DISTRIBUTION OF BREEDING *PHYLLOSCOPUS* AND *SEICERCUS* WARBLERS IN THE HIMALAYAS: ROLE OF ECOMORPHOLOGY AND COMPETITION

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By

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CERTIFICATE

This is to certify that the thesis of **Ms Mousumi Ghosh** entitled **"Distribution of breeding *Phylloscopus* and *Seicercus* warblers in the Himalayas: role of ecomorphology and competition"** is an original and independent research work submitted to the Saurashtra University, Rajkot (Gujrat), for the award of the degree of **Doctor of Philosophy in Wildlife Science.**

Ms. Mousumi Ghosh has carried out the research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted for any degree of any other University or Institution.

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Contents

List of Figures

List of Tables

List of Plates

List of Appendices

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EXECUTIVE SUMMARY

Understanding the drivers of species distribution and community structure has been a major theme in ecological research. Both abiotic and biotic ecological factors interact and operate at various spatial scales to determine the observed patterns of species occurrence at any site, while the biogeographic species pool from which species are derived is largely a consequence of historical factors acting at large temporal scales. Hence, ecological determinants of species distribution need to be investigated at both the broad geographical scale based on current ecological niche constraints as well as at the local scale with emphasis on species interactions within communities. Similarly, phylogenetic relatedness needs to be taken into consideration to assess the relative importance of historical factors.

The Old World leaf warblers (genus *Phylloscopus*) have been the subject of some notable ecological studies investigating ecological segregation and speciation on continents, owing to the remarkable species diversity, close relatedness among species, and very similar morphology and ecology. In addition, the phylogeny of most of the species is well worked out which allows better understanding of ecological relationships by controlling for phylogeny. Previous studies have examined the nature of ecomorphological relationships and competitive interactions which influence the observed breeding community structure at one site. However, factors influencing the broad distribution pattern of these widely distributed speciose clades across the continental scale have not been investigated.

I carried out this study with the overarching goal of understanding the ecological and historical determinants of geographic and altitudinal distribution of sixteen breeding *Phylloscopus* and *Seicercus* species in the Himalayas. The broad research objectives were as follows:

1. Assess the availability of arthropod resources across the eastern and western Himalaya along the elevational gradients.
2. Identify the climatic correlates of the breeding distribution of Phylloscopidae.
3. Examine the geographic variation in foraging ecology of Phylloscopidae across the Himalayan bioclimatic gradient.

4. Evaluate the drivers of community assembly using phylogenetic community structure of breeding leaf warblers across the Himalayas.

Across east and west Himalayas, I identified sixteen sites situated in relatively undisturbed forested habitats along nine elevational transects. Transects were chosen to cover relatively long continuous forested habitats along a more or less similar aspect. The field sampling was conducted during the breeding season (April-June) over three years (2008-2010). In general, sites situated along elevational gradients in the east were cooler and received more precipitation than sites situated at comparable elevation in the west. I quantified arthropod prey for these strict insectivores using the bagging method from all the sites. Vegetation characteristics were similarly measured from representative plots in multiple sites to broadly characterize the habitats in the east and the west. I carried out fixed-radius point counts at every 25m rise in elevation along the nine elevational gradients. The relative abundances and breeding elevational range for each species was derived for east and west separately by combining data from all the elevational transects situated in each region. I opportunistically collected data pertaining to the foraging ecology of the study species.

Arthropod abundances varied spatially along elevational gradients and across east and west corresponding with the variation in climatic factors. This study provides the first broad-scale assessment of variation in distribution patterns of foliage-dwelling arthropod orders along elevational gradients located across an extensive precipitation gradient in the Himalayas. Abundances declined significantly from the east to the west and peaked at intermediate elevations along elevational gradients. The observed decline in overall and taxon-specific abundances could be related to decline in temperature above the respective peak elevations, while a combination of precipitation and temperature appeared to influence a general increase in abundance from the low-elevations to the intermediate elevations.

By incorporating occurrence records from the breeding distribution range and environmental layers, this chapter predicted environmentally suitable areas across the Himalayas for species restricted to the east and west to test whether lack of suitable climatic niche is responsible for their inability to range across the west and the east, respectively. Annual precipitation and maximum temperature were the environmental variables which contributed the maximum information to the geographic distribution models. In most cases, environmental niches as defined by climatic variables does exist in the other region (where the species is absent), suggesting that climate alone is inadequate in explaining the observed pattern of breeding distribution.

Across the terrestrial environment more species occur in warm wet areas than in cold dry areas, with explanations broadly classified as historical and unsaturated, or ecologically deterministic and at equilibrium. In the latter hypothesis, more "niches" are available in warm wet areas, but this has been difficult to evaluate. Here, I introduce a test of the alternative explanations based on assessment of geographical variation within species whose ranges straddle species-poor and species-rich regions. Under historical models we predict niche expansions in species-poor regions, because species numbers are further from any ecological carrying capacity. I studied geographical variation in 10 species of Old World leaf warblers (Phylloscopidae) across the Himalayas. Elevational range and feeding method showed niche contractions in the species-poor western communities with respect to species-rich eastern communities, whereas prey size did not vary geographically. For the two traits showing niche contractions, patterns are in the opposite direction to that predicted on the basis of absent congeners but consistent with measurements of resources. Further, species abundances are closely correlated with food availability. Results provide strong support for local determinism in driving species numbers. Other less dispersive taxa may be expected to show a stronger imprint of historical processes.

Finally, in an effort to assess the factors structuring elevational diversity patterns, I examined the patterns of ecological dispersion and phylogenetic structure of Old World leaf warbler communities along elevation gradients distributed in the eastern and western regions of the Himalayas. Blomberg's K statistic was computed to test for niche conservatism in key ecomorphological traits. Phylogenetic structure for each community was quantified using Net Relatedness Index (NRI) and ecomorphological spacing metrics were computed. Linear mixed models were used to relate patterns of species richness and NRI to arthropod abundance, maximum temperature and precipitation seasonality. Among the Phylloscopidae, phylogenetic community structure varied along the elevational gradient. The 16 communities composed of two to eight species ran the entire spectrum of significance in terms of their phylogenetic structure, resulting in many clustered communities at low elevations and few over-dispersed communities at higher elevations. Maximum temperature, resource abundance and precipitation seasonality determined the

variation in net relatedness indices so that warmer, low elevation sites had species more closely related than expected by chance while cooler sites at higher elevations had species from more diverse lineages. Given that ecological traits were niche conserved, maximum temperature appears to act as an environmental filter for this group at lower elevation habitats so that species belonging to only a few lineages have to ability to persist in these sites. In contrast, the communities at higher elevations tended towards over-dispersion, thereby implying heightened inter-specific competition. Examination of ecomorphological space metrics provided greater insights into these contrasting processes.

CHAPTER 1

Introduction

1.1 BACKGROUND

A major goal in ecology has been to understand the drivers of species distribution and community structure. Abiotic constraints, dispersal limitations and biotic interactions have often been identified as the three main drivers which interact to determine the observed patterns of species occurrences (Soberon 2007). While the fundamental ecological niche of a species may be delimited by the intrinsic physiological constraints imposed by abiotic factors (Chase and Leibold 2003), dispersal capabilities of the species and niche conservatism owing to historical legacies might be critical in preventing a species from occupying a suitable climatic niche (Vellend et al. 2007; Wiens et al. 2010). Biotic influences include availability of resources as well as positive and negative inter- and intra-specific interactions which regulate the ability of a species to persist and its abundances (Russell and Clout 2004; Hakkarainen et al. 2004). These factors may influence species distribution patterns at varying spatio-temporal scales (Kneitel and Chase 2004). Hence, patterns of species occurrences and their determinants need to be investigated at both the broad geographical scale based on current ecological niche constraints defined by species distribution models, and at the local scale with emphasis on species interactions within communities (Hulbert and White 2007). Finally, since it is well-recognized now that the functional and ecological similarities of species are shaped by common ancestry, considering the phylogenetic inter-relationships between species also assumes critical importance in studies investigating ecological patterns (Felsenstein 1985; Harvey and Pagel 1991).

At the local scale, investigation of habitat selection is essential to identify the ecological interactions of species within its range (Cody 1985; Morrison et al 1998; Illera 2001). Habitat selection is most often investigated in terms of resource availability (Schluter 1982; Janes 1994), morphological adaptation to vegetation structure (Leisler et al. 1989; Price 1991; Forstmeier and Keßler 2001), and inter-specific competition (MacArthur 1972; Cody 1985; Price 1991). Detailed investigation into habitat selection not only reveals ecomorphological adaptations of the species to the habitat characteristics, but also provides insights into nature of intra- and inter-specific interactions and phylogenetic relationships, particularly among closely related species (Forstmeier et al. 2001).

The genus *Phylloscopus* has been the subject of some notable ecological studies of this nature, owing to the remarkable species diversity, close relatedness among species, and very similar morphology and ecology (Gaston 1974; Price 1991; Price et al. 1997; Forstmeier et al. 2001). In addition, the phylogeny of most of the species is well worked out based on mtDNA sequences (cytochrome b), which allows better understanding of ecological relationships by controlling for phylogeny (Price et al. 1997). While, studies examining the nature of ecomorphological relationships and competitive interactions which influence the observed breeding community structure at one site have been carried out (Price 1991; Price et al. 2003; Forstmemier et al. 2001; Forstmeier and Keßler 2001), factors influencing the broad distribution pattern of these widely distributed speciose clade across the continental scale have not been investigated.

1.2 LITERATURE REVIEW

1.2.1 *Phylloscopus* and *Seicercus* clade (Phylloscopidae)

The Phylloscopidae are small entirely insectivorous, warblers. The genus *Phylloscopus* comprises of the Old World leaf warblers most of which breed in the temperate areas of Europe and Asia, and overwinter in Africa, Southern Europe, India, and Southeast Asia. Including 15 species (six in Africa, eight in Southeast Asia and one in Canary Island) which are known to be non-migratory (Price et al. 1997), more than fifty-five species of the genus have been described (Monroe and Sibley 1993; Alstrom et al. 1992; Olsson et al. 1993; Alstrom and Olsson 1995). *Seicercus* species are distributed primarily in eastern and southern Asia from northern China to Timor in the Lesser Sundas (Del Hoyo et al. 2006) and represented by no less than ten species. Both the genera are comprised of small warblers (5-10g) that forage by picking or flypicking insects from arboreal substrates and air. Recent genetic analyses have shown that neither *Phylloscopus* nor *Seicercus* is monophyletic as recognized in recent taxonomic treatments (Watson et al. 1986; Sibley and Monroe 1990; Dickinson 2003), but together they do form a monophyletic clade (Olsson et al. 2004, 2005;

Päckert et al. 2004) comprising of over 80 species. Nineteen species occur in the Indian Himalayas (Martens 2010; Price 2010). They form the dominant components of many forest communities along the entire elevational gradient in the east (ca. 300 m-4500m) and the west (ca. 600m – 4000m, Price et al. 2011). Most species are migratory and retreat to low altitude foothill forests and the tropical regions of peninsular India and Southeast Asia in the non-breeding season.

1.2.2 Distribution in the Himalayas

The *Phylloscopus/Seicercus* clade is represented by 19 species along the Himalayas, which represents one-third of species found in mainland Eurasia (Johansson et al. 2007). The observed high species diversity was previously attributed to adaptive radiation within the Himalayas (Richman and Price 1992; Price and Gross 2005). However, recent phylogenetic analyses suggest that the Himalayan species assemblage is predominantly composed of immigrants from both the Palearctic and Indo-Malayan zoogeographical zones (Johansson et al. 2007). Except for two sister pairs, all Himalayan species have their closest relative outside in Central China or Southeast Asia. In eight cases, subsequent vicariance between the Himalayan and ancestral populations after dispersal of the ancestral species into the Himalayas has resulted in Himalayan endemics. In two cases (*P. pulcher/P. maculipennis* and *S. affinis/S. poliogenys*) where speciation within Himalayas appears plausible, Southeast Asia receives equal support as likely ancestral area. Based on these results, the study concluded that adaptive diversification is not always coupled with speciation.

1.2.3 Ecological studies

The genus *Phylloscopus* has been the subject of some notable ecological studies owing to remarkable species diversity, close relatedness among species and very similar morphology (Plate 1.1) and ecology (Table 1.1; Gaston 1974; Price 1991; Price et al. 1997; Forstmeier et al. 2001). Price (1991) studied a community of 8 *Phylloscopus* warblers breeding along an altitudinal gradient in Kashmir and observed some striking ecomorphological associations. Body size (PC1) was found to be correlated to prey size, habitat occupancy (median breeding elevation) showed a correlation with a measure contrasting tarsus length and beak size (PC2) and foraging method was related to a measure of beak shape (PC3). Another study by Forstmeier and Keßler (2001) focused on seven species breeding in Siberia and showed that both species morphology and vegetation structure influence foraging behaviour. While species with short wings and large hind limbs foraged closer to the ground in dense vegetation using the gleaning technique, more open vegetation and sallying techniques were used by species having long wings and large bills. In general, smaller species foraged higher in the vegetation and used hover flights more frequently than larger species. The influence of vegetation structure on efficiency of foraging methods was significant. However, this study did not support the hypothesis forwarded by Price (1991) that large bills and short tarsus are adaptations for foraging in coniferous trees. Based on these observations, Forstmeier and Keßler (2001) concluded that morphology presumably adapted to allow more efficient exploitation of the selected habitat. Studies in the wintering grounds have revealed parallel modes of ecological segregation among sympatric species (Gross and Price 2000; Katti and Price 2003; Ghosh et al. 2011).

1.2.4 Statement of research

From the west to the east, the Himalayan Phylloscopidae range across a broad bioclimatic gradient from the west to the east. Corresponding to the decline in precipitation and increase in temperature seasonality, only half the number of species breed in the west as compared to the east (Price et al. 2003, Price et al. 2011). Similarly, climatic changes along the elevational gradient are associated with a turnover of species and variation in species richness (Price et al. 2011, Acharya et al. 2011). While ten of the sixteen species under consideration have breeding ranges straddling the east and the west, four occur only in the east and two are restricted to the west (Table 1.1). The four species restricted to the east are all low-elevation, mostly flycatching species (*Seicercus spp.*) having a South Asian, tropical origin (Päckert et al. 2012); on the other hand, the two species restricted to the west breed at higher elevations and originated in the boreal forests (Päckert et al. 2012). In other words, the distribution of these restricted species appears to be associated with some climatic affinities (tropical and temperate, respectively). Therefore, species distribution models based on environmental layers could be employed to investigate whether the observed distribution is a consequence of lack of suitable climatic niches in either region.

In terms of ecological traits, since the flycatching warblers are missing in the west (Table 1.1), it needs to be tested whether lack of resources (flying insects) is the constraint. It is expected that if resources are indeed limiting in the west, in general, species common to both east and west would standpick more in the west. On the contrary, if resources are not limiting in west, then it would be expected that species would flycatch more in west to fill the vacant niche. Being strict insectivores, arthropod prey constitutes their primary resource base and need quantification to establish relative availabilities in the two regions to test the aforementioned predictions.

