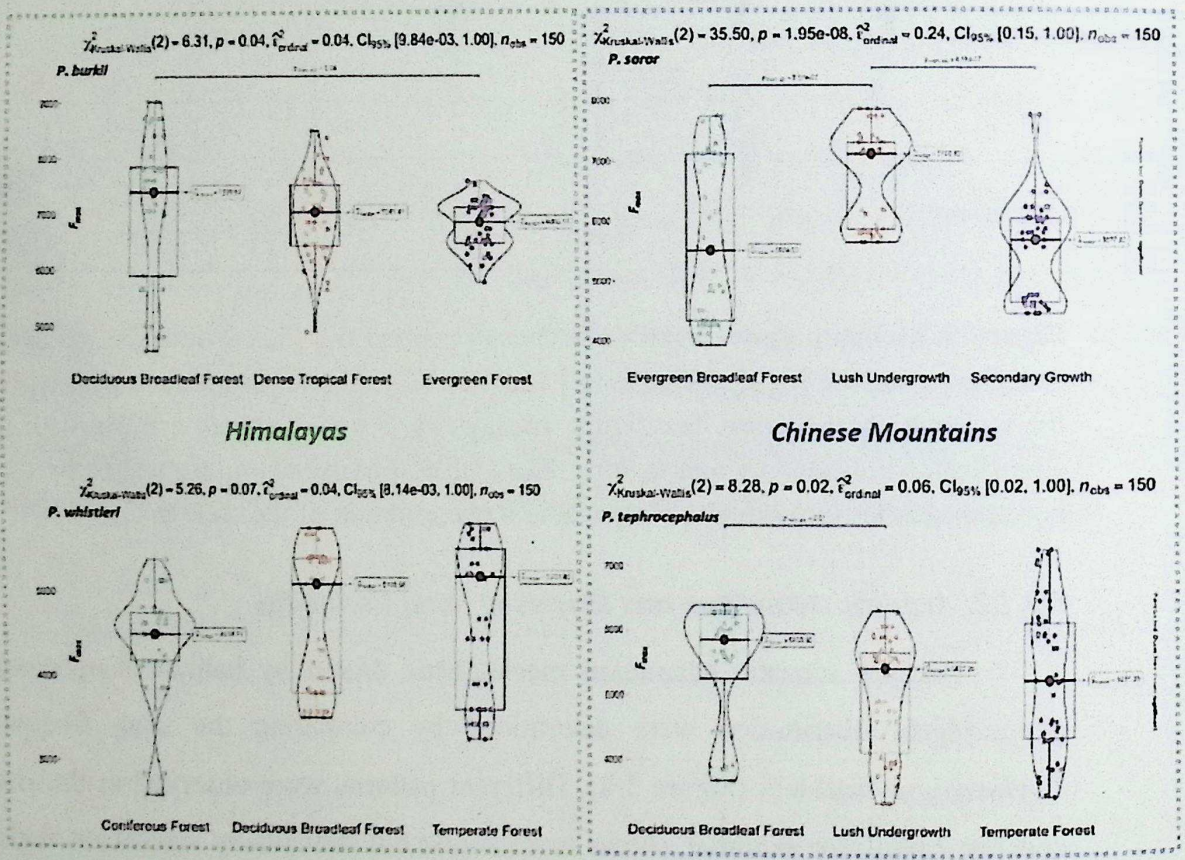


Figure 5.4. Graph representing differences between the highest frequency (F_{max}) within songs of individual species across different forest types according to the Kruskal-Wallis test and Dunn's pairwise comparison (Holm *adjustment* for multiple comparisons).

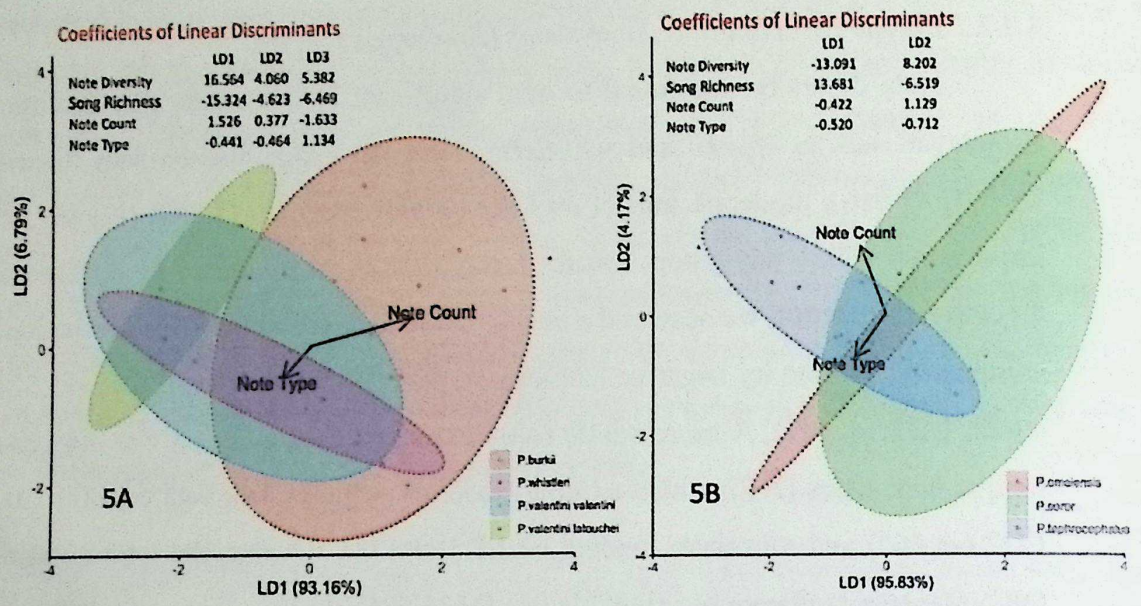
5.3.2. Species Recognition Hypothesis

5.3.2.1 Linear Discriminant Analysis of Himalayan species

Note diversity was found to be a significant characteristic that distinguishes the Himalayan species (*burkii* and *whistleri*) along the major discriminant function (LD1: 16.564). It has a moderate impact on LD2 (4.060) and LD3 (5.382) (Figure 5.5A). This implies that within this group, species recognition is greatly aided by differences in note diversity. In contrast, we observed a negative link between species discrimination and song complexity, as seen by negative loadings across all LD functions (LD1: -15.324, LD2: -4.623, LD3: -6.469). A more subtle role in species differentiation was suggested by the unique note types (NT), which exhibit moderate negative loadings on LD1 (-0.441) and LD2 (-0.464) and a positive loading on LD3 (1.134), whereas the total number of notes (NC) played a moderate positive role in LD1 (1.526).

5.3.2.2. Linear Discriminant Analysis of Chinese species

In the case of the sympatric Chinese species (*omeiensis*, *soror*, and *tephrocephalus*), acoustic divergence was found to be more significantly influenced by song complexity. While song complexity shows a positive association with LD1 (13.681), note diversity shows a negative correlation with LD1 (-13.091) and a moderately positive correlation with LD2 (8.202) (Figure 5.5B). This suggests that the primary factor influencing the acoustic differentiation of these Chinese warblers is song complexity rather than note diversity.



Figures 5.5A and 5.5B. LDA plot illustrating the relationship between acoustic characteristics and the first two LD's in the *burkii* complex and the spatial arrangement of its acoustic attributes, as depicted by LD1 and LD2. The ellipses represent the 95% confidence interval for the centroid of each group.

5.3.3. Song Richness (Structural Equation Models)

Phylloscopus species showed unique patterns when the association between habitat variables and SRI was investigated, with substantial differences between Chinese and Himalayan species. Elevation and song complexity are consistently positively associated with Himalayan warblers. *burkii* showed a negative relationship between canopy cover and song richness ($\beta = -0.645$, $R^2 = 0.42$) and a strong positive relationship between elevation and SRI ($\beta = 0.645$, $R^2 = 0.49$). *whistleri* demonstrated a stronger positive correlation between elevation and SRI ($\beta = 0.811$, $R2 = 0.66$), indicating that higher elevations promote more complex songs in this species. In addition, *whistleri* shows a substantial negative correlation between canopy height and SRI ($\beta = -0.389$, $R2 = 0.88$), suggesting that higher canopies may limit song richness (Figure 5.6). This is either because of habitat constraints or because of poor acoustic transmission in the undergrowth where the species usually occurs. Chinese species, on the other hand, exhibit distinct patterns. In contrast to the Himalayan species, *soror* exhibits a negative correlation between elevation and song richness ($\beta = -0.529$, $R2 = 0.28$), with SRI declining at higher elevations. Notably, there is a positive association between canopy cover and SRI in *soror* ($\beta = 0.466$, $R^2 = 0.22$), indicating that song complexity increases with denser vegetation. *tephrocephalus* exhibits

an intermediate pattern, with elevation and SRI showing a moderate positive association ($\beta = 0.673$, $R^2 = 0.45$), however, no relationship was observed between canopy cover and song richness ($\beta = 0.006$, $R^2 = 0.04$).

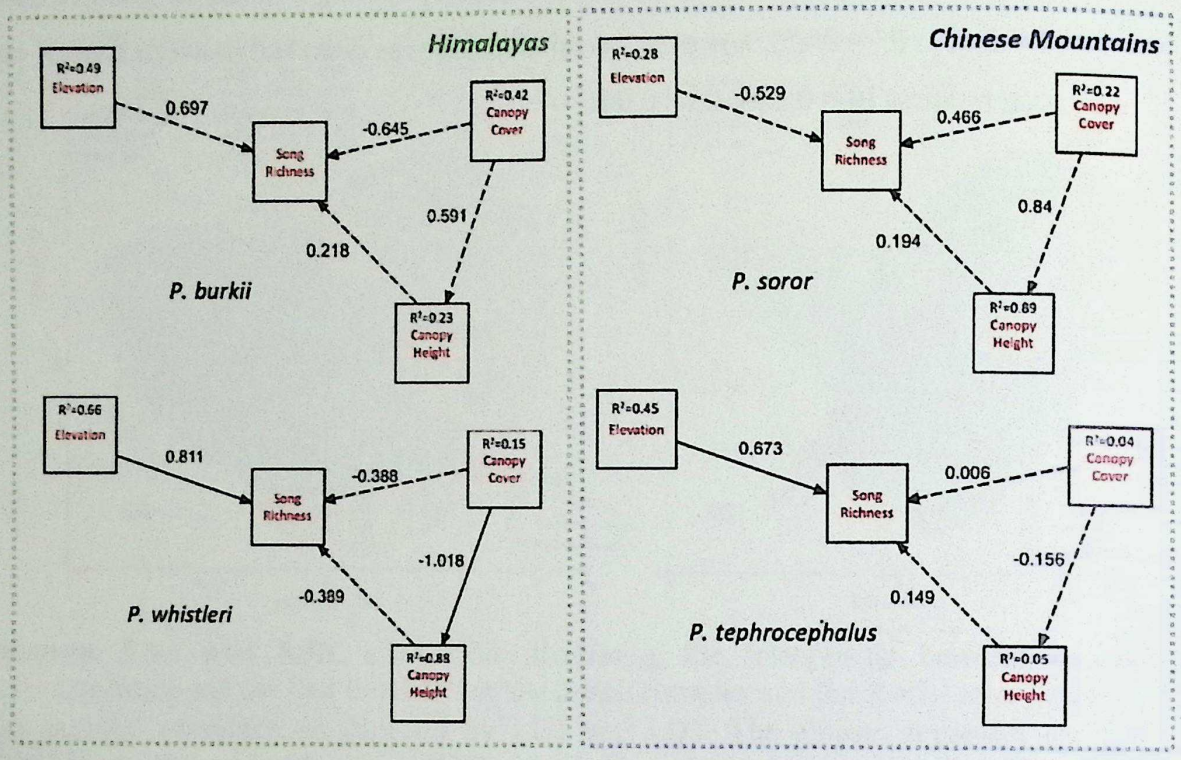


Figure 5.6. The figure depicts SEM's used to assess the relationships between the 'SRI' and the three environmental variables: elevation, canopy height, and canopy cover. The arrows represent the variables' respective paths of influence. A relationship is perfectly positive when the value is 1, perfectly negative when the value is -1, and not at all when the value is 0. The values signify the nature and intensity of these interactions.

5.3.4. Phylogenetic signal in Acoustic Traits

Our Blomberg's K estimates revealed evidence for a phylogenetic signal for song evolution, with distinct strengths across parameters. Note duration exhibits strongest structure (K = 0.891, $p = 0.06$), almost achieving statistical significance. Bandwidth (K = 1.07, $p = 0.13$), and peak frequency (K = 0.884, $p = 0.18$), exhibits values close to one, suggesting Brownian motion like evolution, without significance (Figure 5.7). LOO analysis however, confirms that estimates of K were stable across taxa (with negligible deviations in magnitude) (Appendix 3- ST3). These observed K's consistently fall within the distributions generated within 10000 simulations. However, the inclination of note duration towards the upper tail of distribution indicates stronger phylogenetic conservatism than expected, consistent with species recognition hypothesis.

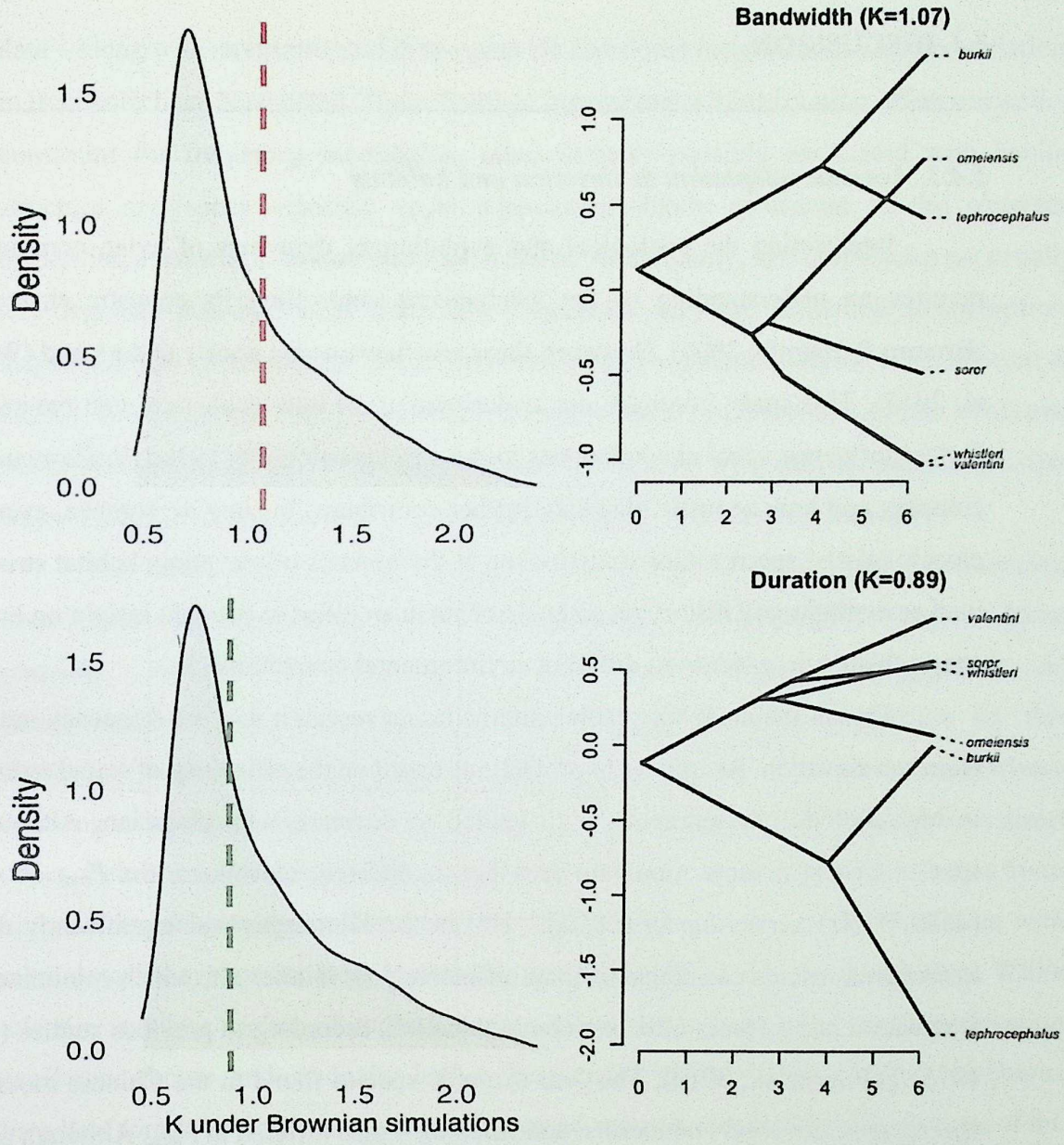


Figure 5.7. Null distributions of Blomberg's K with respective phenograms for acoustic traits (Bandwidth and note duration) under 10,000 Brownian motion simulations.