The distribution of ten leaf warbler species across the broad gradient of climatic conditions and species diversity in the Himalayas offers an excellent opportunity to test alternative hypotheses driving species richness patterns. In general, more species occur in warm wet places than in cold dry places, with explanations broadly classified as historical and out of equilibrium or local and deterministic. A major difficulty in assessing these alternatives is that resource distributions differ qualitatively across regions, making them logically incomparable. However, ecomorphological associations, being related to both the morphology and pattern of resource exploitation, can serve as comparable niche dimensions to test such broad ecological hypotheses. Among Phylloscopidae, certain obvious ecomorphological associations have been identified in studies on breeding communities. Since these patterns have been documented from a single study site in the Himalayas (Kashmir, Price 1991), the generality of these relationships needs to be tested from multiple sites representing broader climatic regimes and biogeographical affinities. Hence, comparison of ecomorphological traits across species common to both the east and the west could provide the means to test the historical and ecological alternatives to uncover the drivers of the species diversity gradient documented across the Himalayas.

Finally, elevational gradients are ideal for studying geographic variation in distribution and abundance of organisms corresponding with the predictable variation in climatic factors (Repasky and Schluter 1995; McCain 2005). In the Himalayas, there exists a gradient of species richness and community composition caused by turnover of species belonging to Phylloscopidae, corresponding to the turnover of habitats as we move from the dry, seasonal west to the tropical, wet east as well as along elevation gradients. In recent years, the availability of well-sampled phylogenies has greatly facilitated attaining a better understanding of the ecological and evolutionary processes that underlie spatial variation in community composition (Algar et al. 2009; Cavender-Bares et al. 2009; Vamosi et al. 2009). This modern framework integrates traditional nomenclatural approach based on taxonomic similarities with information on the phylogenetic relatedness between species constituting the communities, towards elucidating the relative contributions of niche-based and neutral processes in shaping communities (Webb et al. 2002; Kembel 2009). Given the availability of a well-resolved phylogeny for the Phylloscopidae (Johansson et al. 2007), the patterns of phylogenetic structure of Old World leaf warbler communities along the elevation gradients distributed in the eastern and western regions of the Himalayas can be related to climatic variables to test alternative explanations structuring these communities such as "environmental filtering" and "inter-specific competition" (Webb et al. 2002; Losos 2008).

1.3 OBJECTIVES

In this study, the overarching goal is to understand the ecological and historical determinants of geographic and altitudinal distribution of breeding *Phylloscopus* and *Seicercus* species in the Himalayas. The four major objectives of the study are as follows:

(a) Assess the availability of arthropod resources across the eastern and western Himalaya along the elevational gradients.

(b) Identify the climatic correlates of the breeding distribution of Phylloscopidae.

(c) Examine the geographic variation in foraging ecology of Phylloscopidae across the Himalayan bioclimatic gradient.

(d) Evaluate the drivers of community assembly using phylogenetic community structure of breeding leaf warblers across the Himalayas.

PLATE 1.1. Pictures depicting (a) Lemon-rumped Warbler, (b) White-spectacled Warbler, (c) Whistler's Warbler, (d) Grey-hooded Warbler, (e) Ashy-throated Warbler, and (f) Blyth's Leaf Warbler in their breeding habitats. (Photo credits: a, c, d: Abishek Harihar)

TABLE 1.1. Brief description of the ecology and habitat of species belonging to the *Phylloscopus* and *Seicercus* clade (Source: Ali & Ripley 1983).

	Species	Body mass (g)	Habitat	Breeding season
1	Yellow-vented Warbler^{e} (*P. cantator-Pca*)	5-7	Dense evergreen forest	April end-June
2	Grey-hooded Warbler (*P. xanthoschistos-Pxa*)	6-8.5	Oak, pine and deodar forests	March-June
3	Blyth's leaf warbler (*P. reguloides-Pre*)	6.9-9.4	Forests of oak, rhododendron, conifer	May-July
4	Western-crowned Warbler^{w} (*P. occipitalis-Poc*)	8-9	Coniferous forests, willow, mixed conifer-deciduous	May-July
5	Hume's leaf Warbler^{w} (*P. humei-Phu*)	5.8-7.2	Coniferous forests, birch forest	May end-July
6	Grey-faced Warbler (*P. maculipennis-Pmc*)	4.8-6	Mixed forest of oak, rhododendron, conifers, with undergrowth	April end-June
7	Lemon-rumped Warbler (*P. chloronotus-Pch*)	5.1-6.2	Forests of fir, deodar, mixed conifer, birch, *Kharsu*oak and rhododendron	May-July
8	Greenish Leaf Warbler (*P. trochiloides-Ptr*)	8-9.5	Sub-alpine mixed forest of fir, birch, rhododendron/ juniper	May-August
9	Large-billed Warbler (*P. magnirostris-Pmg*)	11.3-12	Birch, mixed rhododendron, fir, invariable close to a torrential stream	June-August
10	Buff-barred Leaf Warbler (*P. pulcher-Ppu*)	6.6-7.2	Mixed conifer, birch, rhododendron and other scrub above tree-line	June-July
11	Tickell's leaf Warbler (*P. affinis-Paf*)	6.3-7.6	Scrub of *Berberis,* willow, juniper, rhododendron, *Hippophae*	June-July
12	White-spectacled Warbler^{e} (*S. affinis-Saf*)	6-8	Dense humid evergreen or pine forest	April-June
13	Green-crowned Warbler (*S. burkii-Sbu*)	6.5-9.3	Upper evergreen, mixed and deciduous forests of oak, rhododendron, birch	May early-July
14	Grey-cheeked Warbler^{e} (*S. poliogenys-Spo*)	6-7	Open evergreen forests and dense bamboo jungle	May-June
15	Whistler's Warbler (*S. whistleri-Swh*)	6.5-9.3	Dense deciduous or mixed forest	June-July
16	Chestnut-crowned Warbler^{e} (*S. castaniceps-Sca*)	4-6	Dense forest of oak	April-June

^{e} and^{w} as superscript refer to species breeding only in east and west, respectively.

1.4 ORGANIZATION OF THE THESIS

The thesis is organized in to six chapters, beginning with the introductory **Chapter 1** describing the broad ecological context of the study, species of interest, existing ecological knowledge, the ecological problem and study objectives. **Chapter 2** begins with a detailed description of the study area including the climatic characteristics of study sites. Thereafter, the field methods pertaining to the study objectives have been collectively described as these remain common to the four core chapters. These four core chapters each address an independent research question and follow a general structure: an introductory section which describes the background to the topic and specific objectives, detailed analytical methods, results and focussed discussion of results and their implications.

Chapter 3 addresses the first objective and describes the distribution of arthropod prey along the elevational gradients in the east and the west Himalayas. The variations in abundance of overall as well as taxon-specific arthropod abundances with elevation and across the two regions have been examined. The observed patterns in variation have been explained in terms of climatic variables and vegetation characteristics to describe the relative availability of resources for the strictly insectivorous leaf warblers.

In **Chapter 4**, the objective was to investigate whether species distribution models based on environmental variables alone can explain the present day breeding distribution of Phylloscopidae. More specifically, climatic niche models were generated using Maxent to examine if the six species which are either restricted to the east or west are unable to range across the Himalayas owing to absence of suitable climatic niches.

Chapter 5 tests the influence of history and ecological determinism using geographic variation in comparable niche dimensions, within species whose ranges straddle species-poor and species-rich regions, to explain the observed patterns of species diversity. Eco-morphological associations were examined along multiple elevational gradients in east and west and observed regional differences were compared against predictions generated under the historical and ecological alternatives.

Finally, in **Chapter 6** the role of inter-specific competition and environmental constraints in determining the distribution of species was examined using data on foraging segregation and phylogenetic community structure. Ecological traits known to influence the community structure of these species were tested for niche conservatism and environmental correlates of phylogenetic community structure were identified.

CHAPTER 2

Study area and field methods

2.1 STUDY AREA

Extending from ca. 60m up to 8000m within 150-200km and comprising tropical/subtropical, temperate, subalpine, and alpine climatic zones, the Himalayas represent the longest altitudinal gradient in the world (Grytnes and Vetaas 2002). They are the breeding grounds for nearly 8% of the world's bird species (Price et al. 2003; Rasmussen and Anderton 2005). Such high species diversity results, at least partly, from the high diversity and turnover of habitats associated with elevation, as well as transition from the wetter eastern ranges to the drier western parts (Martens and Eck 1995; Price et al. 2011).I studied the altitudinal distributions and foraging behaviours of breeding leaf warblers in relatively undisturbed forest habitats across multiple elevational transects within the west and the east Himalayas. I define the *east* as all study sites east of Nepal (in the Indian states of Bengal, Sikkim and Arunachal Pradesh) and the *west* as all study sites west of Nepal (in the states of Himachal Pradesh and Uttaranchal, Fig. 2.1). I combined data from four elevational transects in the west and five transects in the east (Fig. 2.1, Plate 2.1). Transects were chosen to cover relatively long continuous forested habitats along a more or less similar aspect.

I conducted field sampling during the breeding season (April-June) over three years (2008-2010) (Table 2.1). Comparison of vegetation from the regions described here has revealed density of trees and foliage differs significantly along the elevational gradients as well as between the two regions (Price et al. 2011). In the west, mostly dry deciduous, open forests occur below 1000m, followed by mixed broadleaf -conifer and pure conifer between 1000m-3200m, and finally by birch-rhododendron (*Betula utilis- Rhododendron campanulatum*) and willow (*Salix sp.*) scrub near the treeline that culminates around 3500±200m asl. Broadleaf moist evergreen forests dominated by lauraceous members occur at the lower elevations till ~ 3500m in the east, followed by a broad belt (3500m-4100m) of sub-alpine forests dominated by several (> 45) species of dwarf rhododendron.

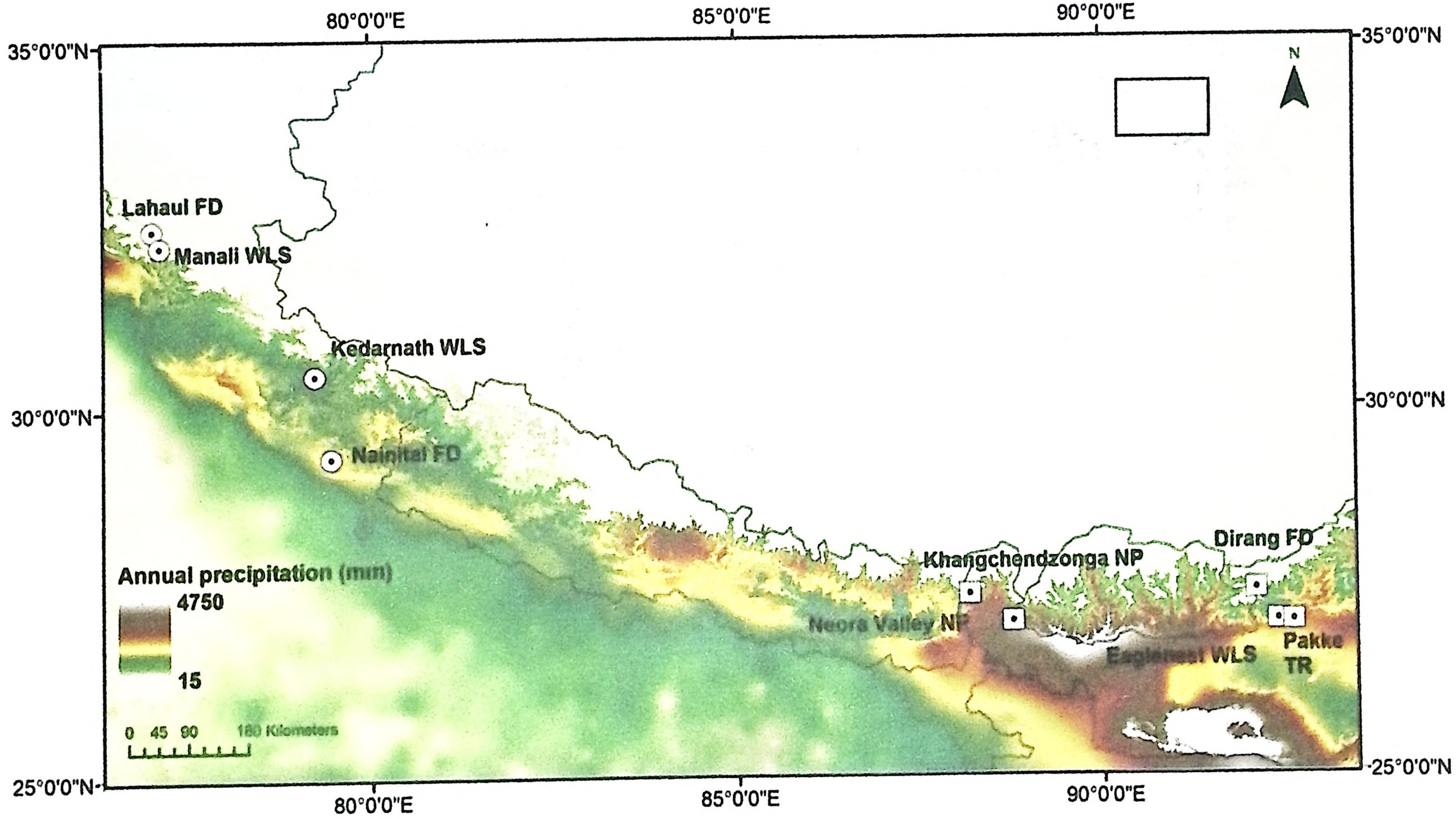


FIGURE 2.1. Annual precipitation across the Himalayas (from Worldclim database; Hijmans et al. 2005) with locations of study sites indicated.

TABLE 2.1. A summary of some important characteristics of the elevational transects and arthropod sampling sites in the west and east Himalayas. The lowest and highest limits of forest habitat of the corresponding transect is indicated. Breeding species include all species for which singing males were observed in a site. Abbreviations can be matched to species using Table 1.1.

Region	Transect	Altitudinal range (m)	Arthropod sampling site	Latitude, Longitude	Sampling period	Breeding species
West	Mooling Reserve Forest	3300-3800	Mooling (3800)	32.4630°N, 77.0178°E	10-16 June 2009	*Poc, Phu, Ptr*
	Manali Wildlife Sanctuary	2000-3900	Manali (3100)	32.2395°N, 77.1214°E	2-4 June 2008	*Pch, Pmc, Pmg, Pre, Swh, Phu, Ptr, Ppu, Paf*
	Kedarnath Wildlife Sanctuary	1600-3800	Tungnath (3600)	30.4835°N, 79.2171°E	26-28 May 2009	*Ppu, Ptr, Pch, Pre, Pmc, Swh*
			Shokharakh (2850)	30.4733°N, 79.2181°E	23-25 May 2009	*Pch, Pre, Pmc, Swh, Pmg*
			Kanchulakharakh (2550)	30.4626°N, 79.2276°E	23-25 May 2009, 26-28 May 2008	*Pch, Pre, Pmc, Swh, Sbu, Poc, Pmg*
			Mandal (1850)	30.4684°N, 79.2636°E	18-22 May 2009, 22-25 May 2008	*Pxa, Sbu, Poc, Pmg*
	Nainital Forest Division	700-1500	Patwadangar (1350)	29.3321°N, 79.4484°E	7 -12 April 2009	*Pxa, Pre*
East	Yuksom-Dzongri Trail	1720-4000	Dzongri (3850)	27.4718°N, 88.1547°E	12-14 May 2008	*Ppu, Ptr, Paf*
			Tsokha (3000)	27.4344°N, 88.1809°E	8-10 May 2008	*Pre, Pch, Pmc, Swh, Pmg*
			Sachen (2200)	27.4157°N, 88.1944°E	26-28 April 2009, 4-6 May 2008	*Sbu, Sca, Spo, Pre, Pmg*
	Neora Valley National Park	600-2200	Thosum (2000)	27.0612°N, 88.7727°E	18 April-24 April 2009	*Sbu, Saf, Spo, Sca, Pre, Pxa, Pca*
	Eaglenest Wildlife Sanctuary	110-2500	Khellong (700)	27.0147°N, 92.4144°E	12-13 April 2010, 10-11 April 2008	*Pca, Pxa*
			Sessni (1260)	27.0475°N, 92.4188°E	14-15 April 2010, 10-13 April 2008	*Pxa, Pre, Sbu, Sca, Spo*
			Bompu (1800)	27.0662°N, 92.4062°E	18-19 April 2010, 15-16 April 2008	*Sbu, Sca, Spo, Saf, Pxa, Pre*
			Lama camp (2350)	27.1600°N, 92.4574°E	21-24 April 2010, 21-23 April 2008	*Sbu, Sca, Pxa, Pre, Pch, Pmc, Pmg*
	Pakke Tiger Reserve	100-160	Pakke (160)	27.0543°N, 92.6176°E	9-11 April 2010	*Pca*
	Sella Pass-Senge	3000-4260	-	27.4885°N, 92.1077°E	25 April-5 May 2010	*Pmg, Pch, Pmc, Ptr, Ppu, Paf, Swh*

2.1.1 Eastern transects

Yuksom-Dzongri trail: The Yuksom–Dzongri trekking corridor (26km long) includes a range of elevations from 1780m to 4000m within the Khangchendzonga National Park in Sikkim. The trekking trail passes through Sachen (2200m), Tsokha (3000m) and reaches Dzongri (4000m) in the southwestern part of Khangchendzonga Biosphere Reserve in Sikkim, India. Yuksom (1780m) is a trailhead for this corridor and leads to the Base Camp, Dzongri, Thangsing, and Gocha La. The vegetation in lower elevations (1780m-2350m) is dominated by *Quercus-Cinnamomum* and *Quercus-Castanopsis*, while in the higher elevations (2350m-3600m) *Quercus-Abies* and *Abies-Rhododendron* are more common (Chettri et al. 2001). Above 3600m, *Rhododendron* is followed by *Juniper* scrub.

Neora Valley National Park: The Neora Valley National Park lies in the eastern Part of Darjeeling district (Fig 2.1). Within the park, I sampled near the Thosum anti-poaching camp, covering an altitudinal belt of 1800-2200m located at the south-eastern end of the park (Table 2.1). The forest type in the sampled area is described as temperate upper hill forest. The forests are dominated by several species of *Quercus* and *Rhododendron* alongside members of family Lauraceae and Aceraceae. Varieties of ferns constitute the ground floras. Dense undergrowth characterizes most places and common shrub species are *Rubus ellipticus, R. niveus, Viburnum colebrookianum, Strobilanthes wallichii, etc.*

Eaglenest Wildlife Sanctuary:Eaglenest WLS (218 km^2) is located in the West Kameng district in Arunachal Pradesh. The elevation between 1700m to 2500m is prone to heavy fog all through the year especially in the afternoons. Six broad vegetation types have been identified including lowland tropical evergreen forest (below 1000m), subtropical (1000m–2000m), temperate broad-leaved and temperate conifers (2000m–4000m) (Kaul and Haridasan 1987). The forests below 800m have been classified as Upper Assam Valley Tropical Wet Evergreen Type (*Mesua*) forest and the forests between 1800m to 3000m have been classified as Eastern Himalayan Wet Temperate Forests. Eaglenest WLS is home to at least 454 species of birds including the Bugun Liocichla (*Liocichla bugunorum*), described in 2006 by Ramana Athreya. Sampling was conducted along the elevational gradient to estimate altitudinal distribution of breeding species, while arthropod sampling was carried out at four sites: Khellong (750m), Sessni (1250m), Bompu (1800m) and Lama Camp (2350m).

Pakke Tiger Reserve: Pakke Wildlife Sanctuary and Tiger Reserve, located in the tropical foothills of western Arunachal Pradesh ranges covers an altitudinal range of 150-1500m asl (Datta 2001). The vegetation type is categorized as Assam valley tropical semi-evergreen forest (Champion and Seth 1968). Sampling for this study was restricted to a single site at 160m situated at the western end of the Reserve, close to Bhalukpong. Very few individuals of Yellow-vented warbler (*P. cantator*) were seen singing during the sampling.

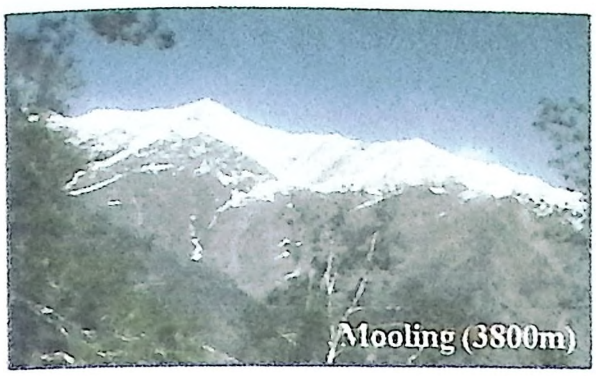
Sella Pass-Senge: Sampling was carried out near the treeline below the Sella Pass (4200m) which lie within the Dirang Forest Division (Fig 2.1). *Juniper* scrub dominates the alpine areas around the pass, while a variety of *Rhododendron*, followed by *Abies-Rhododendron* dominates the forests below. Forest patches were discontinuous along the transect owing to extensive deforestation along Army camps and labour camps between 3200-3600m.

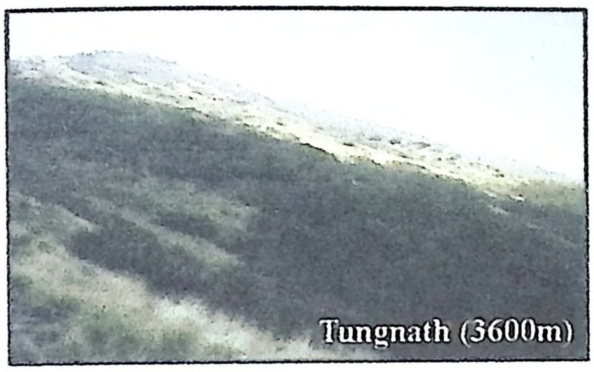
2.1.2 Western transects

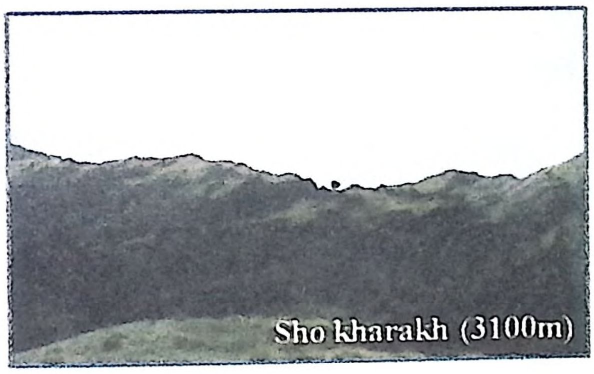
a. Mooling (Lahaul Forest Division): Mooling village is situated within Lahaul Forest Division in the Trans-Himalayas. Situated on the southern bank of river Chandra (Fig. 2.1), the forest slopes above the village are covered with blue pine (*Pinus wallchiania*), birch (*Betula sp.*), *Juniper* scrub, spruce (*Picea smithiana*) and deodar (*Cedrus deodara*).The forests are not continuous, and are frequently interrupted by glaciers and cliffs. The vegetation can be broadly classified into temperate (< 3500m) and alpine (> 3500m to tree-line). The area remains snow covered almost for six months and the temperature ranges between -19°-32° C (Sinha and Samant 2010).

*b. Manali Wildlife Sanctuary:*Manali Wildlife Sanctuary (32km^2) is a watershed and the main river runs west to east (Singh et al. 1990). Altitudinal range is from ca. 2000m (just outside the town of Manali) to above tree-line (Fig. 2.1). The south facing slopes in Manali have more extensive Kharshu oak, *Quercus semecarpifolia* whereas north facing slopes have more extensive fir, *Abies pindrow*. Above 3000m lies a belt of *Rhododendron campanulatum* and birch (*Betula utilis*), followed by *Juniper* scrub above tree-line.

West


Mooling (3800m)


Tungnath (3600m)


Sho kharakh (3100m)


Kanchulakharakh (2500m)

East


Dzongri (3800m)


Below Sella Pass (3500m)


Tsokha (3000m)


Thosum (2200m)

Low-elevation sites in the east

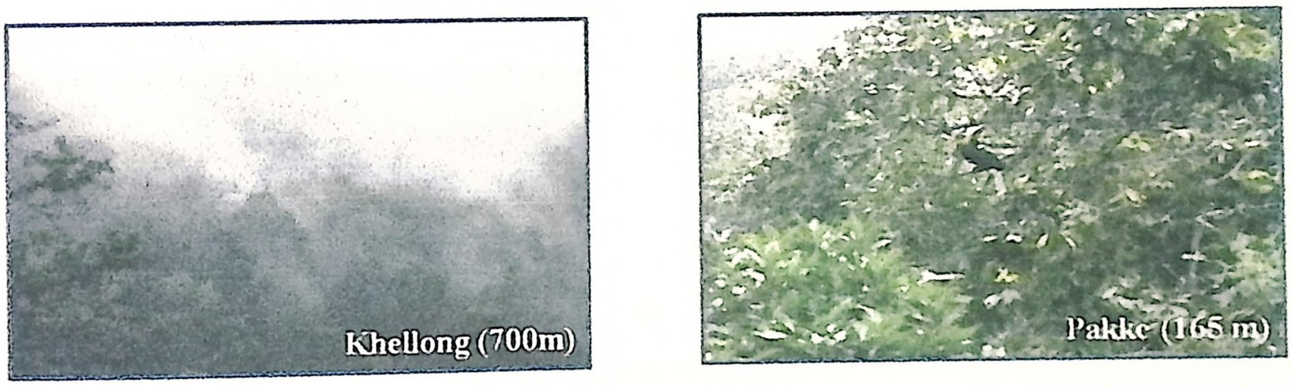


PLATE 2.1. Study sites located at comparable elevations in the west and the east Himalayas showing differences in vegetation characteristics.

c. Kedarnath Wildlife Sanctuary: Kedarnath WLS (975km^2) is located in Uttarakhand and covers an elevational range that varies from 1200 to 7068m (Fig. 2.1, Table 2.1). It lies in the upper catchments of Alaknanda and Mandakini rivers, two major tributaries of Ganges. Kedarnath is influenced by the southwest monsoon in summer and by the passage of belts of low pressure in winter (Mani 1974). The major vegetation types include sub-tropical pine (*Pinus roxburghii*), temperate broad-leaved oak (*Quercus leucotrichophora, Q. glauca, Q. floribunda*) and associated species, sub-alpine oak (*Q. semecarpifolia*), fir (*Abies pindrow*), birch (*Betula utilis*)-

rhododendron (*Rhododendron campanulatum*), and alpine scrub, meadows, and pastures.

d. Nainital Forest Division: The forests situated on the south-facing slopes covered an altitudinal range between 1000m-1500m (Fig. 2.1, Table 2.1). The area receives an average annual rainfall of 2500mm, making it the wettest site in the west. The forests are dominated by pine (*Pinus roxburghii*) mixed with Sal (*Shorea robusta*), *Mallotus phillipensis*, *Terminalia .sp.*, in the lower stretches, while species as *Quercus leucotrichophora, Rhododendron arboreum Aesculus indica,* co-occur on the upper reaches.

2.2 CLIMATIC CONDITIONS

I extracted climatic data for each of the sites using ArcMap 10 from the WorldClim database with 30-s spatial resolution (<www.worldclim.org>; Hijmans et al. 2005) to describe the general climatic characteristics of the sites across the elevational transects and the two regions. I focussed on four Bioclim variables (annual precipitation, precipitation seasonality, maximum temperature and temperature seasonality) which have been used to adequately represent the climate of the study area and describe its influence on range limits of Himalayan birds (Price et al. 2011).

On comparing the sites situated along elevational gradients in the east and the west, it is evident that sites in the west are warmer than sites situated at comparable elevation in the east (Fig. 2.2a). Patterns of spatial variation in annual precipitation revealed that there exists a substantial difference in amounts of precipitation received up to an elevation of 3200 m, with sites in the east receiving more rainfall (Fig. 2.2b). However, at higher elevations these differences no longer exist. This indicates that while lower elevations are drier in the west, higher elevations in both the regions receive similar amounts of precipitation. Based on data extracted for every 200m within comparable grid cells in the east and west, it is evident that while elevations lower than 2200m are climatically dissimilar in the east and the west (west is drier and more seasonal), higher elevations experience very similar climatic conditions (Price et al. 2011).