5.4. DISCUSSION

5.4.1. Acoustic adaptation to elevation and habitats

Interpreting the ecological and evolutionary dynamics of avian communication requires an understanding of the mechanisms controlling its acoustic characteristics (Brumm & Naguib, 2009). However, these mechanisms are poorly understood (Wilkins et al. 2013). This study improves our understanding of how ecological and environmental factors influence vocal characteristics in the species belonging to the *Phylloscopus burkii* complex and how acoustic plasticity further contributes to song divergence, even among closely related species. Our study looked at the impacts of elevation, habitat structure, as well as evolutionary history on song elements in an effort to provide insight on how avian songs change in response to different environmental constraints.

One of the most noticeable patterns in our research was the frequency modulation based on elevation. According to projections based on the efficiency of sound transmission in high-altitude environments, F_{max} tended to decrease with elevation. Although both species live in a same mountain area but at different elevations, the F_{max} of *whistleri* (4688.79 Hz) versus *burkii* (6852.81 Hz) in the Himalayas was significantly different. Lower frequencies can transmit more effectively in thinner air, which minimizes signal attenuation and ensures effective communication, according to previous studies (Morton, 1975; Tobias et al., 2010). The four syntopic species found in the Chinese mountains—*tephrocephalus*, *soror*, *omeiensis*, and *valentini*—also differed in F_{max}. Although the broad decrease in frequency with elevation is compatible with the F_{max}, frequencies may vary with vegetation structure, canopy density, air density, and humidity. The observed frequency pattern may be viewed as consistent with habitat-mediated acoustic filtering, rather than as a direct causal effect of elevation. Thus, elevation is best treated here as a composite ecological gradient that includes vegetation-related changes, rather than as an isolated driver of acoustic divergence.

Another aspect is that physical limitations, such as body mass or vocal tract size, affect song frequencies; as a result, small species cannot generate low-frequency songs (Greenewalt 1968; Ryan & Brenowitz, 1985). In the context of our system, morphological

data—along with environmental data—provide additional insight about whether variations in frequency have been noted. These findings suggest that while elevation offers a selection constraint for frequency modulation, other factors—possibly associated with habitat structure and species-specific vocal adaptations—likely contribute to the observed disparities, even within similar elevational bands. Additionally, low frequencies are usually less degraded than high ones since high frequencies are more vulnerable to absorption, dispersion, and reverberation by the environment and vegetation (Aylor 1972; Marten & Marler, 1977; Martens 1980). As a result, it was crucial to find out if this pattern holds true in different environments or if ecological traits have altered frequency modulation in other ways. Therefore, it was necessary to analyze the songs on the basis of habitats.

Our results demonstrated that habitat structure greatly affects song frequencies, even though the specific patterns vary between species and geographical regions. More precisely, a variety of latent factors, such as plant species richness, canopy cover, and canopy height within a certain geographic area, are probably responsible for this fluctuation. In the context of AAH, our results should therefore be interpreted as evidence that song traits vary along elevation-vegetation gradient, rather than as evidence for a direct effect of elevation alone. Even though a general trend could suggest that dense forests favor higher frequencies with simpler syntax and open habitats favor lower frequencies with more complex syntax, the truth is more complicated than the frequency variation. While *whistleri* exhibits a clear altitudinal pattern, using lower frequencies in high-elevation coniferous forests and gradually higher frequencies within lower-elevation deciduous broadleaf forests (possibly as a result of increased acoustic competition), *burkii*, one of the Himalayan study species, exhibits slight variations in F_{max} within its range. Another argument is that low-frequency bands are more vulnerable to degradation over high-frequency bands when transmitted via undergrowth because of greater interference between both direct and reflected pathways (Römer 1992). Thus, vegetation structure may partly confound the apparent elevational signal, and both variables should be interpreted jointly.

Similar findings were obtained when we took into account Chinese species, where there is a discernible habitat-dependent acoustic variation in *soror*, with larger F_{max} in lush undergrowth compared to secondary growth in evergreen broadleaf forests. With the

exception of a few species, such as *tephrocephalus*, which show little habitat-specific variation, this indicates that the species has evolved to dense, competing acoustic conditions (see Hansen 1979). This habitat-driven variation, while not consistent, emphasizes the importance of environmental selection in forming avian vocalizations and suggests that frequency modulation is a reaction to certain habitat types as well as ecological stresses and competition that could be species-specific. Therefore, habitat-driven vocal alterations show the fine-scale functions of ecological selection throughout the complex, while elevation offers a selective framework. Overall, our findings support an association between acoustic traits, habitat structure, and elevation, but they do not allow direct causal attribution to either elevation or vegetation alone.

5.4.2. Song Richness and structural divergence in sympatry

The combined impacts of canopy cover, canopy height, and elevation were better understood using SEM, which revealed that these factors work together to affect song variability. Elevation exhibited an independent impact on frequency modulation, while habitat variables like canopy cover and canopy height mediated these effects, affecting song transmission efficiency and acoustic adaptation. The finding highlights the relationship between biotic and abiotic factors in influencing avian vocal communication and suggests that a combination of direct and indirect environmental variables causes song divergence. In light of the SEM findings, we expanded our focus to determine if frequency-based adaptations alone account for song divergence or whether other acoustic traits contribute to species differentiation. LDA provided a more thorough perspective by incorporating other song attributes like note diversity and song richness. Our LDA results show that a range of structural features affect interspecific difference, although frequency modulation continues to be the predominant contributing factor. It's interesting to notice that sympatric species exhibited more divergence in note diversity and song richness, supporting the idea that certain acoustic parameters were chosen in response to ecological and evolutionary factors. This lends credence to the species recognition concept, which holds that sympatric species retain differences in song patterns despite overlapping frequency ranges or bandwidths.

5.4.3. Evolutionary history and phylogenetic constraints

Our findings imply that song characteristics often vary, with temporal characteristics such as note durations exhibiting a moderate-strong phylogenetic signal. This suggests that, contrary to what would be predicted by chance, closely related species maintain comparable temporal structures in their songs. Such partial conservatism in temporal characteristic may also suggest contribution to species recognition, maintaining a inherited signature that discriminates among related taxa (Arato & Fitch, 2021). Contrastingly, spectral features (bandwidth, peak frequency) exhibit non-significant or a weak signal, which is consistent with higher ecological lability in response to sympatry. The observations, however, are in line with studies pertaining to morphology and songs (Porzio et al. 2024). Together, these patterns suggest a dual process. Temporal structuring remained phylogenetically conserved (supporting species recognition), while spectral attributes diverge freely (increasing the distinctiveness in sympatry). The observations favour SRH where evolution of songs balances the requirement of recognisable signals within clades (against need to diverge), thus preventing hybridisation in areas of overlap. Our phylogenetic signal analysis provides a comparative framework to link song characteristics to evolutionary history.

5.4.4. Synthesis and implications

The Himalayan distribution of *whistleri* is consistent with its altitudinal frequency gradient, which shows adaptation to reduce acoustic attenuation in dense, high-altitude habitats. The lower F_{max} in high-elevation coniferous forests (4,558 Hz) vs. the higher frequencies in lowland deciduous forests (5,203 Hz) (also see Tietze et al., 2015). Similar to its genetically close relative *tephrocephalus*, which exhibits negligible habitat-linked frequency shifts (5,655 Hz vs. 5,231 Hz), *soror's* extreme F_{max} variation in lush undergrowth (7,109 Hz vs. 5,509 Hz in broadleaf forests) reflects niche partitioning in acoustically competitive environments. The findings offer a structural framework; acoustic divergence is further influenced by ecological elements like habitat and elevation. These findings highlight how closely related species' interactions are shaped by both ecological selection and evolutionary history, underscoring the need for an integrative methodology for understanding the evolution of avian vocalization. Lastly, our results show that social

preference (sympatry), ecological pressure (habitats and elevation), or phylogenetic conservatism all play a joint role in the evolution of song in the *Phylloscopus burkii* complex.

CHAPTER 6. MORPHOLOGICAL CLASSIFICATION: COMPUTER VISION AND DEEP LEARNING

Although Chapter 5 addressed the ecological and evolutionary dynamics of vocal divergence, it also brought up a more general problem that goes beyond vocalisations: in cryptic groups such as the *burkii* complex, minute morphological differences make precise field identifications or observations very difficult. Higher erroneous rates are frequently caused by the fine-scale characteristics and almost identical plumages of cryptic species that live in overlapping areas. This issue is particularly prevalent in public repositories or citizen science platforms, where a large amount of data is labeled by uneven observer ability and a lack of adequately reliable diagnosis. This chapter uses the same group as a test case for deep learning and computer vision techniques to overcome these constraints. We are attempting to approach these models as filters that reduce errors and improve the data set quality in addition to our scientific objectives. This is essentially a social experiment: if machine learning can help us standardize identifications across public domains, we are directly addressing real-world problems by making our repositories cleaner, which is beneficial for long-term monitoring, conservation planning, and ecological research.

The ability to identify and recognize various species has significantly increased because to the quick development of image recognition technology, particularly with the aid of YOLO algorithms. This chapter centers around the *Phylloscopus burkii* cryptic species complex, which is difficult to identify precisely due to its lack of phenotypic variation. We propose an improved YOLOv5-based model that uses a part-based technique that separates part detection from identity classification to facilitate the separation of elements of this complex. In addition to investigating the variety of image attributes of the species within the *burkii* complex, we want to ascertain if photographs captured in real environments can yield statistically reliable identifications.

6.1. INTRODUCTION

Bird population studies provide valuable indicators for environmental monitoring, and changes in bird communities help track climate change (Koskimies, 1989) (Lindström et al. 2013). Counts and numbers are often used in these biodiversity monitoring studies (Larsen et al. 2012). The popularity of adopting a "Big Data" approach in recent years has made it possible for citizen science projects all around the world to gather enormous volumes of data online. However, identification errors have happened (see de Freitas et al., 2022), and this data is sometimes too vague to describe how the observations were generated (Kelling et al. 2018). The difficulty of handling visually cryptic species is shown by this high field identification error rate, especially for smaller polytypic species like *Phylloscopus burkii*.

The classic polytypic *P. burkii* is a prominent example of cryptic speciation since several species have essentially similar morphologies and plumage (Packert et al. 2004). With six currently recognized species (Packert et al. 2004; Martens 2010), this group of sister species had a complex evolutionary history that resulted in both local sympatries, vertical and possibly horizontal parapatry, and extant vicariance throughout the Sino-Himalayan range (Alström & Olsson, 1999, Martens et al. 1999). Despite the fact that some of the species are nearly entirely separated altitudinally, the distribution of four of these species (Figure 6.1) clearly shows overlapping species ranges (Alström 2020). Three of these species were previously reported to be present along a single forest edge during the breeding season by Martens (2002, 2011). The areas where two or more of these species cohabit are where observation errors are most likely to happen.

Image classification has been a more and more prominent topic in deep learning and machine learning methodologies to overcome these flaws (Alter and Wang, 2017). Accurately identifying bird species from images is difficult, though, because it requires recognizing different bird species by their unique shapes and appearances, taking into account background variations, managing different lighting conditions in photos, and adapting to the dynamic postures of birds (Vo et al. 2023). In order to tackle this problem, our study split the identification procedure into two parts: identity classification and part detection. We propose an enhanced You Only Look Once version5 (more specifically,

YOLOv5)-based method for part detection that is capable of managing a variety of environmental factors including partial overlap between part objects.

The principal aim of this research was to ascertain if the application of computer vision and machine learning (ML) could facilitate the differentiation of *P. burkii* complex members according to morphological traits. In order to establish the basis for the development of a reliable and accurate method for automating the identification of at least some *P. burkii* species using morphological data, our investigation's specific goals were to: i) ascertain whether simple in-natural-setting photos could yield statistically accurate identification of visually similar co-occurring warblers of the *burkii* complex, and ii) document the extent to which any differences between groups show continuous or disjunct distributions in the image feature space. The outcomes will reduce identification errors during monitoring by enabling prompt and accurate recognition of cryptic species.

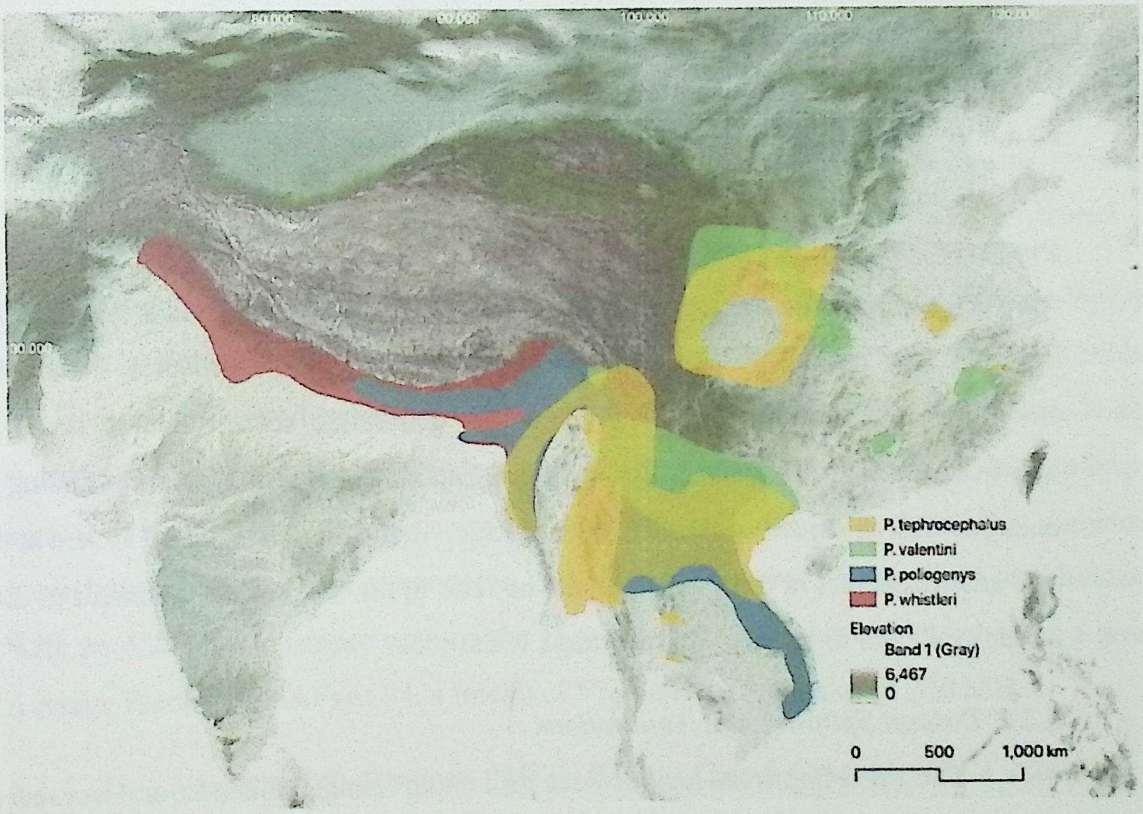


Figure 6.1. A distribution map of *P. tephrocephalus, P. valentini, P. poliogenys, and P. whistleri,* depicting their respective geographic ranges and areas of overlap. For understanding common zones where ranges converge, color-coded portions reflect each species' breeding grounds. Distribution data adapted from *www.birdsoftheworld.org*

6.2. MATERIALS AND METHODS

6.2.1. Data Collection and Pre-processing

We supplemented our dataset with images from a variety of online databases (iNaturalist, eBird, and Wikimedia Commons) for four species (*tephrocephalus, whistleri, valentini* from *P. burkii* complex, and *poliogenys*-outgroup) and produced sets of images specifically for each species. Two significant filtering aspects were explicitly taken into consideration: a) minor indicators such as the supercilium, wing bars, color of the bill and legs, flanks, and—above all—the eye ring are essential for identification in species with few distinguishing characteristics, such as *Phylloscopus* warblers. Because of the intricacy of these markers, it was necessary to concentrate on side-profile photographs to ensure that all of these traits were easily visible (this filter nearly cut the dataset in half), and b) that these images can be used for research and analysis while adhering to copyright laws since they are licensed under the Creative Commons license. The images were uploaded and manually tagged using Supervisely's polygon tool after passing the filter check. *tephrocephalus* (69), *whistleri* (73), *valentini* (59), and *poliogenys* (88) were among the annotated 289 images (218 from secondary sources and 71 personal observations). These were augmented 10 more times resulting in 2890 images (Appendix 4, SF3). In order to improve the model's robustness in identifying the target species under different environmental conditions and its ability to generalize across diverse scenarios, we improved the dataset substantially by flipping, making slight rotations, introducing random noise, as well as adjusting contrast and saturation in the images. We also looked at the label size and placement in order to calculate the ratio of the label center ordinates to the image heights ('y') and its abscissa to the image width ('x')

6.2.2. Dataset Splitting and Annotations

The 2,890 improved images were split into training, validation, and test sets in order to offer reliable model training and unbiased evaluation. 2,312 (80%) of these images were used to train the YOLOv5 model, while 578 (20%) were used for validation to monitor performance and modify hyperparameters. Additionally, 370 images from an additional dataset collected simultaneously with the original sample were reserved just for testing.