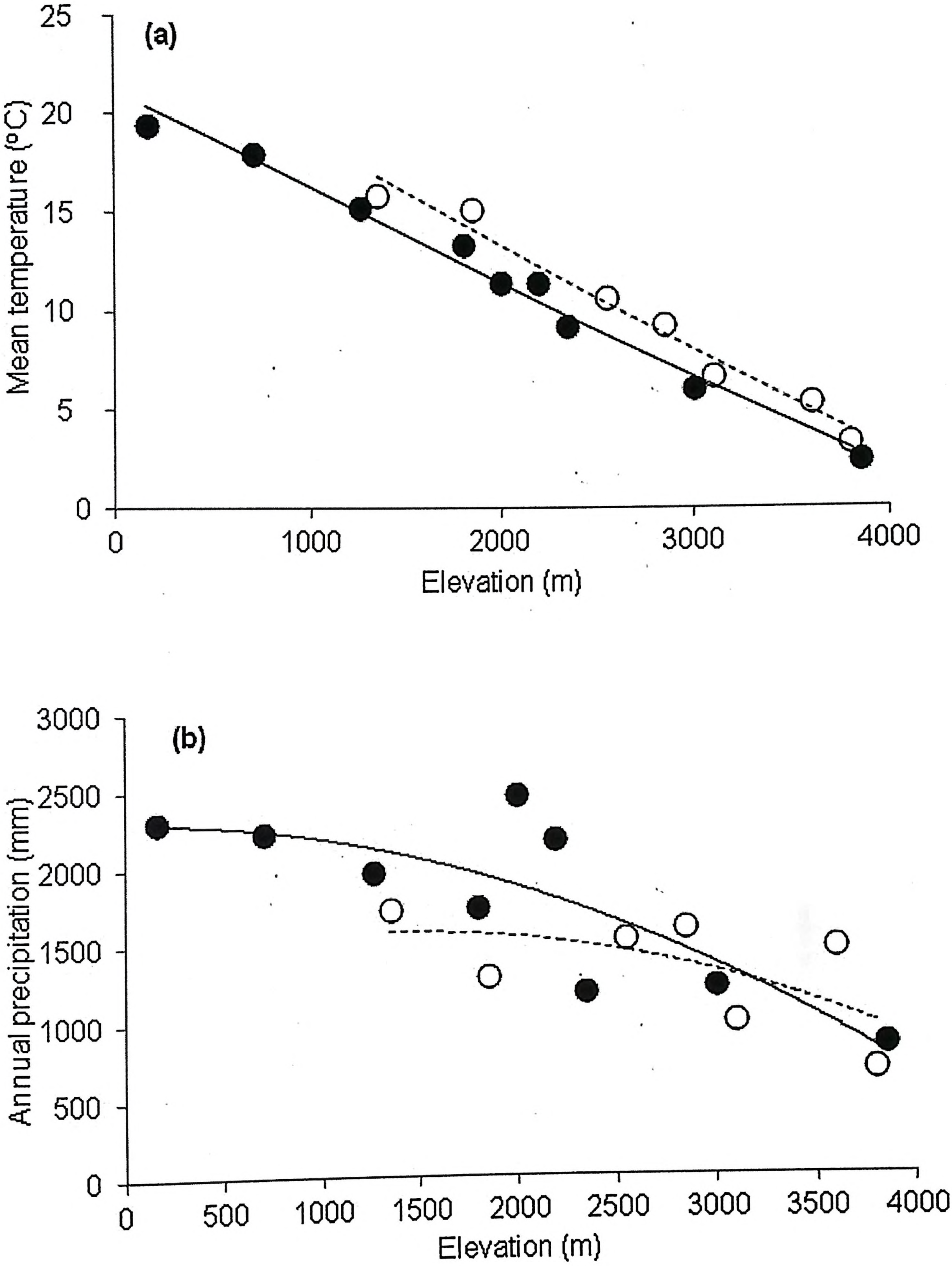


FIGURE 2.2. Variation of (a) mean temperature and (b) annual precipitation along the elevational gradient in the east (closed circles, solid line) and the west (open circles, dashed line) Himalayas (based on Worldclim dataset; Hijmans et al. 2005).

2.3 FIELD METHODS

2.3.1 Resource quantification

Arthropod resources: I used a bagging-method for sampling (Katti and Price 2003), which has been successfully used in both the breeding season in North America (Morse 1976) and the non-breeding season in India (Katti and Price 1996; Ghosh et al. 2011). Nearly 99 % of the arthropods are known to be extracted by this method when the branches are placed in the sampling bag (Morse 1976). One limitation of this technique is that it tends to underestimate the abundance of larger, strongly flying, insects, which escape as we approach. But the fact that the warblers are primarily foliage-gleaners with negligible intake of these insects, and that I was more interested in comparisons across sites than in obtaining absolute abundances, makes this method an efficient way to collect reasonably large samples across multiple locations.

At each site, from plants selected at every 50m along forest trails, a small branch (50-60 cm in length) from up to 5m height was chosen and enclosed within a large plastic bag (~200 litres) and then broken off. On an average, 10-15 branches were investigated per day and sampling was carried out only on bright, clear days, between 1100 and 1400 hours. Branches were sampled from plant species selected to adequately represent the dominant vegetation type at each site. The arthropods were anaesthetized within the bag using a piece of cotton soaked in chloroform, carried to the base camp where they were sorted and identified to Orders within two-three hours. In addition, they were also sorted into two size classes (viz., large and small) based on whether the total body length of the insect was greater or less than 4mm (Katti and Price 1996; Price and Gross 2005). From each branch the total number of leaves was counted and the foliage was carefully investigated for insects concealed inside. I restricted the time to search through a bag to a maximum of 20 minutes, which based on preliminary tests leads me to believe that all large arthropods were collected from each bag, but a few small ones may be missed from bags with many arthropods. Given that sampling was carried out consistently across sites using identical bags and by me, I believe that the estimates of relative abundance of arthropods are comparable across sites.

Foliage density: At multiple sites along several of the elevational gradients, as well as ones not visited by me, TDP established 5ha grids, and sampled tree density (as the number of trees within a 5m radius of 15 randomly chosen points), tree type (coniferous vs. broadleaf) and foliage density (as the number of leaves an imaginary pole extending to the sky would intersect, over 30 random points). The sites at which these data were collected often differed from those over which the ecological studies were made, and can be considered a general sample of western and eastern habitats. Further details of these methods are in Price et al. (2011).

2.3.2 Ecological measurements of warblers

Altitudinal distributions: Obtaining altitudinal distributions of breeding birds in the Himalayas has been difficult because distributions vary from one river valley to the next (Martens and Eck 1995), and breeding, migratory and wintering records have been difficult to disentangle (e.g. Inskipp et al. 2000). Further, the complete elevational gradient (foothills to the treeline) cannot be sampled in a single transect owing to discontinuity of forested stretches, particularly in the west. Here, I combined data from all elevational transects within each region to estimate an altitudinal breeding range for each species in each region. On a single morning from 0600 to 1000 I surveyed a 500m elevational band. At every 25m, as measured with an altimeter, along segments, we counted all singing birds seen or heard within ~ 25m radius for 5 minutes. Each interval was covered twice during the study. Price et al. (2003) showed that this census method gave repeatable results across years in one location (Manali, Himachal Pradesh). Here I define an "altitudinal distribution" as the upper and lower limits of the breeding range; i.e. where at least one male was recorded singing (isolated males >100m above or below other males were excluded). Estimates of altitudinal distributions are approximate but should be sufficiently reliable to allow for broad comparisons between the two regions. In addition, the method was used to obtain reliable estimates of site-specific relative abundances of the species in the breeding season.

Foraging behaviour: I selected different forest trails to avoid sampling the same individuals and actively searched for the target species. Once located, a bird was followed until it captured a prey item and, thereby, each individual constitutes an independent observation. At the time of prey capture I recorded: foraging manoeuvre (standpick, hoverpick, flypick and flycatch), foraging height (in meters), substrate (leaf, twig, branch, conifer needles and air), tree height (in metres) and prey size. I defined a foraging manoeuvre as (a) standpick if the bird picked a stationary prey without involving any flight, (b) hoverpick if the bird searches and picks a stationary prey while on wings, (c) flypick if the bird caught a prey resting on a substrate which was observed while perched or hopping, through the use of flight, (d) flycatch if the bird sallies from a perch to catch a flying prey (see Plate 2.2). For many of the analyses these feeding methods were categorized into two, based on whether the bird used flight in prey capture, i.e. standpicks vs. flypick plus flycatch plus hoverpick (aerial manoeuvres). A prey item was defined prey as large if it was seen in the bill and required mandibulation or small if the prey was not visible in the bill.

Morphology: Museum specimens were measured at The Field Museum of Natural History, Chicago, and at the British Natural History Museum, Tring, by Ulf Johansson and TDP *(personal communication)*. Specimens from Nepal eastwards were included in the east sample, and specimens through Kashmir were defined as belonging to west (Table 1, Appendix 1). The following morphological variables were measured following Price (1991): wing length, tail length, tarsus length, beak length, beak width, and beak depth.

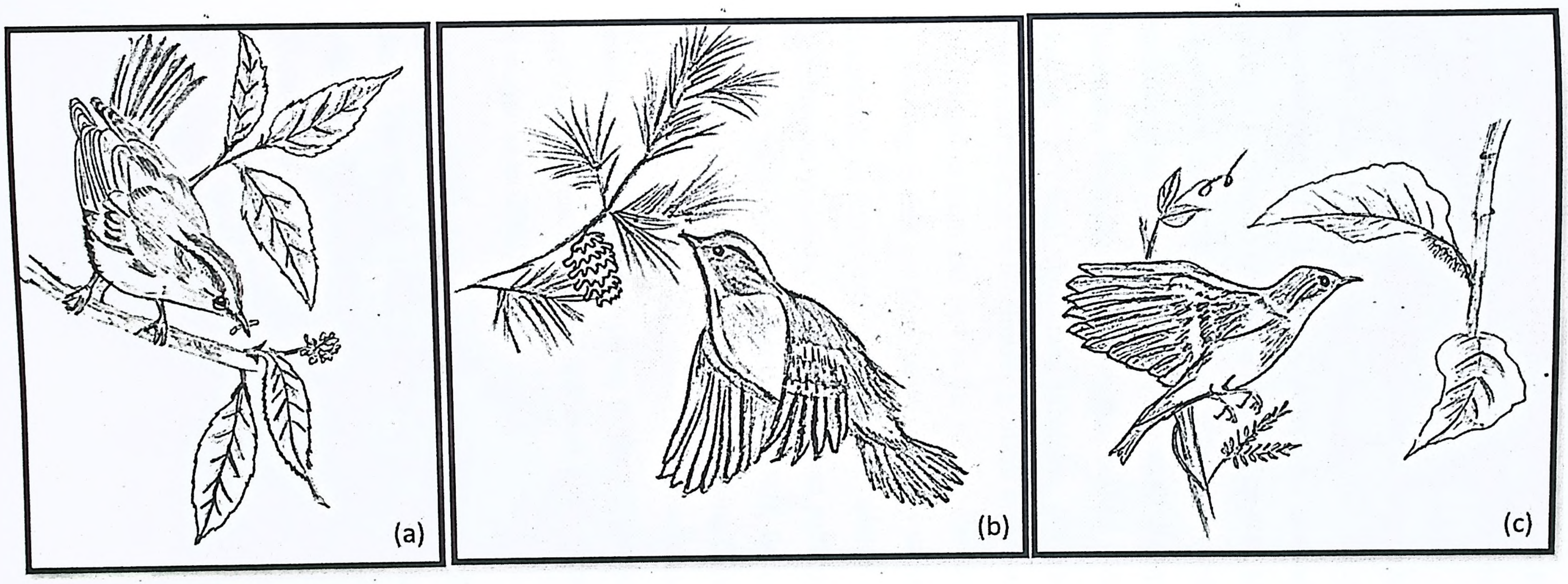


Plate 2.2. The three categories of foraging manoeuvres used by leaf warblers: (a) standpick; (b) flypick and (c) hoverpick. Flycatch is a variant of 'flypick' wherein the bird sallies into the air and picks up a flying insect.

CHAPTER 3

Distribution and abundance of foliage-arthropods

3.1 INTRODUCTION

Analyzing broad biogeographical patterns in species assemblages constitutes a critical step towards elucidating the factors shaping them (MacArthur 1972; Rosenzweig 1995). In general, differences in species diversity correlate with spatial variation in climatic conditions (Schowalter et al. 1999; Evans et al. 2005). Studies on elevational gradients have been especially useful owing to changes in various environmental factors over relatively small distances (McCoy 1990; McCain 2005). Extending from ca. 60 to more than 8000m within 150-200km and comprising of tropical/subtropical, temperate, subalpine, and alpine climatic zones, the Himalayas represent the longest bioclimatic gradient in the world (Bhattarai et al. 2004). Further, the transition from the east to the west is associated with a gradient in rainfall and responding to this gradient, nearly twice as many bird species breed in the eastern Himalayas as compared to western Himalayas (Price et al. 2011). Studies have documented variation in species richness patterns of vascular plants (Oommen and Shankar 2005; Grytnes and Vetaas 2002), ferns (Bhattarai et al. 2004) and birds (Acharya et al. 2011; Price et al. 2011) along Himalayan elevational gradients. Here, I present the first data on arthropod distributions, which have not been addressed in similar manner, possibly owing to the difficulties involved in adequately sampling, sorting and identification of this most species-rich group (Novotny and Basset 2000; Longino et al. 2002).

Arthropods are particularly sensitive to climate owing to their ectothermy and small size (Danks 1992; Thomas et al. 1994) and hence, are known to respond to climatic gradients through changes in community structure and abundances (Landsberg and Gillieson 1995; Hysell et al. 1996; Progar and Schowalter 2002). Along elevational gradients, influence of variation in temperature on arthropod community structure and distribution can be particularly regulatory (Gaston and Chown 1999; Sanders et al. 2007). Precipitation may also alter the composition of foliage arthropod assemblages by influencing the structure and composition of vegetation (Ribeiro et al. 1998; Progar and Schowalter 2002). In this note, I present the variation in abundances of foliage-dwelling arthropod taxa along the broad bioclimatic gradient present across the Himalayas (Table 3.1). This sampling was carried out to quantify spatial variation in relative availability of arthropod prey for foliage-dwelling Old World Leaf warblers (Phylloscopidae) in the breeding season. From the east to the west annual precipitation declines gradually, while temperature seasonality increases, particularly in the lower elevations (Price et al. 2011). Similarly, both temperature and precipitation declines towards higher elevations. Therefore, I predicted that arthropod abundance should vary from (a) east to west, and (b) lower elevations to higher elevations. In order to understand the generality of the observed elevational and regional patterns, I examined the variation in abundance of multiple arthropod taxa across the environmental gradients.

TABLE 3.1. General climatic characteristics of the 16 study sites situated in the west and the east Himalayas. Climatic variables were extracted from the WorldClim database (www.worldclim.org; Hijmans et al. 2005). N indicates the number of bags sampled.

Region	Site	Elevation (m)	Annual precipitation (mm)	Max Temp (°C)	Min Temp (°C)	N
West	Mooling	3800	696	17.9	-11	41
	Tungnath	3600	1486	17.8	-6.8	31
	Manali	3100	998	20.3	-6.4	32
	Shokharakh	2850	1619	21.3	-2.2	20
	Kanchlakharakh	2550	1542	22.6	-0.7	30
	Mandal	1850	1299	27.9	3	45
	Patwadangar	1350	1737	29	3.1	40
East	Dzongri	3850	849	15.1	-10	29
	Tsokha	3000	1235	17.5	-5	30
	Lama Camp	2350	1203	22.3	-3.3	44
	Sachen	2200	2190	21.2	2.1	30
	Thosum	2000	2485	21	2.3	30
	Bompu	1800	1754	25.4	1.7	35
	Sessni	1260	1986	26.9	3.9	45
	Khellong	700	2241	29.2	6.9	33
	Pakke	160	2313	30.5	8.3	20

3.2 ANALYTICAL METHODS

Arthropod abundance was calculated as mean number of individuals per bag using all the bags sampled at each site. For sites (Khellong, Sessni, Sachen, Lama Camp, Bompu, Mandal, Kanchulakarakh), which were sampled for arthropods across two years (during summer months, see Table 2.1), no significant inter-annual variation could be detected (t-tests, $P > 0.05$). Therefore, within a site, arthropod samples were averaged by combining the data from two sampling years to obtain an arthropod abundance value. The optimum elevations for total and taxon-specific abundances were calculated using quadratic regression based on the data from all sites (Table 3.2). Thereafter, two separate ANCOVAs were conducted for each order below and above the peak elevation since the primary objective was to test for variation in arthropod abundances across the elevational gradient and the two regions. Following a backwards-stepwise procedure, all variables and interaction (elevation×region) were initially included and the since the east and west regression slopes on elevation were similar for all the models, the non-significant interaction terms were not retained in the final models. To correct for multiple comparisons, I used the sequential Bonferroni correction (Gotelli and Ellison 2004). In particular, leaf warblers in the breeding season are known to segregate in terms of their large prey (> 4mm, Gross and Price 2000) based on their body sizes. Hence, the variation in large prey abundance as well as proportion of large prey was also examined similarly using ANCOVA.