This independent test set was left out of both the training and validation phases in order to provide an impartial evaluation of the model's performance. All images in the training, validation, as well as test datasets underwent the same annotation procedure in order to reliably compare predictions to ground truth during performance evaluation. While following conventional deep learning techniques used for reliable model training, we made sure that the dataset splitting strategy took into consideration independent assessment of the model's generalization to unknown data. This systematic approach made it possible to evaluate the model's performance in a way that closely resembled actual circumstances.

6.2.3. The CNN Models (YOLO Architecture)

Convolutional neural networks are perfect for image classifications since they consist of several convolution layers that extract information from input images and offer a typical pattern for recognizing the species evaluated after training the datasets (Szegedy et al., 2015). CNNs' YOLO family of detection algorithms divides input images into grids, where each grid cell identifiable as an object. It covers test time augmentation, model ensembling, and hyperparameter evolution. We used the YOLOv5x6 variation of YOLOv5 (Redmon et al., 2016), which performs very well and allows for high-quality photos using bigger models (x signifies "extra-large," and 6 for P6 tiers in the model's architecture).

In order to collect the necessary semantic information, the method first employs the aggregation network for detection after combining the feature extraction network to extract the input bird image's feature information (Liao & Tian, 2021). This architecture is also exceptionally adept at handling bounding boxes (Appendix 4, SF1-SF2), which makes it perfect for identifying bird species with bounding boxes and managing numerous predictions using non-max suppression and Intersection over Union (IoU) thresholding. With an AWS EC2 instance running the Nvidia V100 GPU, this model achieved a mean Average Precision (mAP) of 94, a Recall of 97.3, and a model size of 270 MB.

6.2.4. The Amazon Web Services (AWS) Elastic Cloud Compute (EC2 instance) Backend

The custom backend used to train the model was connected to Supervisely as a compute cluster. Since the Supervisely platform currently offers the well-established service for Amazon Web Services (AWS)-Elastic Cloud Compute (EC2), we decided to

move forward with this strategy. For all model training tasks, the AWS backend was used. After the model was trained using annotated data to correctly identify the target species, it was tested with untrained annotated input to compare actual and predicted results. In order to improve model performance, network architecture, learning rates, and batch sizes were optimized by hyperparameter tuning using cross-validation approaches. Supervisely's UI made it simple to maintain datasets and track training progress in real time. Scalable resources offered by AWS EC2 made it possible to analyze larger data sets effectively. After the model was verified, it was further modified to improve the accuracy of species identification.

6.2.5. Workflow Pipeline

A systematic approach to this machine learning technology is described in the workflow pipeline (Figure 6.2). Initially, the annotations were thoroughly reviewed and updated. The machine learning model YOLOv5 was further trained and assessed using this data. The model was then evaluated on fresh footage to see if it converged. The model was deployed if the performance evaluation report found that its accuracy was sufficient; if not, the dataset or hyperparameters were adjusted, and the model was retrained to increase its capacity for detection. Before the model was used in real-world situations involving species identification, this iterative procedure ensured that it was reliable and strong.

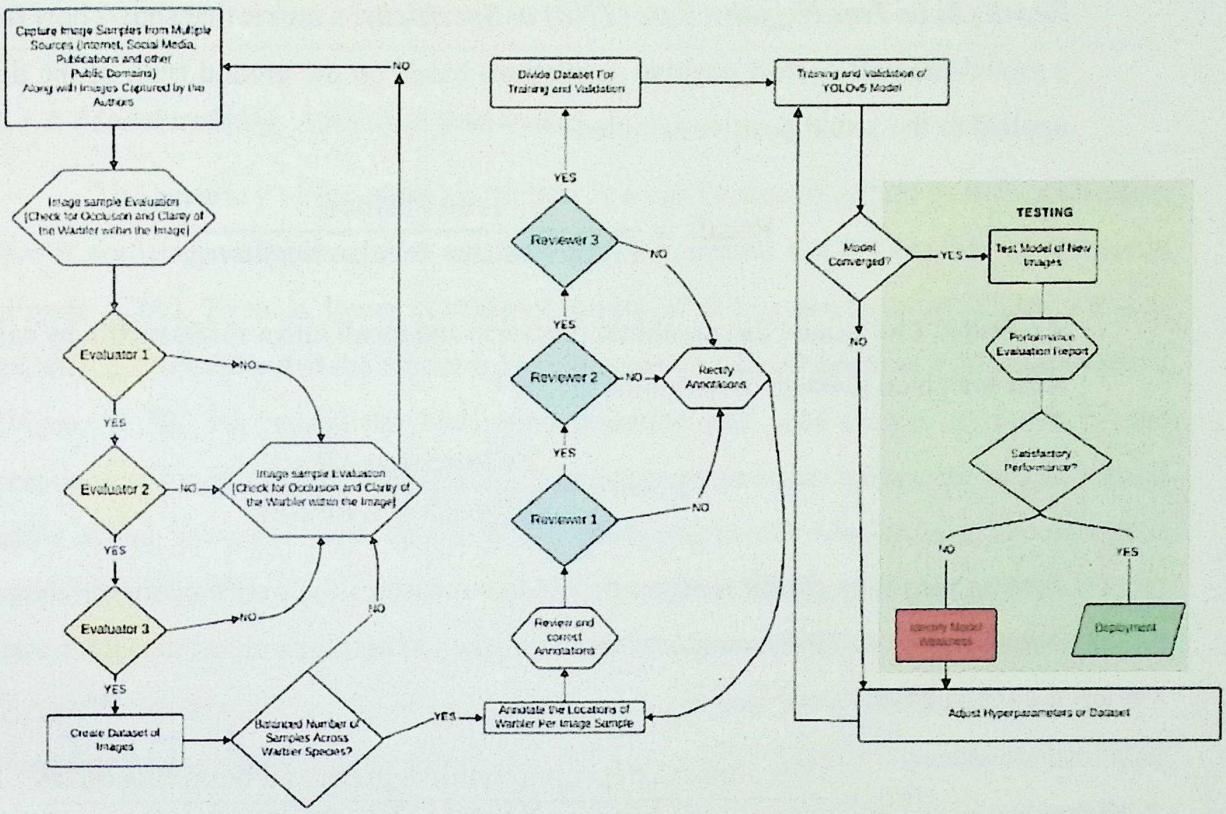


Figure 6.2. Image classification workflow for annotations, model training, and validation.

6.2.6. Evaluation Metrics

Average confidence: The average confidence is determined by adding the confidence levels for true positives, true negatives, false positives, and false negatives. The average confidence is then divided by the total number of occurrences.

Accuracy: A model's accuracy is measured by how well it predicts both positive and negative instances in each scenario.

$$\text{Accuracy} = \frac{\text{True Positive} + \text{True Negative}}{(\text{True Positive} + \text{False Positive} + \text{True Negative} + \text{False Negative})}$$

Precision (P) or True Positive Rate (TPR) or Sensitivity: a measure of how often a model produces the correct positive prediction out of all positive predictions.

$$\text{Precision} = \frac{\text{True Positive}}{(\text{True Positive} + \text{False Positive})}$$

***Recall (R) or True Negative Rate (TNR) or Specificity*:** a metric that shows how frequently a model predicts correct positive predictions based on the ground truth of the data when applied to the actual positive samples.

$$\text{Recall} = \frac{\text{True Positive}}{(\text{True Positive} + \text{False Negative})}$$

F1 Score: a technique that combines precision and recall into a single metric by calculating their weighted average or harmonic mean.

$$\text{F1 Score} = \frac{2 * \text{Precision} * \text{Recall}}{(\text{Precision} + \text{Recall})}$$

Intersection over Union (IoU): a metric that measures the overlap between the predicted bounding box and the ground truth bounding box to assess an object detector's accuracy on a given dataset.

$$\text{IoU} = \frac{\text{Overalp area of ground truth \& predicted bounding boxes}}{\text{Total area of ground truth \& predicted bounding boxes}}$$

Generalised Intersection over Union (GIoU): a measure of the distance between boxes and an enhancement over IoU that accounts for situations where there is no overlap by calculating the overlap between predicted and ground truth bounding boxes.

$$\text{GIoU} = \frac{\text{IoU} - \text{Area of minimum box enclosing both ground truth and predicted bounding boxes}}{\text{Area of minimum box enclosing both ground truth and predicted bounding boxes}}$$

Mean Average Precision (mAP): The trade-off between precision and recall is represented by the area under the precision-recall curve, which is the measure of average precision.

$$mAP = \frac{l}{n}\sum_{k=1}^{n} APk$$

In order to evaluate the model's performance in real-life scenarios, we generated a test set of frames using recently taken photos of the species under examination.

6.3. RESULTS

6.3.1. Model training, validation and testing

The accuracy of the model is highest at a confidence threshold of 0.75, indicating that it performs well because its accuracy persists beyond the 0.5 confidence threshold (Figure 6.3A). Even at lower confidence levels of 0.2, a precision of above 0.6 was estimated, indicating that the model is largely accurate when it predicts a positive instance (Figure 6.3B). The model has both good precision and good recall, as shown by the precision and recall graph (Figure 6.3C). Even at high precision values, the model's recall value is high, indicating that it is accurate in predicting positive instances and proficient in identifying all positive instances in the data (Appendix 4, SF4). Additionally, Figure 6.3D shows that the model has a good recall at a confidence threshold of 0.75, indicating that it is capable of detecting positive cases in the data and maintains the recall above the 0.5 confidence level. Model training performance trends over 100 training epochs are provided along with the model performance confusion matrix for making predictions (Appendix 4, ST1). With scores that are prominent across the diagonal, the confusion matrix indicates that the model has less confusion since it can make predictions that are close to the ground truth (Figure 6.4A). Training curves appear to improve over 100 training epochs, according to the model training performance trends (Figure 6.4B). The model performance on a small number of detection samples is shown in Figure 6.5 based on the confidence scores per detection.

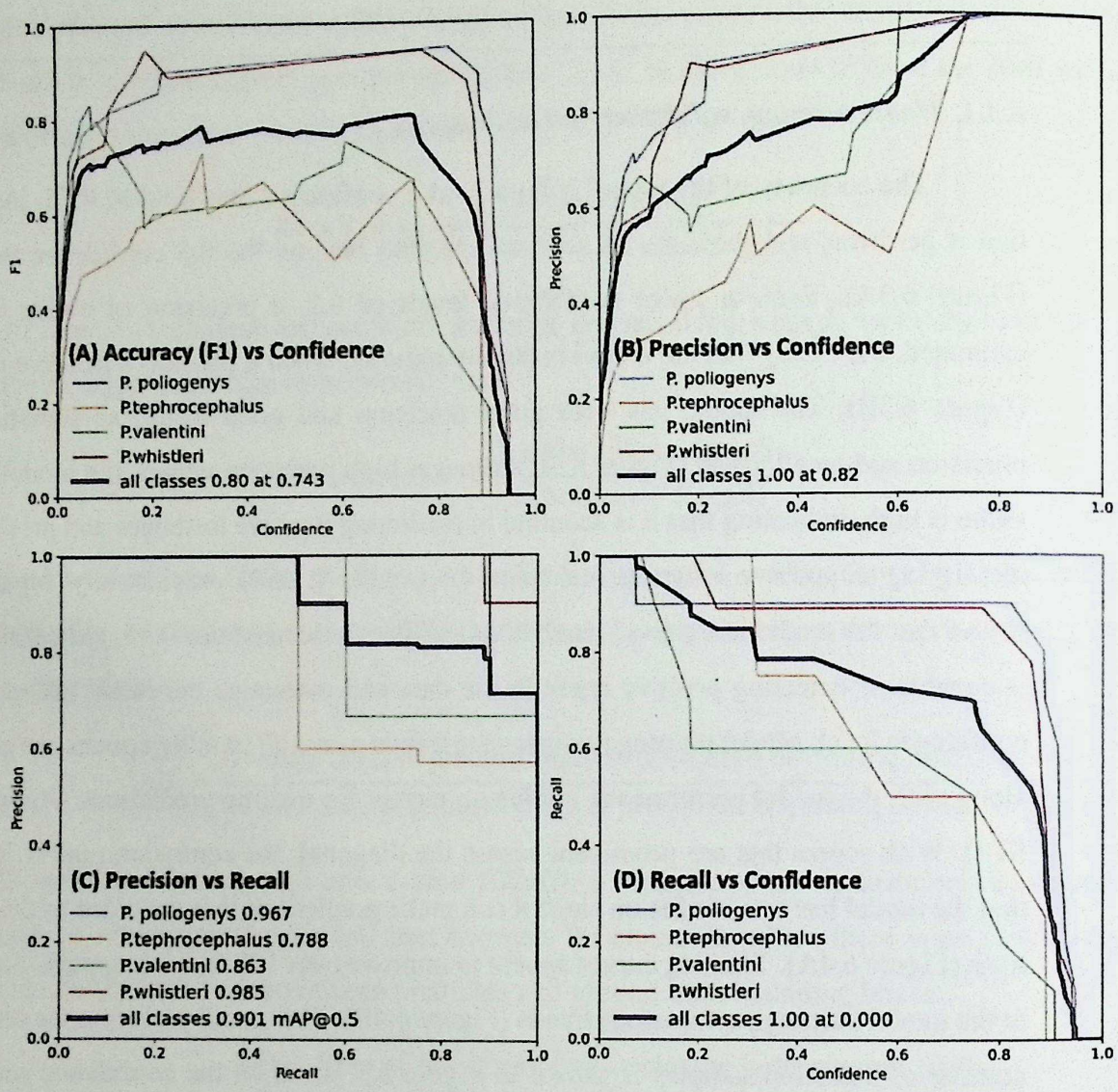


Figure 6.3. Based on the predictions that the model makes given an input image, for a set of test cases in the dataset, the following graphs are generated: **(A)** Graph showing the trade-off between the model's overall accuracy and confidence, **(B)** between the model's overall precision and confidence, **(C)** between the model's overall precision and recall, and **(D)** between the model's overall recall and confidence.

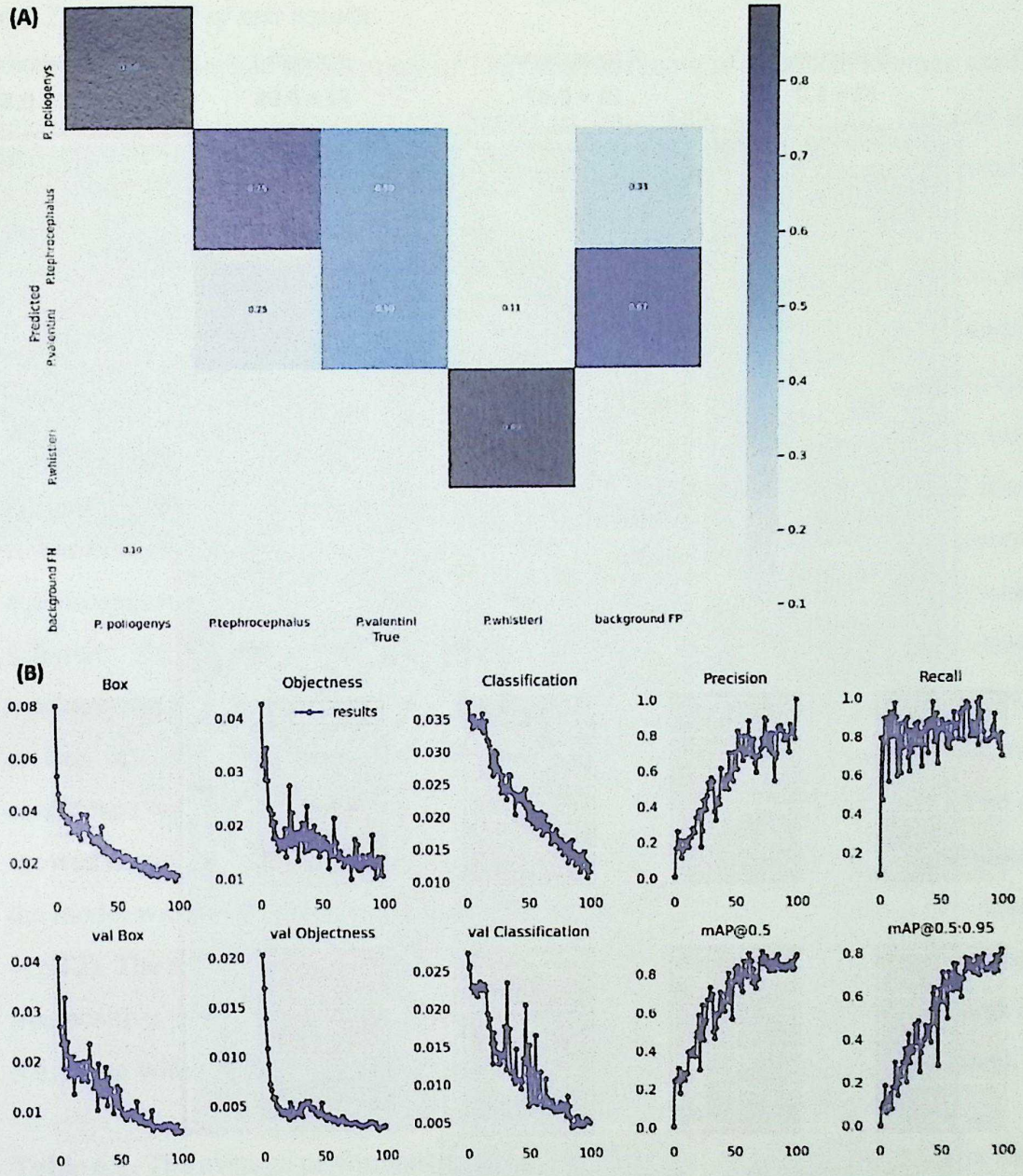


Figure 6.4. Comprehensive Evaluation of Object Detection Model Over 100 Training Epochs **(A)** Confusion matrix illustrating the classification performance of the detection framework. Correct identifications are concentrated along the diagonal, indicating species that were successfully distinguished. Off-diagonal values reflect occasional misclassifications among highly cryptic taxa **(B)** Training and validation metrics, including box loss, Classification loss, Precision, Recall, mAP@0.5, mAP@0.5:0.95) demonstrating stable convergence and improving model performance across epochs.



Figure 6.5. Confidence scores for each detection used to create a sample set of model detection over test datasets. Links to the photographs featured in this figure with respective copyrights is provided in Appendix 4- List 1. Species with more distinct morphological or plumage characteristics generally were detected more consistently (*poliogenys*), and generally showed higher confidence values, whereas species with highly similar external morphology (*valentini* and *tephrocephalus*) exhibited lower confidence scores and occasional overlap in predictions.

6.3.2. Inference of test results

The model had an accuracy of 1, a precision score of 1, and an average confidence level of 0.86 for the *poliogenys* test dataset (n_train=880, n_test=100). The fact that the *poliogenys* is the most unusual of the four species due to its distinctive gray head might assist in clarifying this result. The accuracy of the model for *tephrocephalus* on the test dataset (n_train=690, n_test=80) was 0.83 having a precision score of 0.6 with an average confidence of 0.62. The model correctly recognized 60 out of 80 samples of *tephrocephalus*, despite a few cases in which *valentini* was confused for *tephrocephalus*. The model's accuracy was 0.92, precision score was 1, and average confidence was 0.64 for the test dataset (n_train=590, n_test=90). Despite the fact that the model identified *valentini* in 60 out of 90 test cases, the model's ability to distinguish between *valentini* and *tephrocephalus* due to their similarities has significantly reduced the confidence scores for *valentini*. Of these 60 accurate detections, the model also produced overlapping *tephrocephalus* detections in 20 of them, leaving just 40 *valentini* detections that were entirely accurate. The model's accuracy was 0.97, precision score was 1, and average confidence was 0.77 for the *whistleri* test dataset (n_train=730, n_test=100). The model showed no significant inaccuracy for this species, indicating that any residual ambiguity in the model will be cleared up by adding more training samples for each species (Appendix 4, ST2). The average confidence, model accuracy, precision, true negative, false negative, true positive, and false positive values for each species are shown in Table 6.1 and Figure 6.6, along with the results of the computations (for precision, recall, and F1 scores).

Table 6.1. The average performance metrics, obtained from the confusion matrix findings over multiple runs, for test datasets, including accuracy, precision, recall, and F1 score.

Species	Average Confidence	Accuracy	Precision	Recall	F1 Score
P. poliogenys	0.86	1	1	1	1
P. tephrocephalus	0.59	0.83	0.6	0.75	0.67
P. valentini	0.53	0.92	1	0.67	0.8
P. whistleri	0.76	0.97	1	0.9	0.95

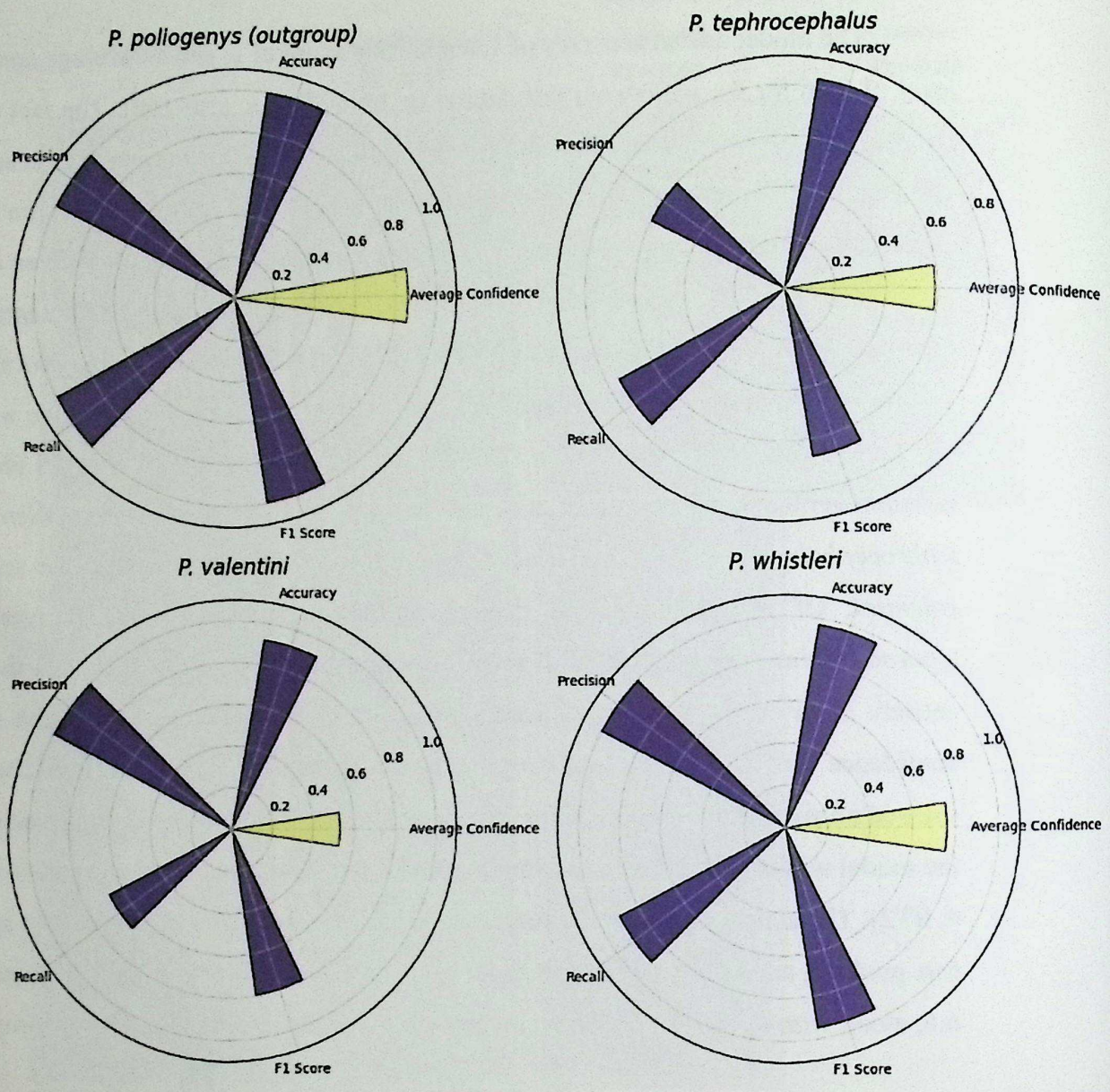


Figure 6.6. Accuracy, Precision, Recall, F1 Score, and Average Confidence distributions for different species are shown in a heat plot, emphasizing the variation in performance across metrics.

6.4. DISCUSSION

6.4.1. Advances in Image Classification for cryptic species

Research on the detection and identification of species has greatly benefited from the quick development of image recognition technology, particularly YOLO algorithms (see Jiang et al. 2022). The use of YOLO v5 models for studies on mammals (Tan et al. 2022, Xie et al. 2023), birds (Ou et al. 2020, Liao and Tian, 2021, Yi et al. 2023), reptiles (Pandey et al. 2023, Afonso et al. 2024), and amphibians (Takaya et al. 2023) has demonstrated notable improvements in accuracy, speed, and model efficiency, even though there are a number of other models available for species recognition, such as Deep Learning Ensembles (Chen et al. 2019), Transfer Learning Models (Wang et al. 2020), and Generative Adversarial networks (Zhang et al. 2023).

6.4.2. Challenges in Morphological Crypticity

Notwithstanding these developments, cryptic species—in our case, *P. burkii* complex—frequently exhibit subtle pattern variation that is difficult for conventional models to account for. Therefore, to increase detection accuracy and manage these minute morphological differences in our study, more validation (see Ma & Yang, 2022) and specialized customization—such as improved data augmentation (Bati & Ser, 2023) and fine-tuning (Kim et al. 2022) of model parameters—were required. As a result, a comprehensive preprocessing and model training approach was used to enhance species classification, which is flexible and adaptable in practical settings. To maintain a concentrated and well-defined research route within this group of birds, we propose that species from different complexes be studied independently rather than in combination. This work proposes a deep learning method based on the YOLO-v5 algorithm to enhance bird species identification in the *burkii* complex.

6.4.3. Performance of YOLOv5 in Cryptic Taxa

Since YOLOv5 can handle the specific challenges of our assignment while providing significant advantages in terms of flexibility, performance, and deployment, it was chosen for classification in our study over other CNN architectures like ResNet. It integrates categorization and object detection into a single, effective process. YOLOv5

does not need a separate detection step, which is especially helpful for applications that need local species identification, in contrast to ResNet, DenseNet, or other CNNs that are only concerned with classification. The value of visual signals alone in identifying species differences may vary depending on how diverse the species' look is in the dataset. The accuracy of image-based classification may be constrained when species show notable visual overlap or minor visual differences. Using complimentary information and combining visual and auditory signals may increase categorization accuracy. However, the primary rationale for excluding acoustic classification was that it would not be feasible to gather high-quality audio data for these species due to the limitations of our study. It is more difficult to get precise and reliable audio recordings of this species since species identification is mostly based on songs and calls sometimes consist of short pulses.

The results of the study demonstrate that simple images acquired in natural settings may, in fact, be utilized to identify cryptic species using statistically sound morphology-based techniques. The YOLOv5 model's strong recall, accuracy, and precision rates show how machine learning algorithms can efficiently use the unique morphological information collected in these images, even when there are minute variations. The model demonstrated strong performance with excellent accuracy, precision, as well as recall at a 0.50 confidence level while retaining precision even at lower thresholds, making it ideal for these sorts of tasks. However, we are presently focusing on expanding the training dataset to make it adaptable because the model occasionally misleads *valentini* (average confidence = 0.64). The model works effectively with *tephrocephalus* and shows exceptional detection and discriminating abilities among *poliogenys* and *whistleri* (average confidence = 0.0.86 and 0.77, respectively). Nevertheless, *valentini* is challenging to handle with the test dataset, which often leads to the confusion with *tephrocephalus*. Solving such issues might improve the model and ensure accurate species identification in ecological study (Shah et al., 2023).

An important future direction involves integration of video-based detection framework, that ay simultaneously combine visual and acoustic information. A multimodal approach as this may substantially improve the accuracy for identification, where subtle plumage similarities frequently overlap with vocal differences. By integrating image recognition and song analysis, future systems may be able to provide more reliable real-

time identifications under natural field conditions, further reducing observer-related errors in citizen-science datasets.

6.4.4. Sources of Error and Recommendations

Even though the image only included *valentini*, there have been instances where multiple bounding box detections occurred in the same image, resulting in bounding boxes for both *valentini* and *tephrocephalus*. This may have been caused by feature overlaps between the two species as well as the inadequate number of images containing both *valentini* and *tephrocephalus* in the present database. To overcome this, we propose (a) doubling the training epochs in the dataset and (b) adding more representative and diverse instances of *tephrocephalus* and *valentini* to the dataset. When differentiating between species like *valentini* and *tephrocephalus*, misconceptions can be avoided by training the model separately depending on the geographic ranges of each species. Identification may be made much easier by concentrating on the unique elevational gradients and ecological requirements that each species favors (see Yang et al. 2023, Parab et al. 2023) (Alström 2020). By using a training strategy tailored to regional distribution (see Opaev & Kolesnikova, 2019), the model can learn the distinctive traits linked to each species' preferred settings, potentially increasing recognition accuracy. To enhance species identification in regions with overlap, regional distribution data must be incorporated into the training process.

6.4.5. Practical Implications and Citizen Science Applications

Our method starts the process of building a more accurate model for the few focal species under consideration, whereas other tools, like Merlin, provide users a list of potential species, mostly aimed at seasoned birders who use their knowledge to make the final decision. Our goal was to create a model that could generate a single, trustworthy forecast so that even inexperienced birdwatchers might eventually come to accept the model's accuracy. We see a feedback system that displays confidence levels next to projections as a possible future improvement. In addition to providing an instructional component that is now lacking in other apps, users would be able to assess the model's predicting accuracy, which would increase confidence. In conclusion, the percentage of incorrect identifications on citizen science platforms may be considerably decreased by using specific models created for species identification. We could raise the standard of the

data gathered by citizen scientists by making these models more accurate. Accurate species identification is crucial to successful conservation efforts because it directly affects the quality of data and our understanding of the environment (Sharma et al., 2019). Using these models will ultimately result in improved ecological research findings and more informed decisions on biodiversity consevation.

6.4.6. Future Directions

The test dataset for this study did not purposefully include non-target species, such as overlapping *Phylloscopus* warbler species as well as co-occurring non-warbler species. The main goal was to assess YOLOv5's performance under controlled circumstances by concentrating on target species identification. Although include non-target species would have provided more information on the universality of the framework, we chose to restrict our focus to target species for the current study in order to preserve consistency and clarity in performance evaluation. We agree that including non-target species would aid in evaluating the model's resilience in practical situations, and we advise future research to concentrate primarily on this.