3.3 RESULTS

3.3.1 Variation in arthropod abundance along elevation

In total, 535 branches were examined which yielded 6163 arthropod individuals representing 11 orders across the 16 sites in this study (see Table 3.1, Table 3.2). The arthropods were identified to the following categories: Hemiptera (both Homoptera and Heteroptera combined), Aranae, Coleoptera, Diptera, Hymenoptera (97.28 % were ants), Lepidoptera larvae, Thysanoptera, Acarina, Dermaptera and others (which included Orthoptera, Blattaria, other unknown adults and larvae). These first six orders have been reported in the stomach samples of these species in the breeding season (Price 1991). Overall, arthropod abundance was significantly correlated to the number of leaves per branch (r = 0.63, N = 410, P = 0.0001).

Mean arthropod abundance is highest at 2000m, and differs significantly between the two regions below this peak (Fig. 3.1, ANCOVA, elevation: n = 7, F= 4.8, P = 0.09, region: n= 7, F = 18.5, P = 0.01). However, above 2000m arthropod abundance declined gradually with elevation, although there was no significant difference between the two regions (ANCOVA, elevation: n = 9, F= 49.5, P = 0.0004; region: n = 9, F = 0.1, P = 0.77). Maximum arthropods abundances were attained at a higher elevation in the west (2543m) as compared to the east (1770m).

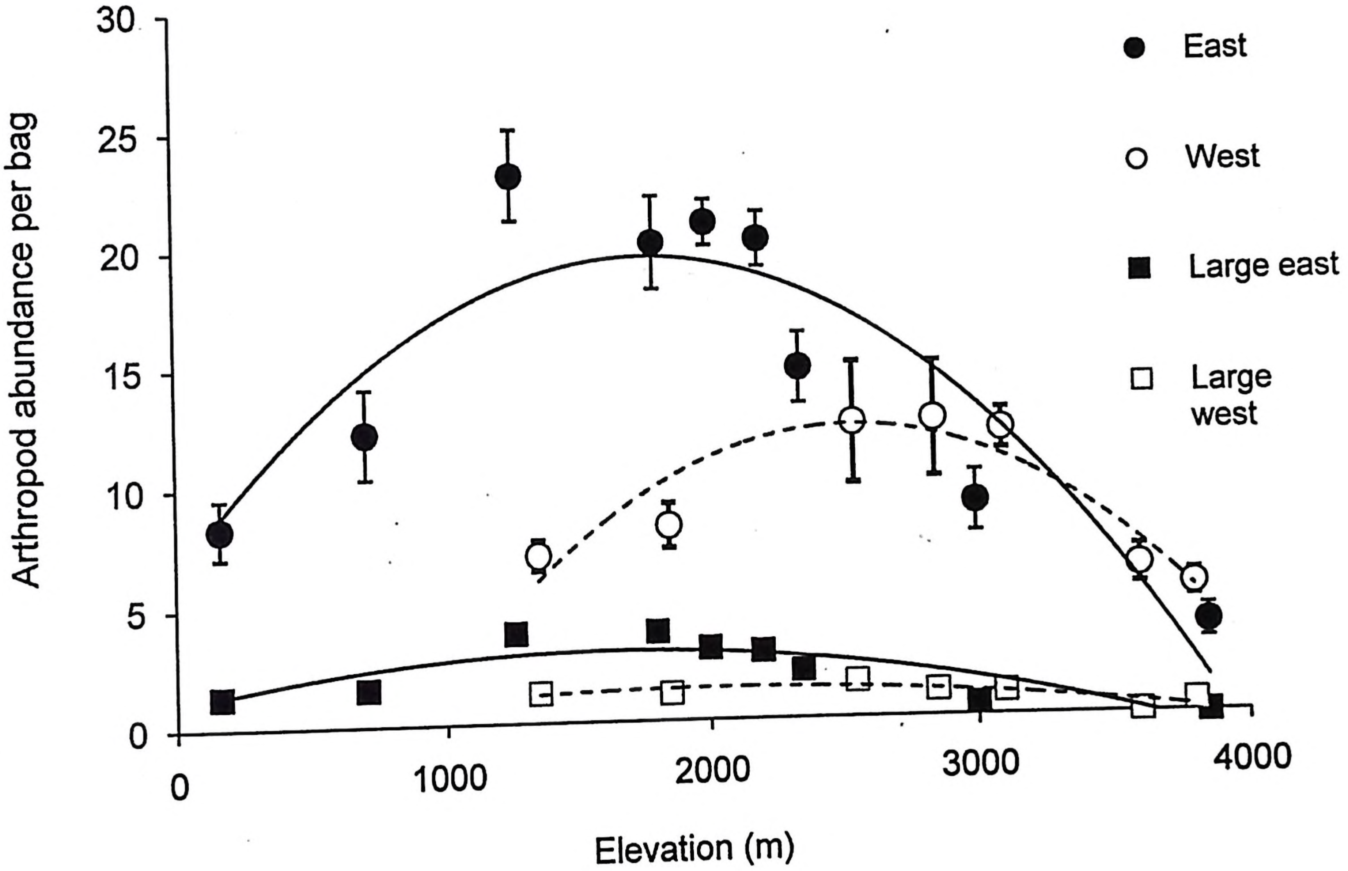


FIGURE 3.1. Arthropod abundance measured as numbers per bag (see Methods) against altitude. Arthropods were sampled at different locations along the elevational gradients in the east (solid lines) and the west (dashed lines) as indicated in Table 3.1. Error bars indicate standard errors based on bag as replicate (*N*=15-46 bags). Large (> 4mm in body length) arthropods are separated as closed squares and open squares for the east and the west, respectively.

TABLE 3.2. Mean abundances of arthropod orders from sixteen sites located in the east and the west Himalayas. Refer to Table 3.1 for sample sizes (number of bags sampled).

Sites	Elevation (m)	Orders									
		Hemiptera	Aranae	Coleoptera	Diptera	Hymenoptera	Lepidopetera*	Thysanoptera	Acarina	Dermaptera	Others
EAST											
Khellong	700	2.34	1.86	1.02	0.71	1.61	0.22	0.05	0.24	0.10	0.10
Sessni	1260	7.17	4.09	3.76	1.90	0.83	0.76	0.05	0.20	0.00	0.29
Bompu	1800	5.15	5.51	3.02	1.07	0.34	0.32	0.00	0.00	0.15	0.05
Neora Valley	2000	1.90	1.84	1.02	1.83	0.07	0.39	0.03	0.00	0.85	0.00
Sachen	2200	5.22	2.63	1.95	2.41	0.37	0.83	0.07	0.12	0.95	0.10
Lama Camp	2350	4.88	4.46	3.32	2.80	0.12	0.32	0.19	0.07	0.10	0.20
Tsokha	3000	4.03	0.83	1.23	2.70	0.00	0.13	0.00	0.20	0.00	0.00
Dzongri	3850	2.32	0.20	0.17	0.24	0.00	0.00	0.00	0.00	0.00	0.00
WEST											
Patwa-dangar	1350	2.48	1.33	1.83	0.00	0.70	0.38	0.20	0.00	0.00	0.02
Mandal	1850	2.20	3.76	1.11	0.62	0.20	0.16	0.00	0.16	0.03	0.03
Kanchula-kharak	2550	4.90	1.30	2.27	1.17	0.13	0.47	0.00	0.33	0.00	0.01
Shokharak	2850	3.15	3.25	4.10	1.70	0.05	0.25	0.00	0.15	0.00	0.01
Manali	3100	1.70	2.38	1.38	2.19	0.00	0.13	0.00	0.31	0.00	0.05
Tungnath	3600	0.87	0.20	2.60	0.67	0.00	0.00	2.00	0.00	0.00	0.01
Mooling	3800	1.80	0.66	0.59	0.29	0.32	0.10	1.76	0.00	0.00	0.00

Large arthropod abundance was similarly influenced by elevation, peaking in abundance at 1650 m in the east and 2040m in the west. Below peak elevation, large arthropod abundance differed significantly elevation and region (ANCOVA, elevation: N = 6, F= 39.2, P = 0.008; region: N = 6, F = 25.1, P = 0.01). At elevations higher than the peak elevations, abundances differed significantly with elevation, although regional differences were no longer significant (ANCOVA, elevation: N = 10, F= 5.8, P = 0.047; region: N = 10, F = 0.16, P = 0.71). The proportion of large arthropod (arcsine-square root transformed; Fig. 3.2) did not vary with either elevation or region below the peak elevation (ANCOVA, elevation: N = 6, F= 0.23, P = 0.67; region: N = 6, F = 0.09, P = 0.78), while it declined with elevation above peak elevation in both regions ((ANCOVA, elevation: N = 10, F= 18.36, P = 0.004; region: N = 10, F = 2.7, P = 0.14).

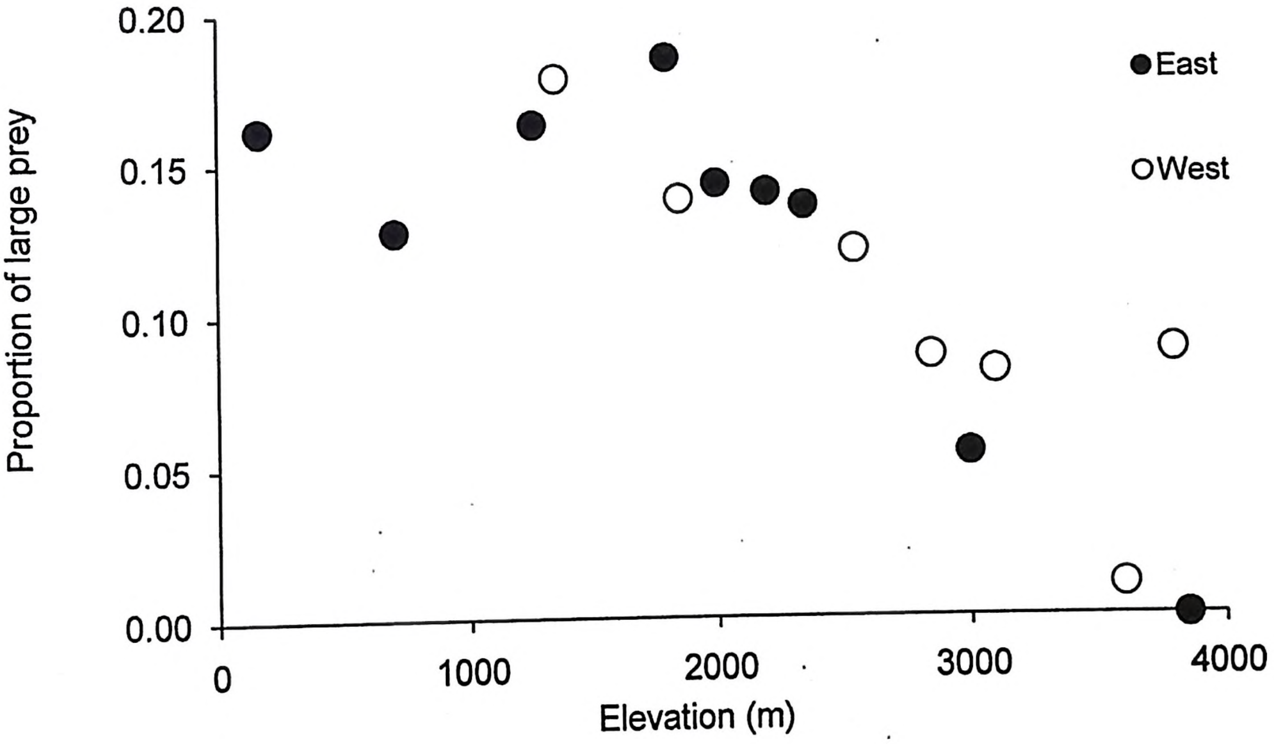


FIGURE 3.2. Variation in proportion of large prey (per bag) along altitude from the 16 sampling sites across east and west Himalayas.

3.3.2 Variation in abundance of various orders along elevation

Each arthropod order peaked in abundance at a different optimum elevation and mean abundances of most orders varied significantly with elevation both above and below their respective optimum elevation (Table 3.3). In general, the decrease in mean arthropod abundance with elevation above taxon-specific optimum elevations corresponded with the decline in mean temperature (Table 3.3, Fig. 2.2).

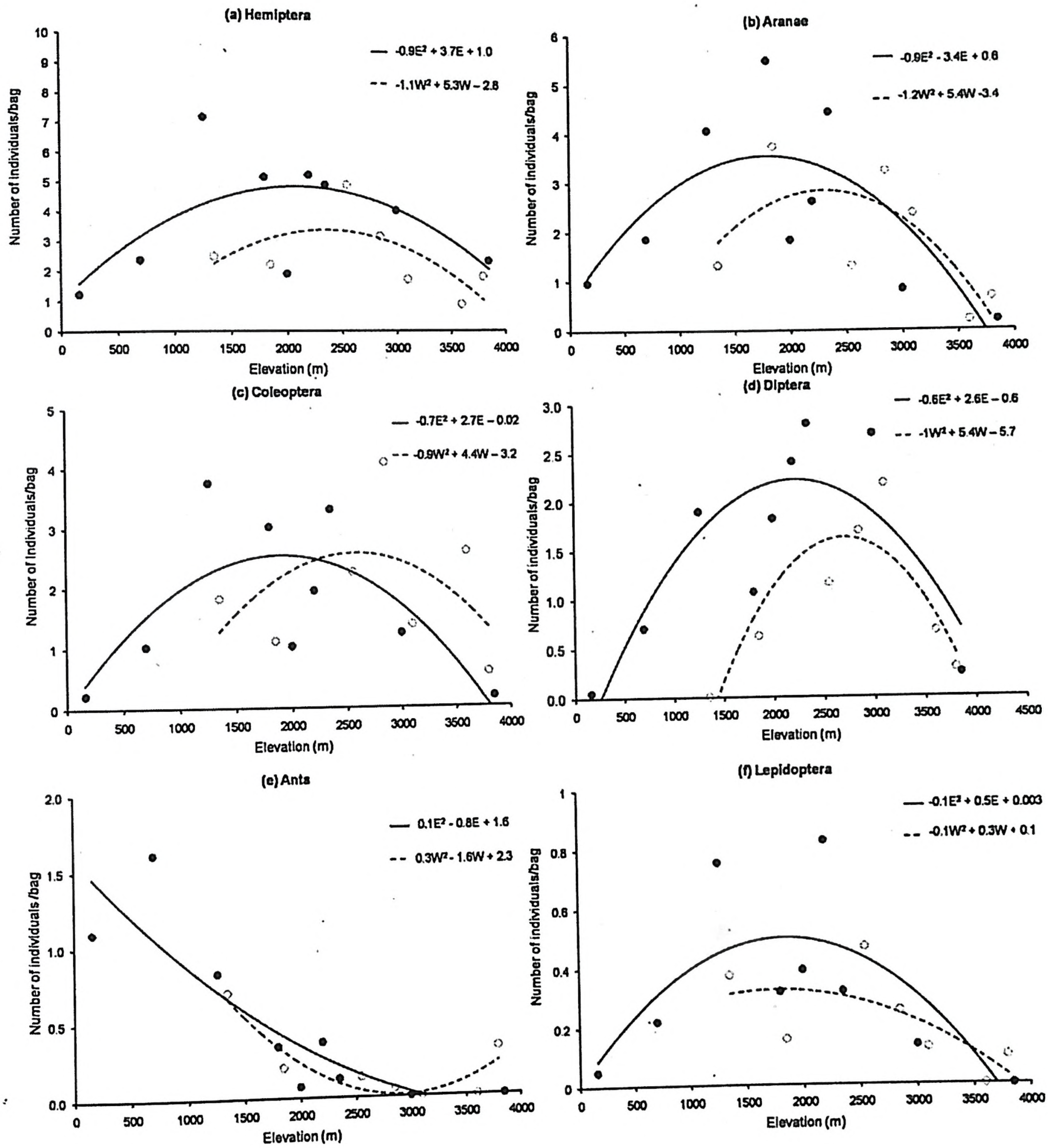


FIGURE 3.3. Variation in mean abundance of the six most common orders along the elevational gradient in east (closed circles, solid line) and west (open circles, dashed line) Himalayas.