CHAPTER 7. CONCLUSION

The thesis examined evolutionary and ecological diversification of *Phylloscopus* leaf warblers by integrating historical biogeography, migration, compositional turnover, vocal divergence, and automated species identification. The central argument that emerges, is that diversity of this group cannot be understood through a single line of inquiry and explanation. Geography, elevation, climate, habitats all interact to shape how these small insectivorous passerines originate, persist, diverge and are recognized.

The historical reconstruction of *Phylloscopus* suggests that this genus was shaped by repeated dispersals and range shifts across Asia and beyond. The Indo-Chinese and Indian regions emerge as important ancestral ranges, but present distribution of the group reflects a dynamic history of isolation, expansion and recolonization rather than a simple radiation from one geographic origin. Seasonal environments, mountain systems, and transition zones appear to have acted both barriers and corridors. They supported dispersal while simultaneously providing opportunities for local adaptation, isolation and eventual divergence.

Migration represents one major outcome of this interaction between seasonality and space. Rather than being a static trait, migratory behaviour in this group appears evolutionary flexible and closely tied to clime niche, habitat use, latitude, and life-history variations. Sedentary species are largely associated with tropical and subtropical environments, complete migrants with temperate breeding systems, and partial migrants with intermediate or montane conditions where seasonal movements along the elevation may be advantageous. This strongly suggests that migration is merely not a movement strategy, but an ecological response to temporal variation in climate suitability and resource availability.

Present day assemblages add on an extra layer, since historical dispersal alone does not explain diversity. Zeta diversity and multisite turnover patterns reflect filtering by environmental gradients such as elevation, snow cover, aridity, productivity and disturbance. Some lineages retain a shared core of widespread species, whereas others show rapid turnover driven by localized, restricted, or habitat-specialised taxa. The result is a landscape in which closely related species can co-exist, remain separated, or replace

one another along these gradients. This compositional structure reveals continuing influence of filtering on a historically mobile lineage.

Where closely related species come in contact (especially in cryptic complexes), species identity must be maintained despite their morphological similarity. The acoustic analysis shows that vocal traits provide one such mechanism. Song variation in one such group, the *burkii* complex, reflects a balance between evolutionary constraint and ecological association. Spectral traits appear more responsive to elevation, vegetation structure, and habitat-mediated signal propagation, whilst temporal features retain a stronger phylogenetic structure. This indicates that divergence in vocal characteristics is not solely governed by acoustic adaptation or species recognition, but by interaction of both. Vocal signals thus carry ecological information while also helping maintain reproductive boundaries among morphologically similar taxa.

The issue related to crypticity also extends beyond evolutionary biology into the reliability of biodiversity data. If species are difficult to separate in field, then surely citizen-science records and public repositories inevitably contain uncertainty in identification. The computer-vision framework developed here addresses these applied consequences of cryptic diversification. Our YOLO-based model demonstrates that simple in-natural photographs too, can provide statistically useful identification tool for cryptic species such as leaf warblers. Machine learning should be therefore viewed not as a replacement of field expertise, but as a filtering tool that may reduce observer error and improve readability and reproducibility of large biodiversity datasets.

Taken together, this thesis shows that *Phylloscopus* leaf warblers are shaped by the continuum of processes operating across different scales. Deep-time dispersal explains us how these lineages reached new regions; ecological and climatic gradients explain how they partition and occupy present landscapes; vocal divergence helps maintain species limits; and automated recognition provides a practical approach in improving the data through which these patterns are studied. The broader contribution of this work lies in treating all these components as connected parts of the same evolutionary problem. In doing so, it positions *Phylloscopus* as a valuable model to understand how cryptic avian radiations diversify, persist, communicate, and remain detectable in changing landscapes.

CHAPTER 8. BIBLIOGRAPHY

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ABSTRACT

Name of the Student: Tushar P. Parab. **Registration No.:** 10BB22A73006
Faculty of Study: Biological Sciences. **Year of Submission:** 2026
AcSIR Academic Centre: MoEF&CC-WII. **Name of the Supervisor:** Dr. Salvador Lyngdoh

Title of the thesis: Biogeography, compositional turnover, morphology and vocal complexity of Genus '*Phylloscopus*'

Historical biogeography, evolution of migration, community turnover, acoustic divergence, and morphology of *Phylloscopus* leaf warblers was assessed using an integrated phylogenetic, ecological, and computational framework. To examine these aspects, we combined species-level phylogeny, ancestral range reconstructions, trait-dependent transition models, climatic niches, diversity estimates, eco-acoustic analyses and an image recognition approach. Our ancestral reconstructions support an Indo-Chinese origin followed dispersal into wider Eurasia, Afrotropics and the Indo-Malayan regions. Trait-dependent models indicate asymmetric evolution of migration, with temperate lineages more likely to gain migration and tropical lineages frequently losing it. Migration correlates with wing morphology, larger clutch size, shorter breeding season, and occupation of more seasonal climatic niches. Community turnover across Eurasia is structured by elevation, aridity, soil moisture and snow cover, indicating strong environmental filtering within superspecies complexes. Within *P. burkii* complex, spectral song traits vary with elevation and canopy cover, while sympatric species show greater divergence in frequency and song richness. Temporal traits are conserved phylogenetically within this complex, supporting both acoustic adaptation and species recognition mechanisms. A part-based YOLO-v5 model achieved high accuracy in identification performance (mAP = 0.94; recall = 0.97), demonstrating the utility of automated approaches for cryptic taxa. Together, these results highlight that integrative approaches are essential for developing a comprehensive understanding of evolutionary dynamics, ecological structuring, and diversification within complex species groups.

APPENDIX

Supplementary information for each chapter can be accessed using following links:

APPENDIX 1: FOR CHAPTER 3- ANCESTRAL RANGES AND EVOLUTION OF MIGRATION
https://drive.google.com/drive/folders/1kJteb6yCJid0cVV2nIBGM3Q594Zhz4Or?usp=sharing

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APPENDIX 2: FOR CHAPTER 4- COMPOSITIONAL TURNOVER: PATTERNS AND DRIVERS
https://drive.google.com/drive/folders/1svErIDhjzkpEY8yFcnuTzRIAh8t5ZEoh?usp=sharing

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APPENDIX 3: FOR CHAPTER 5- VOCALISATIONS: SONGS, ELEVATION AND SISTER SPECIES
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APPENDIX 4: FOR CHAPTER 6- MORPHOLOGICAL CLASSIFICATION: COMPUTER VISION AND DEEP LEARNING
https://drive.google.com/drive/folders/1vA65T3UIoXazTxXo9ob3P73JDAe8mxmf?usp=sharing

Codes used for the analyses of chapter 6 can be accessed through following GitHub:
https://github.com/tusharrparab/yolov5_Warbler

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1) List of publication(s) in SCI Journal(s) (published and accepted) emanating from the thesis work, with complete bibliographic details.

- **What Defines the Groupwise Compositional Turnover of Eurasian *Phylloscopus* Warblers? Insights From Zeta (ζ) Diversity and MS-GDM.**

  Parab, T., Singh, A., Alashi, N., Modak, N., Singh, A.P., Bhave, M., Nagarale, S. and Lyngdoh, S., 2025. What Defines the Groupwise Compositional Turnover of Eurasian Phylloscopus Warblers? Insights From Zeta (ζ) Diversity and MS-GDM. *Journal of Biogeography*, *52*(3), pp.657-669. https://doi.org/10.1111/jbi.15060

2) Abstract presented (poster) at Indian Conservation Conference,2025. (Chapter 5)

Evolution or ecological adaptation? Signal transmission in *Phylloscopus burkii* complex.

Animal Behaviour

Objectives: This study examines the effects of sympatry and habitat structuring on song divergence of the *Phylloscopus burkii* species complex inhabiting Sino-Himalayan ranges.

Methods: We analyzed bird songs using non-parametric tests and calculated song richness indices based on note diversity and repetition. Cross-habitat comparisons and structural equation models assessed how elevation, canopy structure, and vegetation complexity influence song traits. Linear discriminant analysis classified vocalizations using extracted acoustic features to distinguish between sympatric species. Genetic analyses using nuclear and mitochondrial DNA sequences established phylogenetic relationships and correlated genetic distance with vocal parameters.

Results: Habitat structure strongly shapes bird song, supporting the acoustic adaptation hypothesis. Elevation drives richer, lower-frequency songs due to less competition, while dense canopies favor higher frequencies for better sound transmission. Sympatric species show distinct vocal traits, supporting the species recognition hypothesis and reducing hybridization. Overall, these patterns reveal that reproductive isolation and environment together shape acoustic signals.

Conclusion: This study concludes by suggesting that (a) elevation drives divergence in frequency ranges, (b) habitat structure filters song syntax and frequency to optimize signal transmission, further mediating acoustic plasticity, and (c) reproductive isolation selects for distinct song structures between sympatric species to minimize hybridization. Our results provide insights into the relationship between biogeography, acoustic adaptation, and the role of habitat in the diversification of bird songs.

Keywords: species recognition, acoustic adaptation, ecological selection, song evolution, reproductive isolation

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RESEARCH ARTICLE

What Defines the Groupwise Compositional Turnover of Eurasian *Phylloscopus* Warblers? Insights From Zeta (ζ) Diversity and MS-GDM

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Keywords: distance decay | leaf warblers | site dissimilarity | spatial turnover | species composition

ABSTRACT

Aim: This study examines how environmental variables determine the co-occurrence of *Phylloscopus* warblers. It was carried out using an integrated zeta (ζ) diversity estimation method and multisite generalised dissimilarity modelling (MS-GDM).

Location: *Phylloscopus* species spanning Eurasia.

Study Period: Observations made during the breeding season for each species from 2014 to 2023.

Major Taxa Studied: We specifically focussed on complexes/superspecies groups within the genus *Phylloscopus* to address this question. The groups defined on recent phylogeny are the *P. castaniceps* complex, *P. cantator* group, *P. borealis* group, *P. burkii* complex, *P. affinis* group, *P. proregulus* group, *P. inornatus* complex, *P. davisoni* group, *P. fuscatus* group, *P. collybita* group, *P. trochiloides* complex and *P. tenellipes* group.

Methods: We used ζ diversity estimations to quantify the extent of compositional turnover and diversity across multiple sites. We further used MS-GDM to gain insights into how various environmental variables impact species composition.

Results: The composition of the groups we analysed is shaped by environmental conditions. The normalised difference snow index considerably impacts turnover within the *P. castaniceps* complex, with species such as *P. castaniceps* showing adjacency to snowy areas. Elevation and gravity anomalies play an essential role in the turnover of species in the *P. cantator* and *P. borealis* groups. The prevalence of positive gravity anomalies (variations in gravitational strength) in hilly areas determines the compositional differences within the *P. burkii* complex. The turnover of the *P. proregulus* group is influenced by both artificial night lights and gravitational anomalies. The turnover in the *P. trochiloides* complex and the *P. davisoni*, *P. collybita* and *P. tenellipes* groups is influenced by soil moisture, elevation, gravity anomalies and aridity index, emphasising the varied ecological niches of these species.

Conclusions: This study improves our understanding of the compositional shift of *Phylloscopus* leaf warblers over space and reveals the mechanisms underlying shifts in their composition across regions and the impact of changes in climatic patterns. As a result, this study is an important resource for ecologists and conservationists.

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1 | Introduction

The scale of the recent climate change has been unprecedented over many centuries if not over thousands of years. The global surface temperature has increased rapidly in the last two centuries and has been predicted to increase further under all the emission scenarios until at least the mid-21st century (IPCC 2021). The impacts of such global warming are manifold (Mendelsohn et al. 2000; Harley et al. 2006; Brander 2010; Tol 2018), including the loss of biodiversity (Habibullah et al. 2022) to which birds are no less an exception (Saunders et al. 2022). Reasonably therefore, recent studies in ecology have focussed on the complex relationships between climatic factors and species composition dynamics across ecosystems encompassing various taxa (Lindström et al. 2013). The availability of large species occurrence datasets such as GBIF (www.gbif.org), improved repository of geospatial data, technological advances in computing systems and improved analytical tools have come to help in such studies. This is particularly important for widespread genera, which demand extensive datasets to support accurate modelling.

In this study, we utilise such large datasets for the Genus *Phylloscopus* (Phylloscopidae: Passeriformes: Aves), commonly known as 'Classic Leaf Warblers'. It is the most species-rich genus inhabiting the Eastern Palearctic as well as the adjacent Indo-Malayan and Australasian regions (Martens 2010). Over the past three decades, the taxonomy of this genus has undergone significant revisions, with the number of recognised species rising from 52 in 1980 (Watson, Traylor Jr, and Mayr 1986) to 77–78 by 2018 (Dickinson and Christidis 2014; del Hoyo and Collar 2016; Gill and Donsker 2017; Alström et al. 2018). Further splits were proposed by Eaton et al. (2016), who identified six new species, including three from Indonesia. Although much focus has been on the systematics of this group of birds due to their morphological elusiveness, studies on other aspects of their life history are not scarce.

Research on *Phylloscopus* over the past five decades has spanned various aspects of their biology, including vocal studies (Mahler and Gil 2009; Tietze et al. 2015; Wu et al. 2023), breeding biology (Wesołowski and Maziarz 2009), community structure (Richman 1996; Ghosh-Harihar 2014) and habitat preferences (Tiainen et al. 1983; Forstmeier, Bourski, and Leisler 2001). Additionally, migration patterns (Norman 1987; Hedenström and Pettersson 1987; Ergen et al. 2017), phylogeography (Johansson et al. 2007; Päckert et al. 2012) and studies on adaptive radiation and speciation (Price 2010) have been well-explored. Nonetheless, these studies have mainly been conducted in the Chinese region (Zhang et al. 2021; Wu et al. 2023; Yang et al. 2023), the Himalayas (Price, Helbig, and Richman 1997) and a few in surrounding areas. The leaf warblers of wider Eurasia and Afrotropics still remain understudied despite thorough systematic investigation. In the current study, we cover this entire range except for Afrotropics due to the unavailability of sizable occurrence records and informative geospatial data belonging to them.

Over the past two decades, while advancements in high-resolution climatic variables have been made (Alizadeh 2022), ecological research has yet to explore these developments, particularly concerning variables associated with human activities, such as burned areas and aerosol levels (Engstrom 2010; Sanderfoot and Gardner 2021; Sanderfoot et al. 2022). Significant factors such as gravity anomalies (defined by high mountains and hilly areas) (Mills, Taylor, and Hemelrijk 2019; Jones and Ward 2020) and atmospheric pressure (Richardson 1978, 1990; Chmura et al. 2020) remain underexplored. The wide distribution of *Phylloscopus* across biogeographic realms presents an opportunity to better understand how climatic, geographical and anthropogenic variables, including those mentioned above, drive global species compositional turnover.

Until recently, the beta (β) diversity approach was a popular approach for studying the compositional turnover of species. However, the β diversity approach typically focusses only on pairwise comparisons between communities and, therefore, can emphasise the dissimilarities in the composition of the narrow-range species and does not include the contribution of common species shared across multiple sites (Latombe et al. 2018). Zeta diversity (ζ), on the other hand, is the number of species shared by multiple assemblages. Therefore, it can capture the full spectrum of diversity across multiple sites or assemblages by measuring the number of species shared among any given number of locations. It assumes that the number of shared species between the sites would decrease as the number of sites and/or the distance between them increases (zeta decline). Depending on the characteristics and preferences of the species, they would either be shared between the sites or will be replaced. ζ diversity captures this as a retention rate. Therefore, a high retention rate suggests communities dominated by common species, while a lower retention rate suggests communities dominated by narrow-range species. Further, it provides a unified framework to better understand species ecology by bridging the gap between incidence-based metrics (presence/absence of species) and ecological patterns (McGeoch et al. 2019). This is achieved by integrating ζ diversity with generalised dissimilarity modelling (GDM) to develop multisite generalised dissimilarity modelling (MS-GDM). This combination of metrics provides deeper insights into the drivers of community turnover and enhances our understanding of ecological dynamics. Although zeta diversity has been typically used to understand the compositional turnover of large communities, we utilised its power of teasing apart the impact of environmental variables on widespread and site-specific species. This is expected to signify species/group-specific effects rather than generalised effects over the community, helping in directed conservation efforts for the taxa being analysed.

Avian species turnover within taxonomic groupings is governed by relationships among habitat specificity, geographic distribution across breeding ranges and ecological constraints. The diverse spatial arrangement and ecological characteristics of breeding ranges, together with geographic limitations, affect the compositional turnover of avian complexes. Thus, we hypothesize that (i) the observed patterns in alpha diversity, ζ decay and retention rates stem from the ecological dynamics within breeding areas and limitations that sometimes prevent species co-occurrence and (ii) variables such as gravity anomalies and soil moisture that are associated with distinct geological features and influence net primary productivity modify co-occurrence within the complexes. In this study, we implied ζ diversity with

climatic, topographical, atmospheric, vegetational, anthropogenic and land cover variables with incidence-based metrics to elucidate global patterns and drivers of species turnover within the genus *Phylloscopus*. Furthermore, cross-continental analysis goes beyond local insights and provides important implications for bird ecology and conservation on a global scale. By comparing avian responses to climatic drivers across diverse biogeographical realms, we aimed to find shared patterns and region-specific differences, which is expected to help understand how these species behave with climate shifts.

2 | Materials and Methods

2.1 | Geographical Extent of the Study

Given that species composition can be unpredictable and may vary across space and time (Rosenzweig 1995; Sala et al. 2000), our research focussed on a large geographic area spanning Eurasia. The Eurasian regions of the Caucasus, Altai-Sayan, Caspian Hyrcanian mixed forests, Mediterranean basin, Mountains of Central and south-west China, the Himalayas and Southeast Asia are characterised by a significant prevalence of endemic species. We initiated a preliminary investigation aimed at evaluating the distribution of the genus *Phylloscopus* within these distinct biogeographic zones (see Johansson et al. 2007; Price 2010; Martens et al. 2004; Helbig et al. 1996; Peterson and Anamza 2017; Irwin et al. 2001). Additional information was obtained from literature focussing on long-distance migratory species (see Stervander, Knudsen, and Kristensen 2017). The details of species distribution have been provided in Table S1.

2.2 | Species Groups and Occurrences

We clubbed and followed the complexes and superspecies groups based on recent comprehensive phylogeny (Alström et al. 2018). The complex groups were (i) *P. castaniceps*, *P. cantator* and *P. borealis*; (ii) *P. burkii*, *P. affinis* and *P. proregulus*; and (iii) *P. davisoni*, *P. collybita*, *P. trochiloides* and *P. tenellipes*. This was to predict the findings with greater precision and to recognise variations and similarities within and among the groups to further make comparisons more targeted and informative. The species that had restricted distributions and were disconnected from allied areas (species such as *P. canariensis* mostly endemic to a single island) were excluded from the study to avoid overrepresentation of narrow-range species. Filtering, standardisation, geospatial validation, temporal consistency and data relevance were considered key components during analysis.

We utilised observations from the GBIF database (www.gbif.org) for species occurrence data, which provided critical insights into species turnover. We conducted an initial data pruning using the '*CoordinateCleaner*' package (Zizka et al. 2019) in the R program to reduce any possible spatial errors occurring due to imprecise location reading by the observer device or post hoc entries from distant locations. This eliminated occurrences with zero coordinates, those located in oceans or those associated with capital centroids, biodiversity institutions or GBIF headquarters. Data from the last decade (2014–2023) were used to reflect dynamic changes in species composition over space and time (Rosenzweig 1995). We used data from 2014, ensuring its consistency to the succeeding taxonomic classifications established between 2016 and 2018 (Alström et al. 2018). Species that were newly described after 2014 did not fit under the scope of this study and therefore were not part of the ecological complexes that were examined. We further filtered occurrences to include only breeding season records, ensuring ecological relevance (www.birdsoftheworld.org). To address potential sampling bias from proximity to roads or cities (Mair and Ruete 2016), spatial thinning was applied by selecting one occurrence per species within a 2×2 km grid (see details of occurrences in Table S2). This grid size is balanced, reducing clustering and minimising data loss, particularly for species with limited distributions, thus ensuring accurate, unbiased model prediction.

2.3 | Selection of Environmental Variables

Initially, a dataset comprising 62 variables considered biologically important for the ecological needs of insectivorous birds was compiled from different sources (see Table S3 for details). To reduce multicollinearity, we applied the Spearman correlation, and only variables with a correlation coefficient of less than 0.7 (i.e., $r<0.7$) were retained for further analysis. This effectively minimised multicollinearity, resulting in a more robust model performance. Different sets of environmental variables were then selected for each species complex and superspecies, based on their unique ecological preferences and habitats (Figures S1–S3). The detailed list of final selected variables that were used in the model is provided in Table S4. These variables were then rescaled to a coarse resolution of approximately 4 km^2 before analysis. The analysis was executed using ArcGIS 10.5 and the R programming language and environment (R Core Team 2019).

2.4 | Patterns of Compositional Turnover

The species turnover within the *Phylloscopus* complexes was explored using the ζ diversity approach (Hui and Mcgeoch 2014; Latombe et al. 2017a, 2017b; Latombe et al. 2018). While zeta diversity was originally developed to quantify the species composition of communities, it still could be utilised for comparing species that belong to the same genus as the framework to evaluate compositional turnover remains consistent even at this scale. The ζ diversity suggests the average number of species shared by i sites. Considering the number of sites (n) as the ζ order, the ζ diversity values for lower orders provide information on the turnover of narrow-range species (e.g., those species shared between two sites), while values for higher orders represent the rate of turnover in widespread species of the community (Leihy, Duffy, and Chown 2018; Hui, Vermeulen, and Durrheim 2018). The ζ diversity at order n can be expressed as

$$\zeta_n = \frac{1}{\binom{N}{n}} \sum_{l=1}^{\binom{N}{n}} \prod_{j=1}^{n} S_{lj}$$

where ζ_n is the ζ diversity of order n, N represents the total number of sites, S_{lj} indicates the presence or absence of species J at site l and $\binom{N}{n}$ is the binomial coefficient representing the number of combinations of n sites from N. As ζ diversity values decline, the

retention rate describes the rate at which species are retained with increasing orders, that is, number of sites (ref). ζ diversity was calculated for each species group separately using the 'zeta.decline' function in the '*zetadiv*' package (Latombe et al. 2017b) in R (R Core Team 2019). Furthermore, we employed the distance decay function from the *zetadiv* package to calculate the spatial distance decay in turnover of ζ diversity. The distance decay of ζ diversity can be represented as $\zeta_n(d) = \zeta_n(0).e^{-\beta d}$ where $\zeta_n(d)$ is the ζ diversity at distance d, $\zeta_n(0)$ is the initial ζ diversity at zero distance, β is the decay rate and d is the spatial distance. Applying ζ decay analysis improves the precision of ζ diversity estimates, especially for widespread genera (Leihy, Duffy, and Chown 2018; Hui and Mcgeoch 2014).

2.5 | Drivers of Compositional Turnover

To further understand the changes in species composition as a function of environmental differences, we used the MS-GDM approach by combining ζ diversity and the generalised dissimilarity models (used along with beta diversity) (Latombe et al. 2018). By applying it to multiple orders of ζ, MS-GDM explains the differences in species composition with different environmental and anthropogenic factors (Alashi and Modak 2023; Latombe et al. 2018). It also includes the spatial distance between sites to determine the relation. We used the Euclidean distance to determine the spatial distances, as it provides a more straightforward mathematical representation of the shortest path between two locations in a multidimensional space. Using a generalised linear model coupled with i-spline functions, MS-GDM addresses the monotonic decline in ζ diversity along environmental gradients. By generating a binomial dataset, this method allows a non-linear analysis of the data, assisting in understanding the complexity of biodiversity response to changing environments (Alashi and Modak 2023; Latombe et al. 2018; Ramsay 1988). A combination of 5000 random sites was set for the sufficient efficiency of the model. The inclination of the splines indicates how the impact varies across the spectrum of values concerning the explanatory variables (Latombe et al. 2018). For instance, a pronounced incline at higher normalised difference snow index (NDSI) levels signifies the variations in snow within regions experiencing high snowfall. Likewise, a gentler incline at lower NDSI levels implies a reduced significance of differences in NDSI within areas with lower snowfall.

3 | Results

3.1 | Patterns of Compositional Turnover

3.1.1 | The *Castaniceps* Complex and *Cantator* and *Borealis* Superspecies Groups

The *castaniceps* complex had the highest initial species richness (alpha diversity = 1.18), followed by the *cantator* group (alpha diversity = 1.02), while the *borealis* group had a very small richness

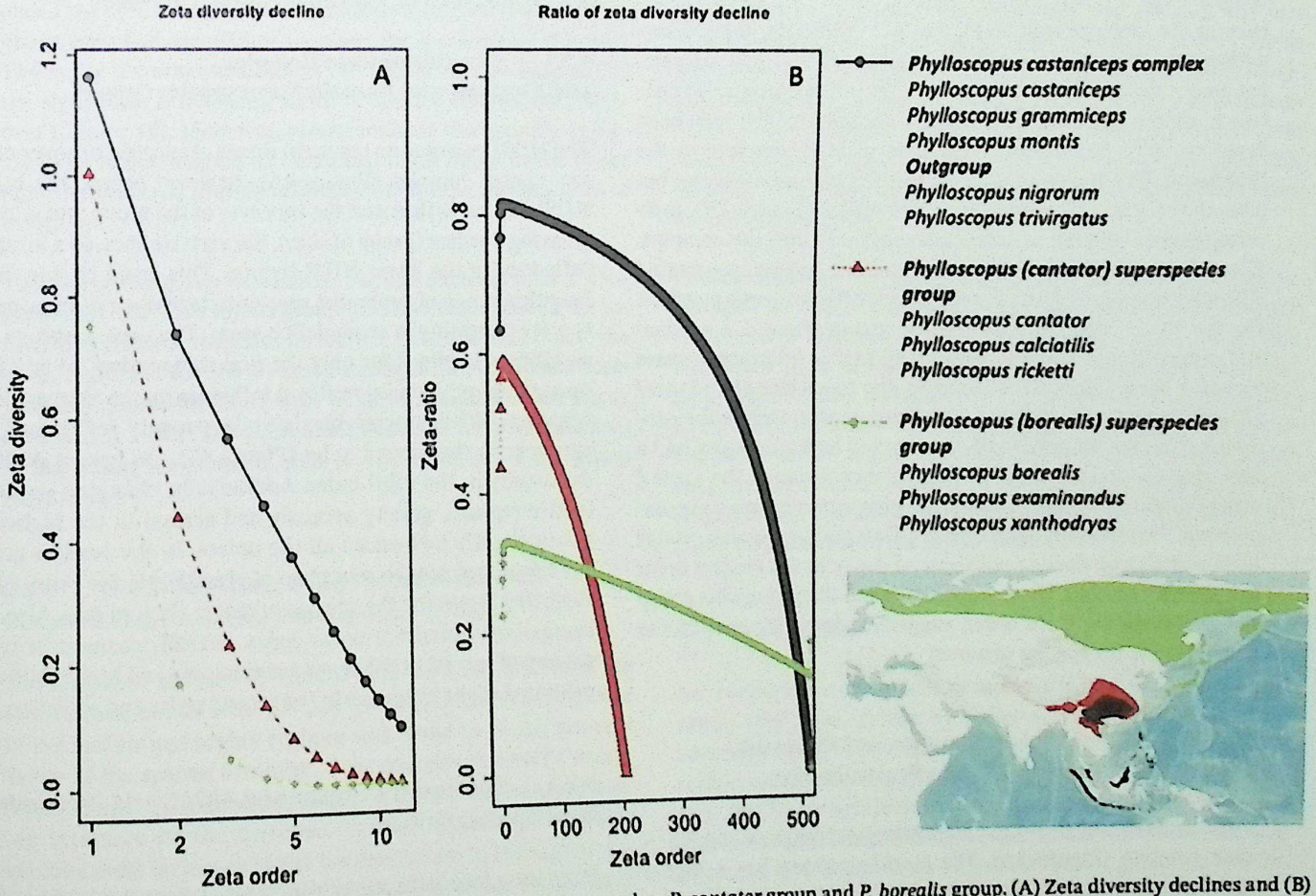

FIGURE 1 | Zeta diversity of the species of the *P. castaniceps* complex, *P. cantator* group and *P. borealis* group. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these three groups is illustrated in the map.

within the site (Figure 1A). All these groups have a minimal increase in ζ-ratio, suggesting a small overlap of all the commoner species. The ζ decay was also lowest within the *borealis* group (more species loss with the increasing number of species in ζ). Although the richness was lowest in the *borealis* group, the retention rate declined gradually, suggesting occupancy dominated by common species, while the retention rate declined sharply for the *cantator* group, suggesting rare/site-specific species influencing the turnover with the increasing number of sites (Figure 1B). The diverse *castaniceps* complex resulted in a gradual decline in turnover, followed by a steep decline after 300 sites, suggesting a species composition of intermediate species among the groups. The distance decay plot shows a gradually increasing regression slope (up to 10 orders) for the *castaniceps* complex, which has a sparse breeding distribution and suggests the influence of distance decay over commoner species turnover (Figure S4). In contrast, the slope demonstrated a downward trend in the *cantator* and *borealis* groups in the second order and followed the same trend in the *cantator* group, having a longitudinal distribution, suggesting a strong influence of distance decay over the rare species turnover (Figure S5). Meanwhile, the trend in the *borealis* group became gradual and had insignificant ζ decline values by the fifth order (Figure S6).

3.1.2 | The *Burkii* Complex and *Affinis* and *Proregulus* Superspecies Groups

Within these species groups, there is only a minimal difference in the alpha diversity (Figure 2A). Similarly, the ζ decay within the *affinis* and *proregulus* groups is also high, suggesting a considerable overlap of species, but interestingly, no species is shared between sites beyond six orders. The restricted *burkii* complex has a higher increase in retention rate in the first few orders due to overlap within the common species but then shows a steep decline up to 200 orders (Figure 2B), indicating higher isolated or restricted species within the complex. The *affinis* group exhibited an intermediate decline, suggesting a limited retention of the rarer species with increasing orders. On the other hand, the *proregulus* group showed a gradual and almost linear decline, suggesting higher common species turnover across sites. This could be due to species abundance/adaptation factors associated with the complex. Unlike the *cantator* group, the longitudinally distributed *burkii* complex had a very gradual decline trend in the distance decay in the same ζ orders (Figure S7), due to its overlapping common species composition. The spatially widespread *affinis* and *proregulus* groups both had a steep decline with spatial decay in the second order (Figures S8 and S9). However, the trend in the *proregulus* group reduced from the third order, suggesting less influence of site proximity on the species turnover.

3.1.3 | The *Trochiloides* Complex and *Davisoni*, *Collybita* and *Tenellipes* Superspecies Groups

This combination showed a contrasting turnover of species in each complex (Figure 3A). The *tenellipes* group has a higher alpha diversity (1.1) and represents a gradual ζ decay, suggesting a lower loss of species with increasing orders or groups of sites. Interestingly, the retention rate was very low, with a sudden drop compared to other complexes, indicating a higher turnover of rarer species (Figure 3B). A similar pattern was observed in the species richness of the *davisoni* group, with common species overlapping only for a few orders, but the retention rate further gradually declined for more than 3000 orders and then reduced, suggesting intermediate species influence on the turnover of the complex.

The *davisoni* and *collybita* groups and *trochiloides* complex show a gradual slope in all the ζ orders of distance decay, suggesting that it influences the intermediate species turnover (Figures S10–S12). The *trochiloides* complex has a linear ζ decay, suggesting no strong influence on the richness of the complex, but there is a steep decline in the retention of common and intermediate species, which can be due to significant overlap within groups of rarer species in the complex. On the other hand, the *collybita* group having a similar linear ζ decay showed a gradual reduction after seven orders. The retention of rare species was still higher in comparison to the common species (steep decline in ζ-ratio, suggesting higher rare species turnover). The influence of distance decay in the *tenellipes* group is shallow on the compositional turnover (although with high diversity) at lower ζ orders (Figure S13). With the increasing number of sites, the decay shows an upward trend (up to the 63rd order, after which the estimated ζ values are insignificant), supporting the high rarer species turnover with proximity in sites.