TABLE 3.3 Results of ANCOVA relating abundance of the six most abundant arthropod orders to elevation and region (east/west) above and below respective peak elevations along with regression coefficients of the quadratic fitted curves (bold indicates $P < 0.05$). F-statistics and associated P-values for the predictor variables are presented. Bold indicates significance after sequential Bonferroni corrections for multiple comparisons. N refers to the number of sites.

	Peak elevation (m)*				Below					Above				
Order	East	R^2	West	R^2	Elevation	P	Region	P	N	Elevation	P	Region	P	N
Hemiptera	2080.79	0.41	2350.49	0.528	0.29	0.62	0.68	0.46	7	27.91	**0**	3.27	0.13	9
Aranae	1791.36	0.56	2300.68	0.442	39.15	**0.01**	25.52	**0.01**	6	5.77	**0.05**	0.16	0.7	10
Coleoptera	1910.38	0.55	2587.41	0.228	2.25	0.18	0.72	0.42	10	3.09	0.18	1.62	0.29	6
Diptera	2223.09	**0.69**	2709.58	**0.761**	21.22	**0**	25.32	**0.001**	11	524.75	**0**	5.31	0.15	5
Lepidoptera	1845.89	0.51	1781.69	0.48	1.54	0.26	0.62	0.46	10	13.29	**0.02**	0.47	0.53	6
Hymenoptera[a]	-		-		23.85	**0**	0.01	0.92	16					

*Peak elevation indicate the theoretical maxima calculated from the quadratic regression curve fitted through the data.

[a] For ants, a single ANCOVA was performed using data from all the sixteen sites.

Hemiptera was represented by the highest number of individuals across sites, and peaked in abundance at a higher elevation in the west as compared to the east (Fig. 3.3a, Table 3.3). Similarly, maximum mean abundances were recorded at a higher elevation in the west as compared to the east among Aranae (Fig. 3.3b), Coleoptera (Fig. 3.3c) and Diptera (Fig. 3.3d). In contrast, Lepidoptera abundances peaked at comparable elevations in the west as compared to the east (Fig. 3.3f). Diptera and Aranae showed significant variation in mean abundances between the two regions below their respective peak elevations (Table 3.3). Ants showed a decrease in abundance with elevation, with a peak in mean arthropod abundance recorded at 750m in the east and 1350m in the west (Fig. 3.3e, Table 3.3).

3.4 DISCUSSION

Arthropods experience considerable changes in environmental conditions along elevational gradients, which drive spatial variation in their distributions and abundance (Progar and Schowalter 2002; Hodkinson 2005; Lessard et al. 2011). This study provides an assessment of variation in distribution patterns of foliage-dwelling arthropod taxa in terms of their relative abundances along elevational gradients located across an extensive precipitation gradient in the Himalayas. In general, total and taxon-specific mean arthropod abundances attained their respective peaks at intermediate elevations which differed across regions and taxa. Furthermore, while relative arthropod abundance is significantly lower in the west as compared to the east below 2000m, abundances are similar above (Fig. 3.1). The patterns documented have further implications in suggesting resource availability for breeding, insectivorous bird species in the two regions which depend on foliage arthropods (e.g. Leaf warblers). In general, while relative resource availability declines in the lower elevations as ones from east to the west, relative availability of large arthropods remains unchanged.

Arthropod abundances declined sharply with decrease in temperature above peak elevations suggesting that low temperatures impose physiological limits on distribution of arthropod taxa (Clarke and Gaston 2006). However, no such limiting influence of temperature is evident below peak elevations. While lower elevation sites receive more precipitation, higher temperatures expose the arthropods to risks of desiccation (Hadley 1970). At intermediate temperatures, relatively lower temperatures are more favourable to persistence of arthropods in addition to increased plant productivity owing to lower maintenance costs imposed by cool nights (Janzen 1973). In the east, tropical moist and broad-leaved vegetation occurs at the intermediate elevations, and regionally this elevational belt (1500-2000m) is known to harbor highest plant species richness (Acharya et al. 2011). Similarly, the highest abundance in the west was obtained in subalpine higher oak–fir forests, with flowering *Quercus leucotrichophora* and fir branches being associated with abundant arthropod. This abundance appeared to be highly seasonal, concurrent with breeding of migratory avian insectivores such as leaf warblers (8 species). Similar trends have been documented for overall arthropod abundance and taxon-specific patterns and have been similarly related to higher plant productivity at intermediate elevations (Janzen 1973; Samson et al. 1997; reviewed in Hodkinson 2005). The only exception to the general unimodal pattern was the order Hymenoptera (mostly ants), which showed a steady decline in number of individuals with increasing elevation. Such a pattern has been reported previously, particularly for ants (Janzen 1973; McCoy 1990; Lessard et al. 2011). The explanation of this pattern hinges upon the hypothesized constraints imposed by low temperature on population size of arthropods at high elevations (Hodkinson 2005; Sanders et al. 2007). Hence, further investigations are required to explain the anomalous response of this group to elevation.

A comparison of climatic conditions across east and west Himalayas reveals similarity in conditions at higher altitudes (>2000m), while lower elevations are evidently wetter and cooler in the east (Table 3.1; Price et al. 2011). Mirroring these patterns, regional differences in total and taxon-specific (Aranae, Diptera) arthropod abundances are evident only below peak elevations possibly responding to the moister conditions in the east (Table 3.3), particularly among the moisture sensitive Diptera (Dial et al. 2006). This trend assumes importance since among leaf warblers (Phylloscopidae) species using more flypicks as a foraging maneuver (3 of 5 *Seicercus sp.* and *P. cantator*), i.e. the ones employing aerial captures more often to catching flying insects, are the ones restricted to the east.

Abundance of foliage-dwelling arthropods is also known to be strongly correlated to foliage area or density (Janzen 1973; Wolda 1978; Dial et al. 2006). Here, a similar association between arthropod abundance and leaves per branch is evident. Density of trees as well as vertical foliage density differs significantly from the east to the west (Price et al. 2011). The lowered availability of foliage arthropods in the low-elevation sites in the west could be a significant contributing factor in explaining the inability of a high proportion of low-elevation forest bird species in extending their ranges into the western Himalayas (Price et al. 2011).

In conclusion, this study assumes importance given the paucity of information on broad-scale spatial trends in arthropods from the Himalayas. The trends in relative arthropod abundances along elevational gradients across the Himalayas appear to be most related to differential responses to climatic variables, and suggest reduced resource availability for forest-dependent avian insectivores in the west. Owing to their strong association with environmental variables, various arthropod taxa can potentially serve as ideal indicators of climate change (Progar and Schowalter 2002). The higher Himalayas, particularly the Greater Himalayan region is very vulnerable to global climate change (Xu et al. 2009). Therefore, gathering baseline information on spatial variation in arthropod assemblages across the Himalayan climatic gradient constitutes a critical first step towards predicting the possible impacts of future climate change on arthropod communities. However, given that the lack of finer level identification of arthropods sampled precluded investigation of species richness and diversity patterns, further research involving more detailed taxonomic resolution is required to attain better ecological and biogeographical understanding of this hyper diverse group.

CHAPTER 4

Climatic determinants of breeding distribution

4.1. INTRODUCTION

Understanding the determinants of observed pattern of species distribution has traditionally been a central theme in ecology. The current distribution of a species is an outcome of a complex interplay of its ecology and evolutionary history acting at various spatial scales (Brown 1995; Gaston 2003). Various factors govern the observed pattern of species occurrence and include (a) abiotic conditions such as climate and physical environment; (b) biotic factors which consist of positive and negative interactions with other species; (c) regions accessible for dispersal; and (d) capacity of the species to adapt to new conditions which can be discerned from evolutionary analyses. Hence, often a two-scale approach is employed in studies looking at ecological correlates of species distribution (Hulbert and White 2007). The first scale uses polygonal range maps to detect environmental factors that limit species distribution at broad biogeographical and macroecological scales, yielding very satisfactory results with well-known taxa (Brown et al. 1996; Gaston 2003).

Estimating the geographic extent of the "fundamental ecological niche", defined mostly in terms of coarse bioclimatic envelope/climatic dimensions, is often the intermediate step in studies addressing issues in evolution (Peterson 2001; Hugall et al. 2002), ecology (Anderson et al. 2002), and conservation (Godown and Peterson 2000; Sánchez-Cordero and Martýnez-Meyer 2000; Peterson and Robins 2003). Ecological niche is often reconstructed by relating species occurrence data with data sets corresponding to environmental dimensions (from GIS layers). Using diverse algorithms (e.g., MAXENT-Phillips et al. 2006; BIOCLIM-Nix 1986; GARP-Stockwell and Peters 1999; DOMAIN-Carpenter et al. 1993; multiple regressions and generalized linear and additive models - Guisan and Zimmermann 2000), suitable environmental variables for each species are identified and projected onto landscapes to predict the potential species distribution range. Hence, essentially this procedure is a correlative approach of ecological niche modeling to identify areas ecologically similar to where the species is known to occur (Soberón and Peterson 2005). Application of such presence-only environmental niche models include identifying ecological requirements of species (Anderson et al. 2002; Vetaas 2002; Diekotter et al. 2006), understanding evolutionary range dynamics (Peterson and Holt 2003), predicting effects of habitat alterations (Manel et al. 2000), climate change (Thuiller 2003) and assessing viability of species in reserve networks (Burns et al. 2003). In recent studies (Cadena and Lioselle 2007; Cadena 2007), distribution models derived in this manner have been employed to elucidate the role played by inter-specific competition, autecology and geographic variation in environment in determining the evolutionary origin of elevational zonation of congeneric species.

Among the Phylloscopidae ten of the sixteen species under consideration have breeding ranges straddling the east and the west, while four occur only in the east and two are restricted to the west (Table 1.1). The four eastern species breed in the low-elevation forests having a South Asian, tropical origin (Päckert et al. 2012). On the other hand, the two western species breed at higher elevations and originated in the boreal forests (Päckert et al. 2012). Furthermore, based on data gathered in the first year, I found evidence for climate tracking among the eastern community of Phylloscopidae. In general, species breeding at higher elevations in the east were the ones ranging further into the west, whereas it is species breeding at lower elevations which dropped out (Fig. 4.1). This indicated the possibility of species with climatically similar high-elevation niches available in the west being able to range into the western Himalayas, while low elevation species being unable to do so.

In this chapter, the primary objective was to assess whether eastern species are tracking their climatic niche to range across the Himalayas. Since the western Himalayan habitats were apparently dry and mostly non-forested during the last glaciation during the Pleistocene (Ray and Adams 2001), it has been hypothesized that majority of the forest species probably retreated to forested refuge in the eastern Himalayas and re-colonized habitats in the west post-glaciation (Price et al. 2011). Hence, I focused on the eastern species, of which four are restricted to the eastern Himalayas during the breeding season. Using species occurrence records from the specified eastern Himalayan grid (covering all the field sites visited during this study) and relevant long-term environmental variables, I generated predicted distribution of the 14 eastern species across the Himalayas. This allowed me to examine whether environmentally suitable areas are present in the west for the eastern species and thereby, if I could attribute the inability of the four eastern species to range into the west to lack of respective climatic niches in the west. A similar approach was adopted to test whether climate alone could explain the absence of the two western species (*P. humei, P. occipitalis*) in the east.

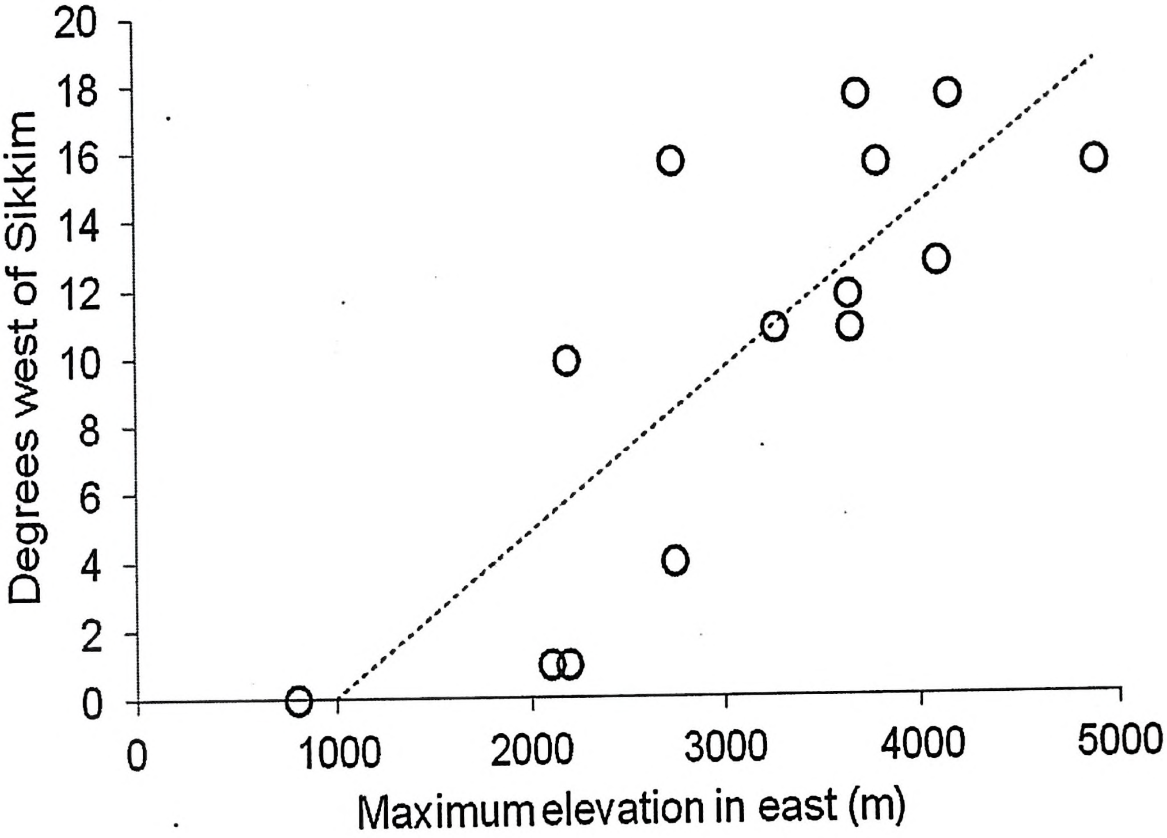


FIGURE 4.1. Maximum elevation where a species was recorded breeding plotted against the western range limit of the species (as degrees west of Sikkim).