3.2 | Drivers of Compositional Turnover

3.2.1 | The *Castaniceps* Complex and *Cantator* and *Borealis* Superspecies Groups

The NDSI emerged as the main driver of species turnover of the *castaniceps* complex (Figure 4A). At lower orders, the higher NDSI regime influenced the turnover of the group, but with increasing ζ orders (group of sites), the variable showed a minimal influence in the lower NDSI regime. This could be due to the breeding range of generalist species independent of snow or the species migrating to snow-deficit areas. The *cantator* group had significant i-splines for only the first three orders, after which no variable exhibited significant influence on the compositional turnover. While increasing latitude strongly influenced the turnover in the second order (Figure 4B), the impact declined drastically in the third order. Additionally, changing longitude (entire regime), gravity anomaly and aerosol in the higher regimes slightly influenced all the orders. In the *borealis* group, the lower and moderate regime of elevation is the primary influencing factor for the species turnover (Figure 4C). Also, the normalised difference water index (NDWI, changes in water content of leaves) in the lower water regime and higher latitudes exhibited slight influence in the second order and elevation.

3.2.2 | The *Burkii* Complex and *Affinis* and *Proregulus* Superspecies Groups

Increasing longitude, gravity anomaly and aerosol turned out to be the influencing factors for the species turnover of the *burkii* complex (Figure 5A). Although the effect of gravity anomaly prevailed beyond six orders, the rest of the factors exhibited

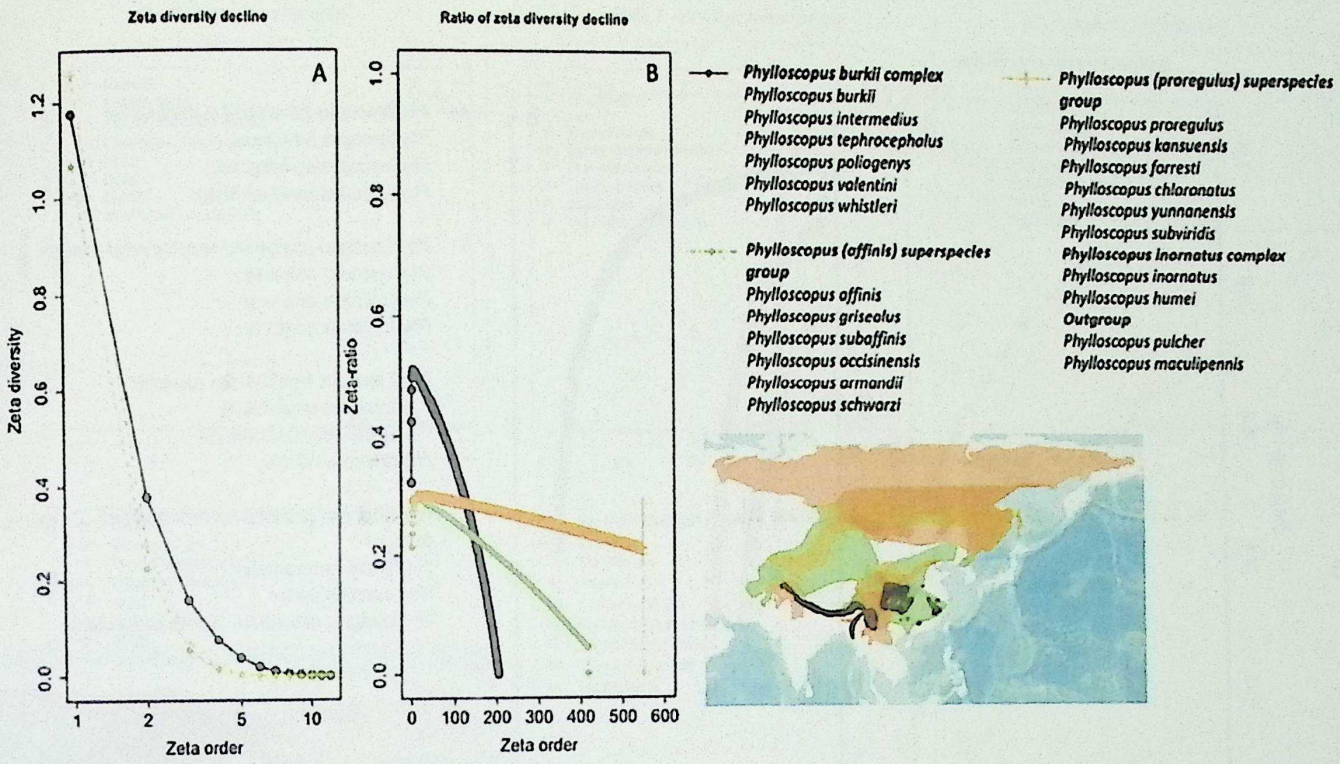

FIGURE 2 | Zeta diversity of the species of the *burkii* complex, *affinis* group and *proregulus* group. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these three groups is illustrated in the map.

a decline in the effect. Also, higher night lights slightly influenced the species complex in the lower orders of ζ. The *affinis* group only had significant i-splines for a couple of ζ orders. The decay disturbance index in the higher regime emerged as the significant influencing factor of species composition turnover (Figure 5B). Moreover, results indicate that gravity anomaly in its middle regime and artificial night lights in the lower light regime could slightly influence the species composition of the group.

The *proregulus* group has similar i-spline declines after a couple of orders like the *affinis* group. Elevation emerged as the influencing factor throughout its regime. In the second order, the lower regime of the NDWI had a strong influence on the compositional turnover, along with the lower regime of the decay disturbance index. The third order exhibited a slight influence of increasing longitude as well on the turnover of the group (Figure 5C).

3.2.3 | The *Trochiloides* Complex and *Davisoni*, *Collybita* and *Tenellipes* Superspecies Groups

The longitude and gravity anomaly are the main drivers of the species composition of the *davisoni* group (Figure 6A). Longitude in the middle and higher regimes was found to be the primary driver of the species turnover of the complex in lower ζ orders (up to 24 orders), after which gravity anomaly shows an increasing influence on the turnover. Further, distance-to-drainage exhibits more influence in the last few orders in the higher distance regime, although we expect this factor to have a minimal impact due to the low i-spline value (i-spline at order 50: 0.13). Additionally, the higher regime of the disturbance index and the lower regime of net primary productivity also slightly influence the species composition of the complex. The *collybita* and *fuscatus* group turnover was found to be influenced mainly due to elevation (lower and middle elevation regimes). The lower longitude and higher latitude regimes are highlighted as an influencing factor in the lower orders (up to six orders) due to the wide breeding distribution of species within the groups (Figure 6B). No other environmental factor exhibited a significant influence on the species group.

For the *trochiloides* complex, longitude in the higher regime emerged as the influencing factor for the species turnover (Figure 6C). Higher soil moisture and distance to settlement had only a slight influence in the first few orders. The *tenellipes* group significantly influenced aridity in the lower aridity index. In contrast, the lower regime of the NDWI, along with the bare soil index in the higher regime, exhibited a fluctuating influence on the species turnover of the species within this group (Figure 6D). In addition, canopy height (in the lower height regime) played a role in the higher orders.

4 | Discussion

An ecological understanding is expected to progress significantly over time, driven by easier access to geospatial data, advanced analytical software and the growing availability of resources and platforms for interdisciplinary research (Bluemke et al. 2017). Alongside these technical advances, citizen science data are of great help. Due to its spatiotemporal extent and ease of access, it has become an important tool for gathering new information and filling in the knowledge gaps (Klemann-Junior et al. 2017). Although citizen science platforms have evolved

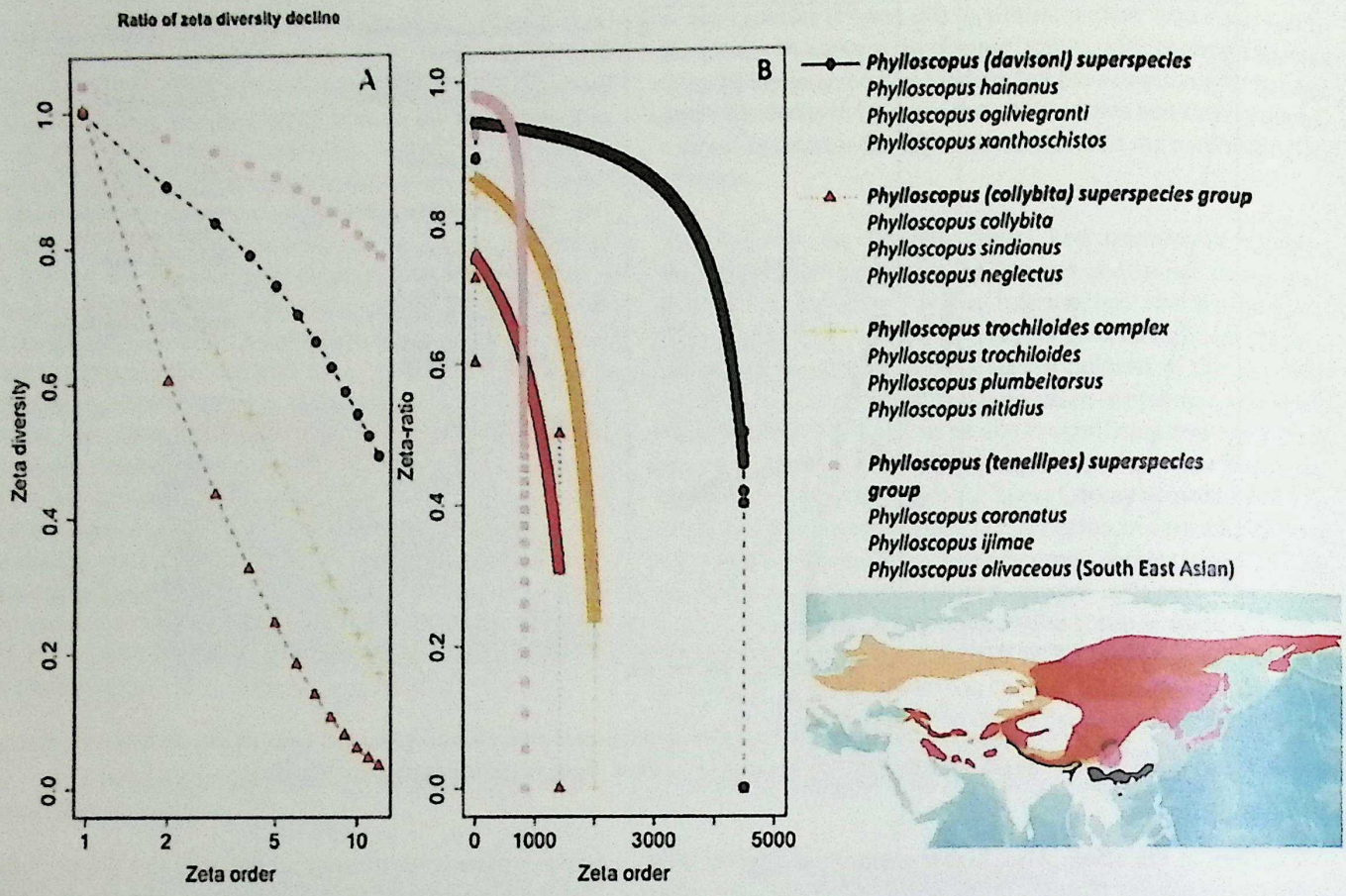

FIGURE 3 | Zeta diversity of the species of the *P. davisoni*, *P. collybita* and *P. tenellipes* groups and *P. trochiloides* complex. (A) Zeta diversity declines and (B) the corresponding zeta ratio computing the retention rate. The distribution of these four groups is illustrated in the map.

over the past 20 years, particularly in terms of improving our understanding of species distribution, the variables influencing this distribution are mostly unknown. Our work fills a major research gap by utilising an integrated strategy to explain the patterns of the continuous change of compositional diversity. Understanding these shifts would be much improved by including more fine-scaled (regional data, effectively adding more data points) data, as the data adds value to sufficiently evaluate variations in composition at a continental scale. Uneven species occurrence across compound communities may be demonstrated by a decline in zeta for complexes, suggesting that niche-based primary assembly processes may exist within the *Phylloscopus* community (see Hui and McGeoch 2014; McGeoch et al. 2019). This approach also contributes to understanding how environmental variables shape the composition of Genus *Phylloscopus* throughout its geographical distribution, which is pertinent in the changing climatic scenario.

4.1 | The *Castaniceps* Complex and *Cantator* and *Borealis* Superspecies Groups

The species composition of intermediate (*P. montis*) and rarer (*P. grammiceps*) species within the group is apparent by the turnover of the *castaniceps* complex, which first decreased gradually, followed by a steep drop. All three of these species are known to intersect in a very small area in the Sumatran mountains (Martens 2010) despite their breeding grounds being separated by a substantial distance (https://birdsoftheworld.org). Among the species belonging to this complex, the breeding territory of only one (*P. castaniceps*) is adjacent to snowfall areas, while the other species primarily reside in Southeast Asia, extending as far as the Thai-Malay Peninsula and Indonesia. This might be the reason why the results suggest that NDSI is the main driver of species turnover in this complex. It is also essential to highlight new locations/ranges from northern China's Nenjiang (Li et al. 2012), where 5 months of snowfall is predicted annually. There have been studies suggesting species' inclination for an intermediate level of snow cover that is consistent with the foraging strategies. Birds either gather fallout of trapped invertebrate prey on the snow surface (Antor 1995) or take advantage of the melting edges of snow fields where they can find an abundance of larvae, one of their favourite and most easy-to-acquire prey items (Cramp, Perrins, and Brooks 1994).

The presence of site-specific species (*P. calciatilis*) influencing the turnover with an increasing number of sites must have driven the retention rate for the *cantator* group to drop sharply. The patchy breeding distribution of *P. cantator* in the Himalayas and southeast Asia can be attributed to the influence of gravity anomaly (positive) as a driver of turnover at higher elevations. The *borealis* group exhibits lower richness within the site along with the lowest ζ decay. A minimal increase in ζ-ratio suggests a small overlap between the species (*P. examinandus*, *P. borealis* and *P. xanthodryas*). Wide Palearctic breeding distribution of *P. borealis* (one of the largest breeding distributions of all *Phylloscopus*) and a comparatively smaller range of *P. examinandus* and *P. xanthodryas* (see Saitoh et al. 2010) provide contrasting details on elevational preferences,