4.2 ANALYTICAL METHODS

4.2.1 Species occurrences

Altitudinal breeding ranges and mean abundances per species were derived from altitudinal point counts separately for the east and the west (Table. 4.1). A rectangular polygon each, encompassing all the sampled elevational transects, was overlaid on the western and eastern region, respectively. Most locations for the 14 eastern species were recorded from field using a handheld Garmin GPS 72. However, since field sampling was restricted to four elevational transects additional georeferenced locations from the region were compiled from literature screening, personal communications and online databases such as Global Biodiversity Information Facility (GBIF; www.gbif.org). Georeferenced locations were overlaid on the digital elevation model (DEM) used by WorldClim (Hijmans et al. 2005) and elevation was extracted using ArcGIS 9.1 (ESRI 2005). For each species only those locations were retained for further niche modelling which lay within the breeding altitudinal range estimated using field sampling (Table 4.1) and fell within the pre-defined areal delimitation with a spatial accuracy of less than 1 km^2. The number of georeferenced locations for the target species ranged between 24-67 (see Appendix 2 for details).

4.2.2 Environmental variables

To predict climatic niches of the eastern species across the Himalayas, four temperature- and precipitation-based Bioclim variables were selected from the WorldClim database (Hijmans et al. 2005) obtained from global land area interpolations of climate point data (years 1950–2000) with 1 km^2 resolution. These variables were selected given the critical role played by these variables in determining in the northerly range limits of Himalayan passerines (Price et al. 2011) and include: BIO5 (maximum temperature of the warmest month), BIO7 (temperature annual range), BIO12 (annual precipitation) and BIO 17 (precipitation seasonality expressed as coefficient of variation in annual precipitation). The four environmental layers were imported as raster map layers ArcGIS 9. (ESRI 2005) and clipped to match the geographic extent of the Himalayas.

4.2.3 Modelling procedure

To predict spatial patterns of climatic suitability for the 14 eastern species and the 3 west-restricted species, I used the maximum entropy method of species distribution modelling or 'Maxent' (ver. 2.3.0; http://www.cs.princeton.edu/_shapire/maxent/) (Phillips et al. 2006). Maxent is a general approach which estimates the distribution with the 'maximum entropy' or most uniform distribution (wherein each grid cell has almost equal probabilities of occurrence) across the study area, given the constraint that the expected values for the environmental variable in the model must match the empirical average calculated over the presence locations. Therefore, the Maxent probability distribution estimates the suitability of each grid cell as a function of all the environmental variables at the locations where the species is known to be present and is able to predict potential geographic distribution (i.e. areas where the environmental conditions are similar to the known distribution of the species). Maxent was chosen over other commonly used algorithms for rules-set prediction (e.g. GARP, BIOCLIM etc.) since (a) Maxent was designed specifically to model species distributions using presence-only data (Phillips et al. 2006), and (b) has performed better than other modelling applications (Elith et al. 2006, Hernandez et al. 2006, Pearson et al. 2007).

To avoid pseudo-replication due to inclusion of multiple locality records within the same grid cell per species, I set Maxent to ''remove duplicate presence records''. I randomly selected 75% of the occurrence records as "training set" to generate the model, while 25% were set aside as "test set". The area under the receiving operator characteristic (AUC) was calculated to test whether the model could distinguish between the test localities and the null generated from 10000 randomly selected points in the background. Since an AUC value of 0.5 (particularly for a model derived from presence random data) indicates that the model is no different from random, I considered values > 85% a baseline for model accuracy (Pearce and Ferrier 2001). The logistic output (ranges between 1-0) was selected to quantify the probability of environmental suitability for each species across the Himalayas. Thus, species distribution models were generated for each of the 4 east-restricted and 2 west-restricted species to test whether climatically similar niches for these species exist in the western grid.

4.3 RESULTS

4.3.1 Altitudinal distribution of breeding leaf warblers

The minimum and maximum elevational limits of species were derived from the altitudinal point count data. These values were used to estimate the mid-point and breeding elevation range of each species in the east and the west. Based on estimates of relative abundances over their respective breeding elevational ranges, Blyth's leaf Warbler (*P. reguloides*) was the most abundant species in the east, while Grey-hooded Warbler (*P. xanthoschistos*) was most frequently encountered in its breeding range in the west.

TABLE 4.1 Altitudinal ranges and relative abundances (±I SE) of leaf warblers in their breeding rangės in the east and the west Himalayas.

	EAST			WEST		
Species	Altitudinal distribution		Abundance (per point)	Altitudinal distribution		Abundance (per point)
	Max (m)	Min (m)	Mean	Max (m)	Min (m)	Mean
P. cantator	1200	120	0.88±0.12	-	-	-
S. castaniceps	2750	1805	0.80±0.08	-	-	-
S. affinis	2200	1750	0.61±0.10	-	-	-
S. poliogenys	2100	1150	0.70±0.10	-	-	-
S. burkii	2200	1700	0.59±0.09	2675	2275	0.55±0.16
S. whistleri	3650	2000	0.66±0.07	3200	2800	0.35±0.08
P. chloronotus	3800	2700	0.63±0.09	3275	2205	0.79±0.09
P. xanthoschistos	2350	700	0.97±0.08	2800	1250	0.98±0.08
P. pulcher	4100	3250	0.63±0.09	3500	3100	0.52±0.11
P. reguloides	3660	1750	1.04±0.07	3300	2490	0.76±0.10
P. maculipennis	3275	2100	0.69±0.07	3200	2650	0.70±0.09
P. trochiloides	4170	3000	0.62±0.08	3700	3400	0.90±0.10
P. affinis	4500	3800	0.51±0.09	3985	3600	0.42±0.12
P. magnirostris	3700	2000	0.19±0.04	3100	1690	0.18±0.20
P. humei	-	-	-	3800	3200	0.88±0.09
P.occipitalis	-	-	-	2900	1900	0.87±0.08

4.3.2 Predicted climatic niches

Species breeding only in east

Yellow-vented Warbler (*P. cantator*): The western extent of the predicted environmentally suitable areas from the maxent geographical output for this eastern species was only up to central Nepal (Fig. 4.2). Within the western grid, there is no predicted distribution of this species (except for a small patch with low probability). The model had a discrimination capacity (i.e. AUC value of the training set) of 0.994. The environmental variable with the highest regularized training gain was temperature annual range followed by annual precipitation (Fig. 1a, Appendix 2).

Grey-cheeked Warbler (*S. poliogenys*): The maxent geographical output predicts areas of environmentally suitable areas within the western grid, although no suitable habitat exists within an intervening area in western Nepal (Fig. 4.3). The AUC value of the training set was 0.993, indicating that the model is able to distinguish between areas with and without the presence of the species 99.3% of the time.

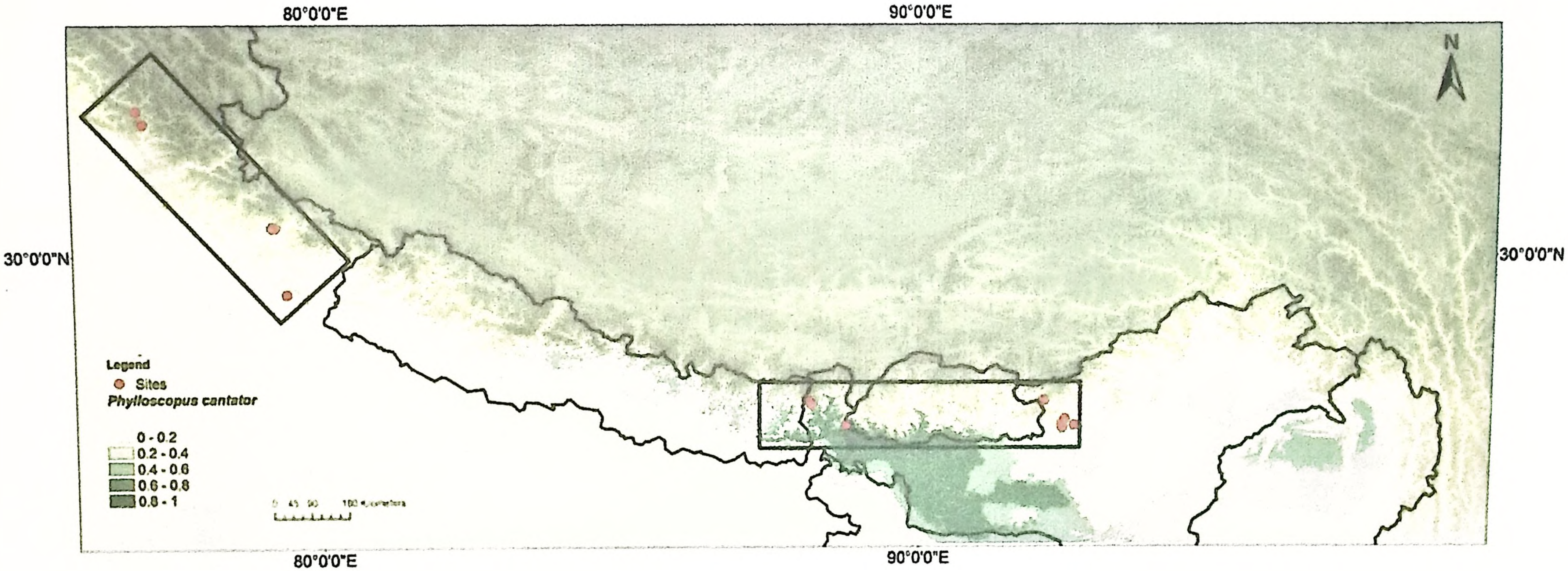


FIGURE 4.2. Predicted geographic distribution of Yellow-vented Warbler (*Phylloscopus cantator*) across the Himalayas using occurrence locations from its breeding range in the east. The study sites have been enclosed within rectangles in the west and the east.

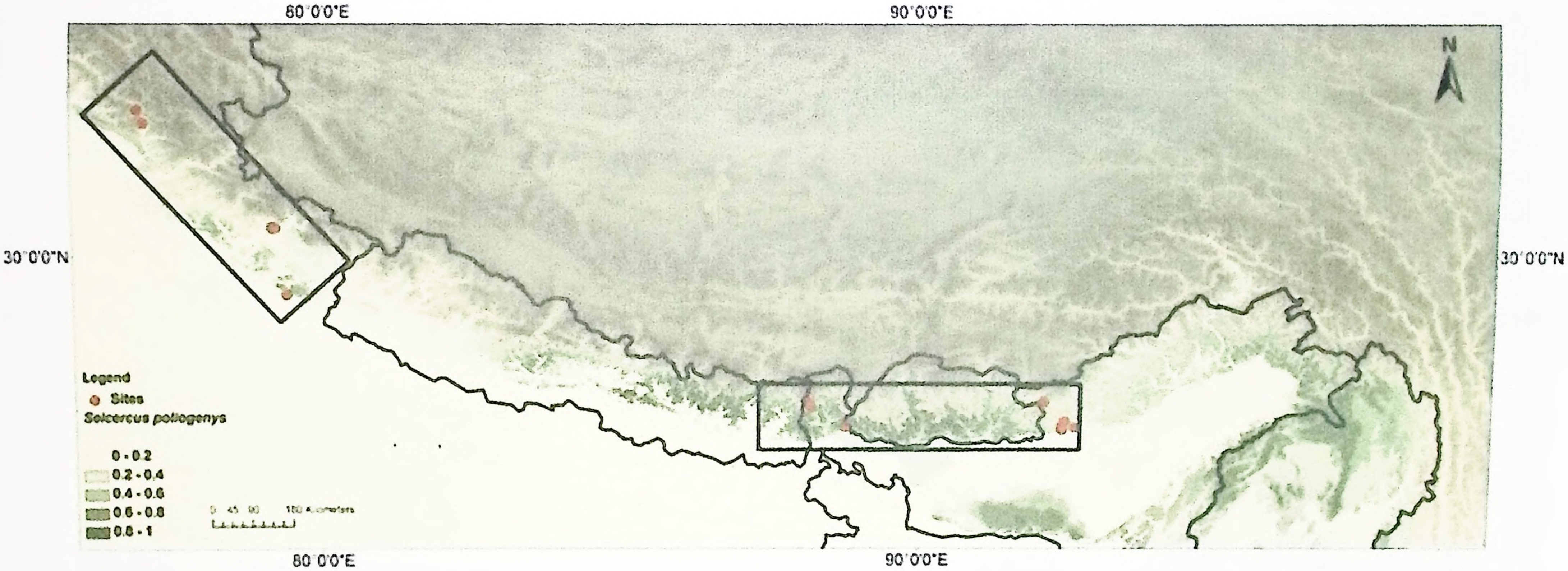


FIGURE 4.3. Predicted geographic distribution of Grey-cheeked Warbler (*Seicercus poliogenys*) across the Himalayas using occurrence locations from its breeding range in the east. The study sites have been enclosed within rectangles in the west and the east.