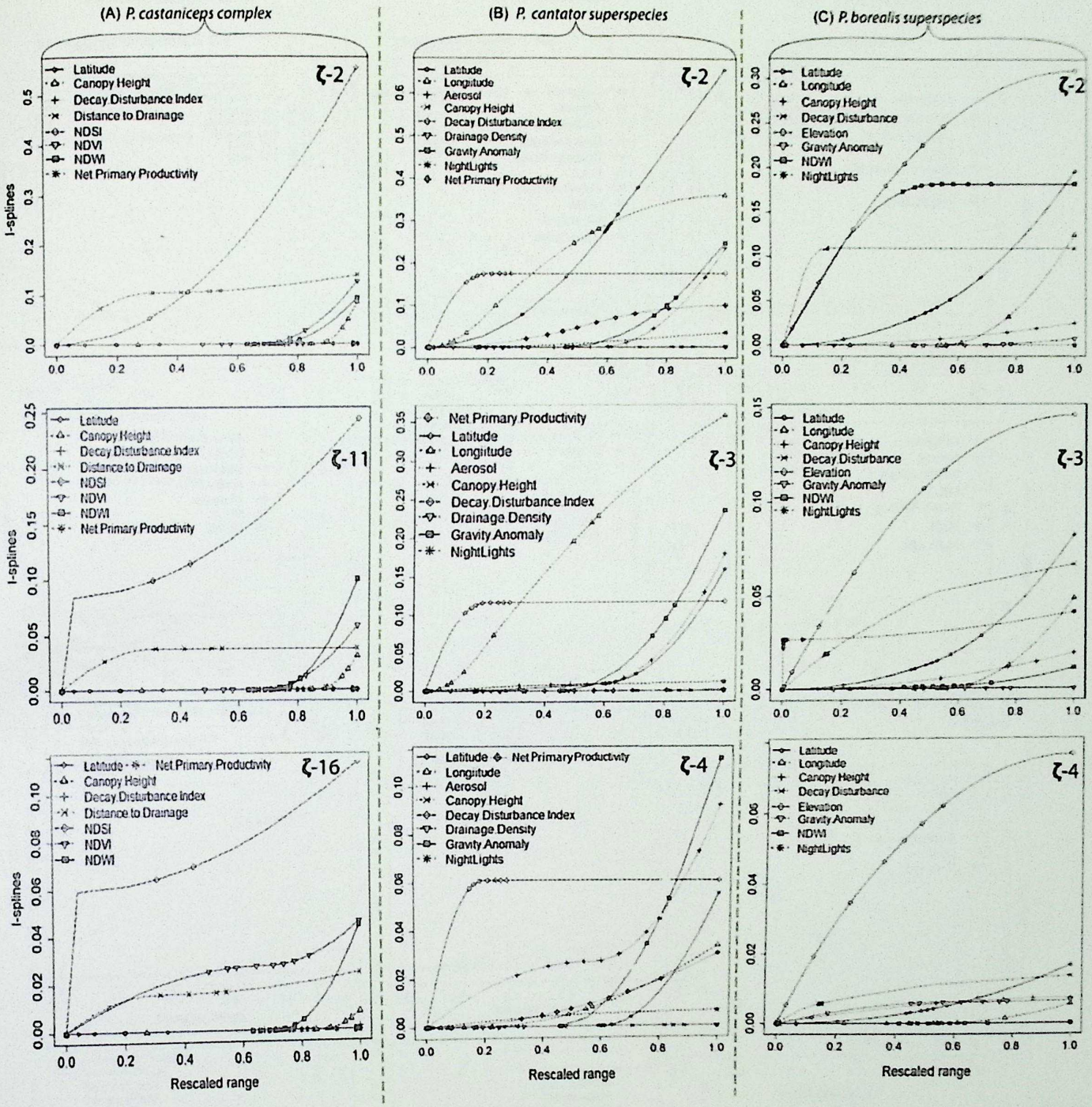

FIGURE 4 | I-splines evaluated by multisite generalised dissimilarity modelling for the *P. castaniceps* complex (at $\zeta_{2,11 \text{ and } 16}$), *P. cantator* group (at $\zeta_{2,3 \text{ and } 4}$) and *P. borealis* group (at $\zeta_{2,3 \text{ and } 4}$), showing the contribution of environmental variables.

which has also emerged as a primary influencing factor for the species turnover in this group.

4.2 | The *Burkii* Complex and *Affinis* and *Proregulus* Superspecies Groups

Throughout its complex evolutionary history, the *burkii* complex experienced both vertical and possibly horizontal parapatry across the whole Sino-Himalayan region, along with vicariance (Alström and Olsson 1999; Martens et al. 1999; Päckert et al. 2004). The majority of the species from this complex inhabit continuous mountain belts at uniform altitudes. (Päckert et al. 2004). Because the breeding ranges of the common species (*P. burkii* and *P. whistleri*) overlap, our results indicate an increase in retention rate in the first few orders. However, a steep fall suggests the presence of more isolated species within the complex, which is likely because breeding ranges of several species (*P. soror*, *P. valentini* and *P. omeiensis*) are scattered throughout tiny, remote mountaintops in China and later two along with *P. whistleri* are likely evolved in northern refuge areas (Päckert et al. 2004). Results also indicate positive gravity anomaly (which is associated with mountainous regions) as a primary driver of compositional turnover within this complex. Gravity anomaly acts as a geophysical barrier for the seasonal migration of various bird species, affecting their energy

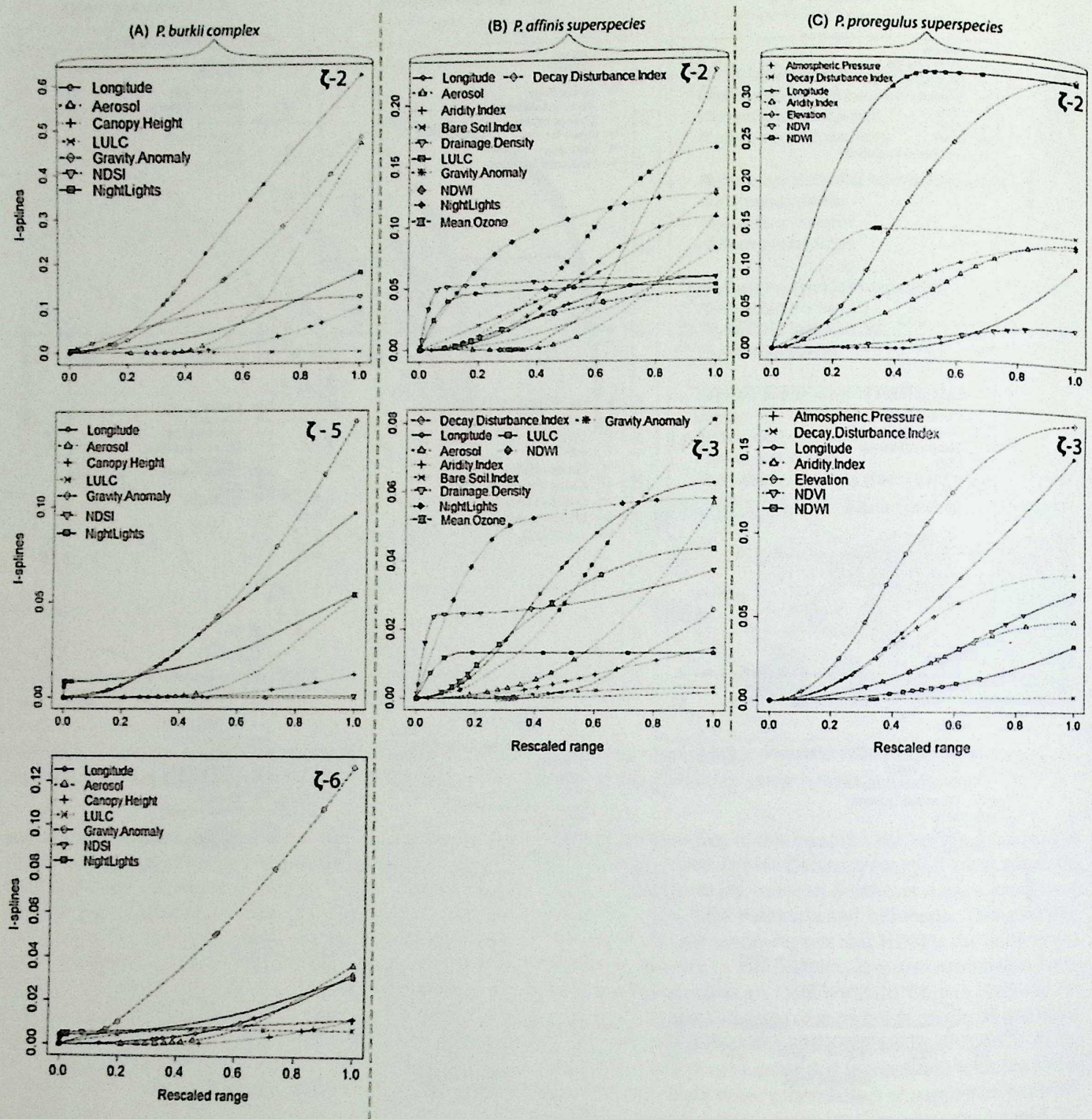

FIGURE 5 | I-splines evaluated by multisite generalised dissimilarity modelling for the *P. burkii* complex (at $\zeta_{2.5 \text{ and } 6}$), *P. affinis* group (at $\zeta_{2 \text{ and } 3}$) and *P. proregulus* group (at $\zeta_{2 \text{ and } 3}$), showing the contribution of environmental variables.

requirements in areas with larger elevational gradients (Blaser et al. 2014). Interestingly, Martens et al. (2003); Martens, Tietze, and Päckert (2011) reported the presence of three species along a single forested edge during the breeding season.

An intermediate decline in the *affinis* group suggests an intermediate retention of the rarer species with increasing orders (presumably *P. subaffinis* and *P. armandii* based on scarce breeding locations). The species composition of the group may be slightly influenced by artificial night lights in the lower light regime and gravity anomalies in the middle elevational gradients, according to our MS-GDM results. The *proregulus* group is another great example of diversification in the Sino-Himalayan region, much like the *burkii* complex (Päckert et al. 2004). The breeding distribution of species belonging to this group is mainly clustered around regions where elevation likely shaped the composition and breeding ranges of this species. Along with this group's lower decay disturbance index regime, the NDWI also considerably influenced the compositional turnover.

4.3 | The *Trochiloides* Complex and *Davisoni*, *Collybita* and *Tenellipes* Superspecies Groups

The geographical forms of this greenish warbler (*P. trochiloides*) complex show significant overlap, as indicated by a steep

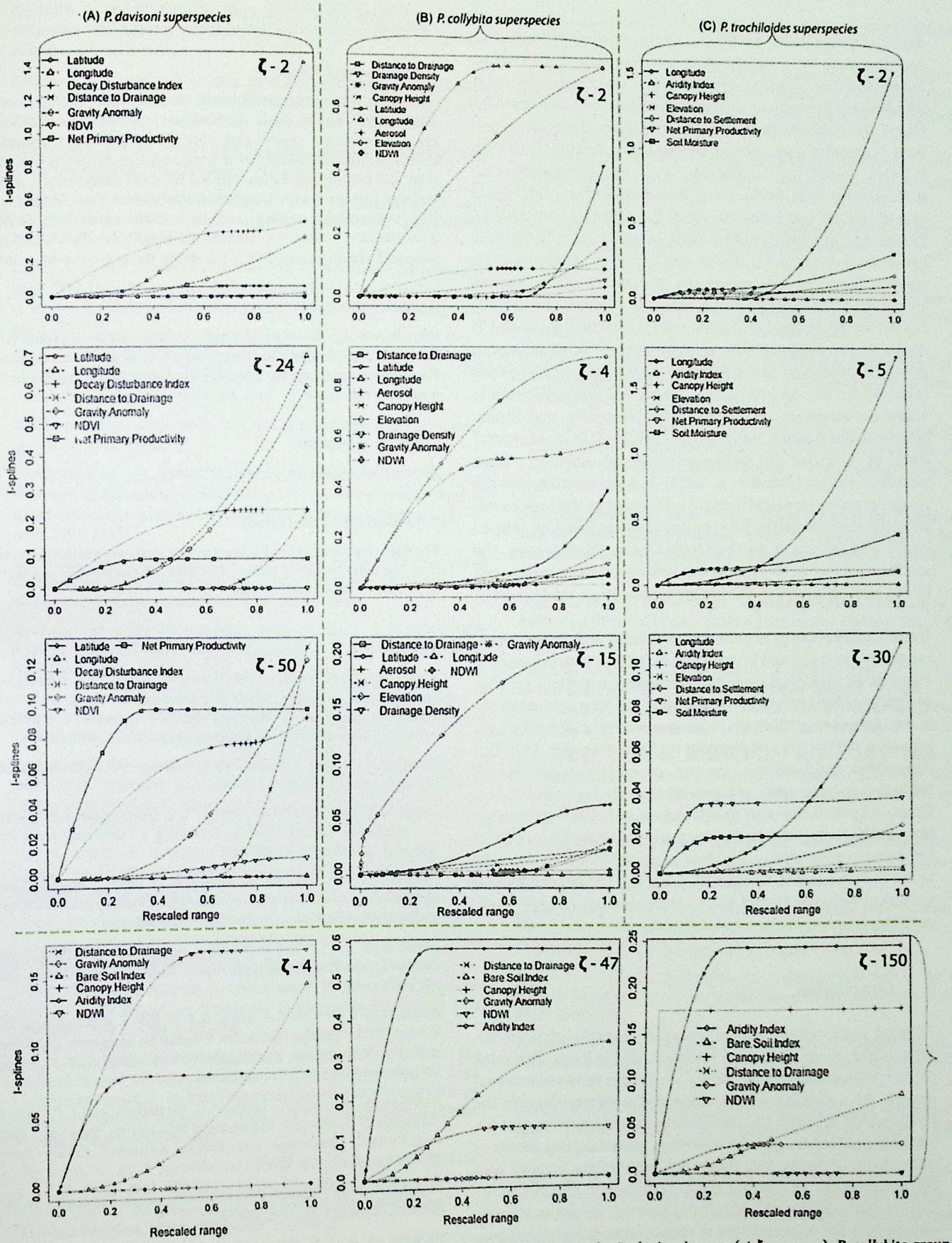

FIGURE 6 | I-splines evaluated by multisite generalised dissimilarity modelling for the *P. davisoni* group (at $\zeta_{2,24 \text{ and } 50}$), *P. collybita* group (at $\zeta_{2,4 \text{ and } 15}$), *P. trochiloides* complex (at $\zeta_{2,5 \text{ and } 30}$) and *P. tenellipes* group (bottom, at $\zeta_{4,47 \text{ and } 150}$), showing the contribution of environmental variables.

decline in retention. According to the results, soil moisture was found to be a contributing variable, which can be attributed to the breeding distribution of *P. trochiloides* itself, which exhibits a gap in the arid, forestless area of northern China (Martens 2010). Although soil moisture primarily governs vegetation composition across areas, it also drives the primary productivity of that region and the abundance of insects (Onrust et al. 2019). These factors may play a significant role in habitat specialisation. Both the *collybita* and *davisoni* groups also exhibit a gradual slope in all ζ orders of distance decay, indicating that it affects the turnover of intermediate species. Elevation emerged as the primary driver for species turnover for the *collybita* group, which is apparent considering the patchy breeding distribution ranges of *P. sindianus* and *P. neglectus* and comparatively wide-ranging *P. collybita*. Again, gravity anomaly was found to be the primary driver for species turnover for the *davisoni* group, which is distributed mainly across the mountainous regions of the Himalayas and China. Similar to the *P. burkii* complex, the movement of these species could be restricted due to the gravitational variation within mountain ranges (Blaser et al. 2014). It is noteworthy that the *tenellipes* group was significantly influenced by the lower aridity index, demonstrating how the composition has been shaped by the arid regions of north-eastern China. Furthermore, the species turnover in this group was also found to be influenced by the bare soil index in the higher regime in an unclear way.

Overall, differences in retention rates, ζ decay and diversity represent the dynamics and interactions that occur within breeding zones on an ecological level. Furthermore, restrictions such as competition for resources, habitat specialisation and environmental factors might limit the coexistence of species, which may influence the patterns of diversity that are observed. This fact strengthens the discussion for our second hypothesis, which holds that co-occurrence patterns within the complexes are influenced by variables such as soil moisture and gravity anomalies, which are linked to particular geological features and affect net primary productivity (which is more prominently observed in the *P. burkii* and *P. trochiloides* complex). When conducting ecological research linked with environmental factors, these variables may be considered in the future.

5 | Conclusion

Targeted conservation efforts are made possible with an understanding of compositional turnover, which helps determine habitat preferences and resistance of species to environmental change. By a detailed examination and understanding of the relationships between the distribution of leaf warblers and environmental factors such as elevation, snowfall, soil moisture and gravity anomaly, this study indirectly offers insights into the impact of environmental and anthropogenic drivers that influence these groups of birds. It expands our ability to identify and analyse the consequences of climate change on ecosystems and biodiversity. Using this understanding, fragile species and ecosystems can be conserved using more effective management practices. To that end, interdisciplinary collaboration is crucial for establishing a detailed ecological understanding in the context of climate change.

Author Contributions

Tushar Parab: conceptualization, investigation, writing – original draft, formal data analysis, methodology, software, visualization, formatting, writing – review and editing. **Ankit Singh:** visualization, geospatial analysis. **Niket Alashi:** methodology, software, writing – review and editing, validation. **Nikhil Modak:** methodology, software, writing – review and editing, validation. **Amar Paul Singh:** formatting, methodology, writing – review and editing. **Maitreyee Bhave:** data curation, resources. **Shashank Nagarale:** data curation, resources. **Salvador Lyngdoh:** supervision, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available on request from the corresponding author. The data are not publicly available due to privacy or ethical restrictions.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.