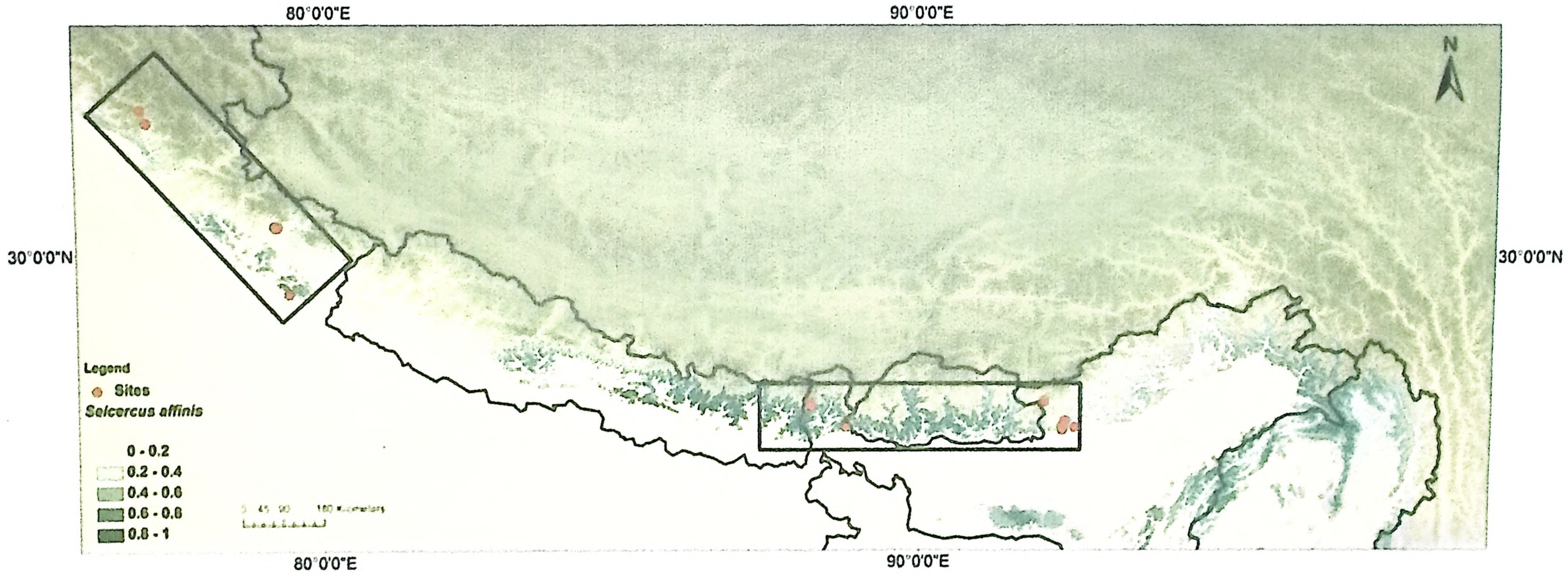


FIGURE 4.4. Predicted geographic distribution of White-spectacled Warbler (*Seicercus affinis*) across the Himalayas using occurrence locations from its breeding range in the east. The study sites have been enclosed within rectangles in the west and the east.

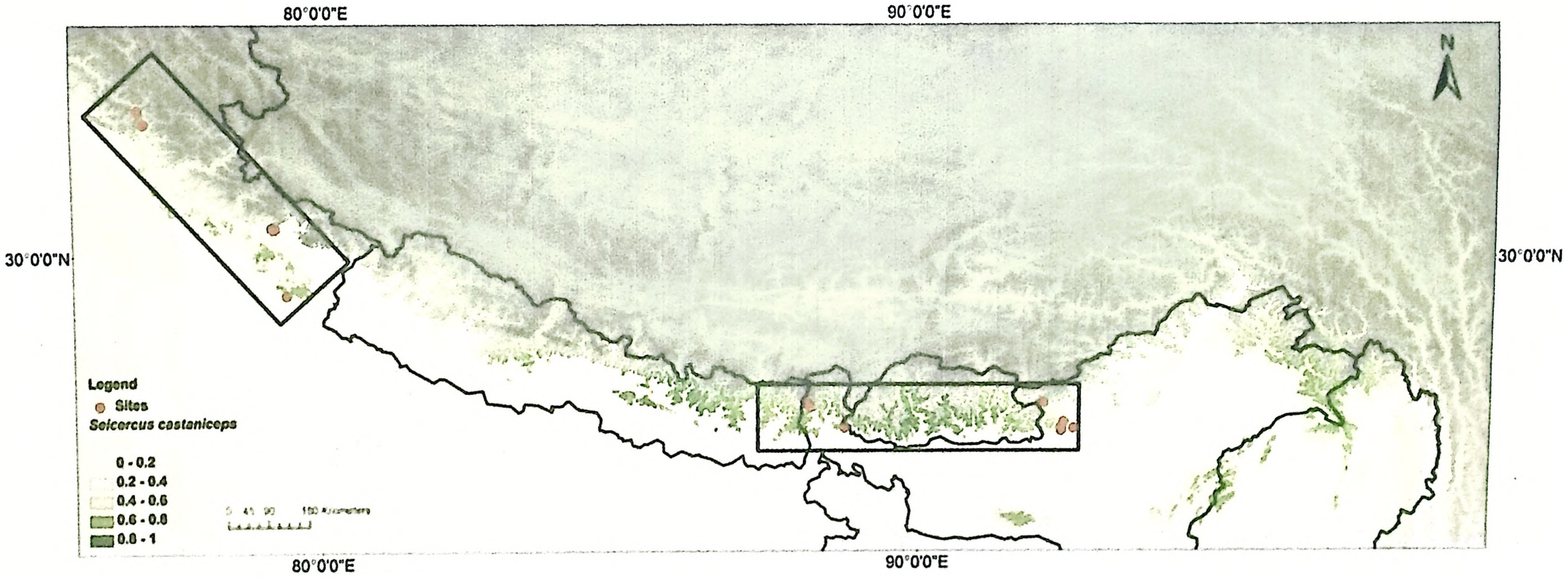


FIGURE 4.5. Predicted geographic distribution of Chestnut-crowned Warbler (*Seicercus castaniceps*) across the Himalayas using occurrence locations from its breeding range in the east. The study sites have been enclosed within rectangles in the west and the east.

White-spectacled Warbler (*S. affinis*): The predicted distribution of the species based on the maxent model depicts areas of suitable areas within the western grid (Fig. 4.4). Similar to the predicted model of the Grey-cheeked Warbler, there is a gap in the predicted distribution in western Nepal. The accuracy of the predicted model is indicated by results of the ROC curve analysis: the AUC of both the training and test sets were 0.99. Temperature annual range and annual precipitation were the most environmental variables in the model (Fig. 1c, Appendix 2)

Chestnut-crowned Warbler (*S. castaniceps*): Environmentally suitable areas were predicted within the western grid by the maxent model, with two gaps in the predicted distribution (Fig. 4.5). The discriminatory capacity of the model was very high with an AUC value of 0.99 indicating the accuracy of the prediction based on the selected environmental layers. The relative contribution of temperature annual range and annual precipitation was greater in the model (Fig. 1d, Appendix 2).

Eastern species ranging across the Himalayas

For the ten eastern species common to the east and the west, the maxent model predicted suitable areas across the Himalayas (Figs. 3-12, Appendix 2). In case of all the predicted models, the discriminating capability was very high as indicated by AUC value of > 0.99 in each case.

Species breeding only in west

Western-crowned Warbler (*P. occipitalis*): The maxent model predicts suitable environmental niche across the eastern grid continuing into South-east Asia (4.6). The AUC value of > 0.99 indicated the accuracy of the predicted model. Annual precipitation and annual temperature range were the variables showing the highest regularized training gain (Fig. 2a, Appendix 2).

Hume's Warbler (*P. humei*): Climatically suitable areas are predicted within a narrow belt in the eastern grid by the maxent model (4.7). However, there exists a wide gap in the predicted distribution across Nepal. The model has high discriminatory capacity as indicated by an AUC value of 0.99. Maximum temperature of the warmest month and temperature annual range are the two variables showing the highest regularized training gain (Fig. 2b, Appendix 2).

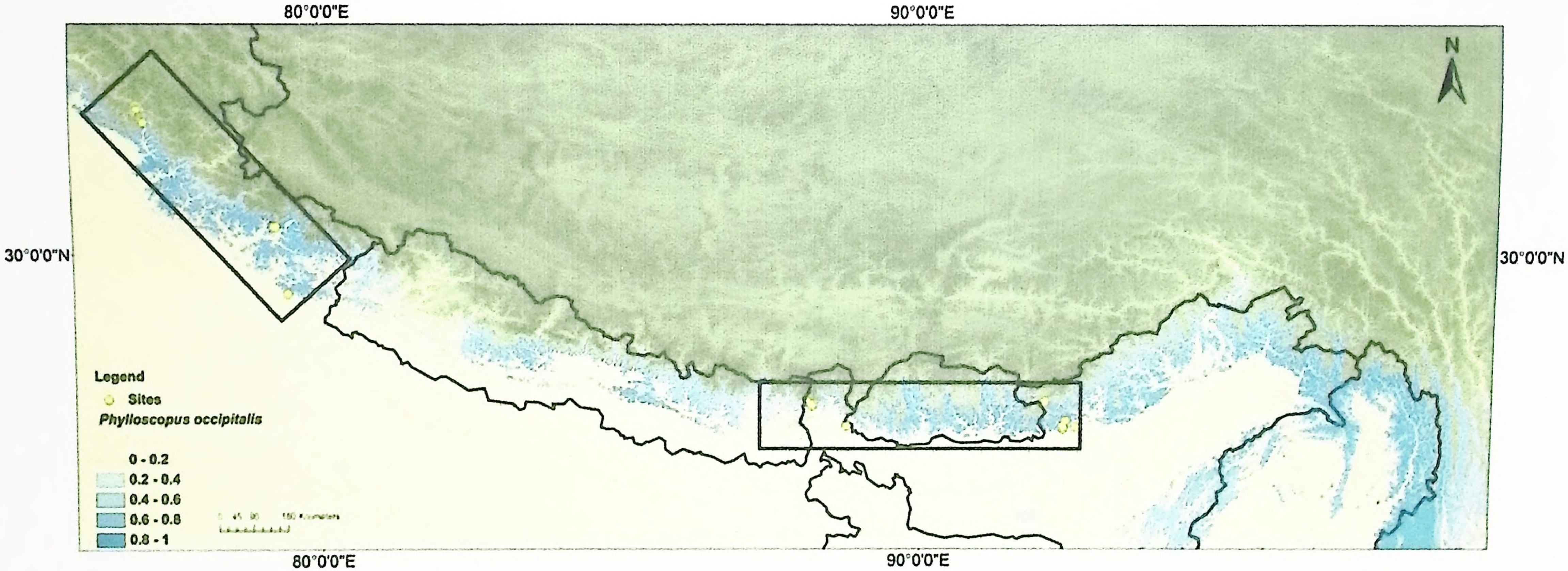


FIGURE 4.6. Predicted geographic distribution of Western-crowned Warbler (*Phylloscopus occipitalis*) across the Himalayas using occurrence locations from its breeding range in the west. The study sites have been enclosed within rectangles in the west and the east.

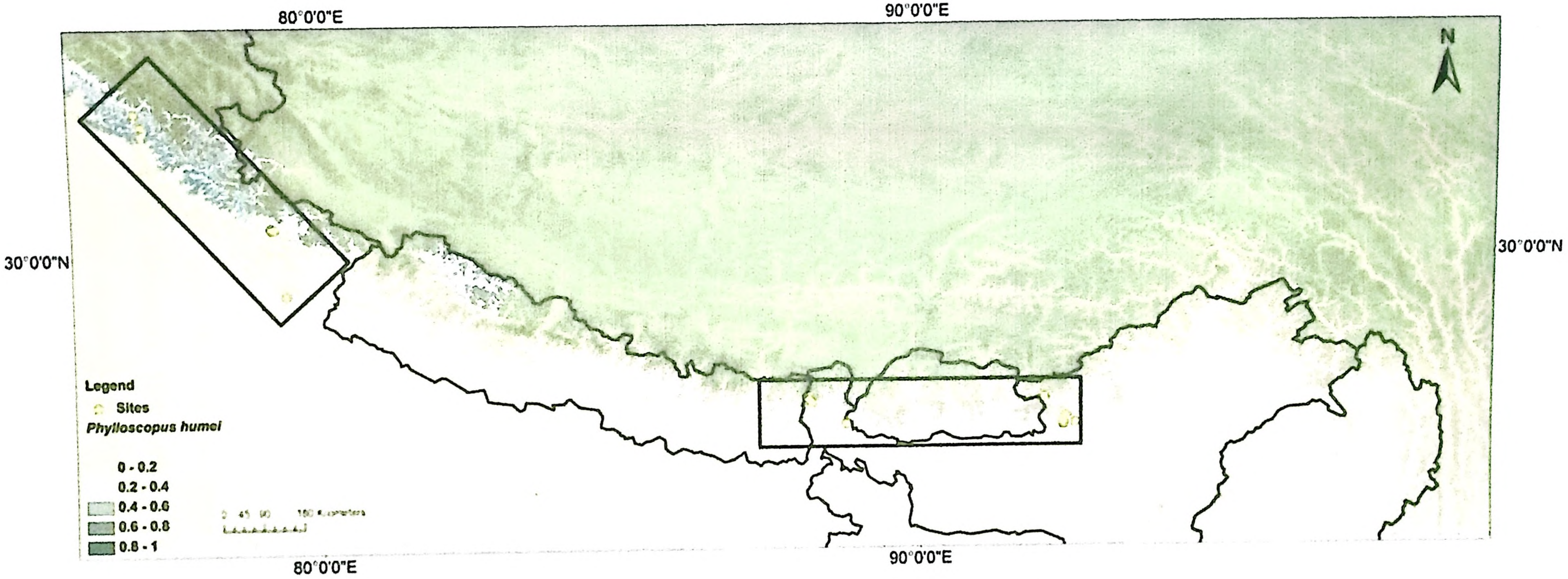


FIGURE 4.7. Predicted geographic distribution of Hume's Warbler (*Phylloscopus humei*) across the Himalayas using occurrence locations from its breeding range in the west. The study sites have been enclosed within rectangles in the west and the east.

4.4 DISCUSSION

The Himalayan range encompasses a broad bioclimatic gradient, with habitats transitioning gradually from dry and seasonal to wet and tropical as we move from the west to the east, particularly in the elevations below 2500m. Species distribution models suggest the non-existence of low-elevation eastern climatic niches in the east and *vice versa* (Price et al. 2011). By incorporating occurrence records from the breeding distribution range, this chapter predicted environmentally suitable areas across the Himalayas for species restricted to the east and west to test whether lack of suitable climatic niche is responsible for their inability to range across the west and the east, respectively. Annual precipitation and maximum temperature were the environmental variables which contributed the maximum information to the geographic distribution models. In most cases, environmental niches as defined by climatic variables exist in the other region (where the species is absent), suggesting that climate alone is inadequate in explaining the observed pattern of breeding distribution.

In case of three of the four east-restricted species, the ecological niche model-based suitability map suggests existence of favourable environmental niche within the western grid, including areas of high suitability as indexed by prediction probability > 0.6. However, in all three cases there exists a considerable 'gap' or environmentally unsuitable area in western Nepal. In case of *P. cantator,* the geographic distribution of suitable areas does not extend beyond central Nepal. In their study on the role of barriers in causing vicariance within the Indian subcontinent, Ripley and Beehler (1990) identified the river gorge Karnali situated in the aforementioned unsuitable area in western Nepal as a 'barrier' between north-western and south-eastern Himalayan forms. It seems that for most of these low-elevation species which originated in south-east Asian tropical and subtropical forested habitats (Packert et al. 2012), lack of suitable areas along the river gorge Karnali has possibly functioned as a dispersal barrier which has prevented these species from occupying suitable areas existing within the western Himalayas. However, on examining the predicted geographic distribution of species common to both regions using similar models, it is evident that similar unsuitable areas have been predicted for species such Grey-hooded Warbler (a low-elevation species) and Ashy-throated Warbler (Appendix 2).

This implies that these species have been able to range across this 'barrier' emphasizing the need for assessing other ground-based characteristics such as habitat structure, resource availability with respect to the ecomorphological adaptations of the species to determine the factors which restrict the distribution range of the restricted species.

To summarize, in most cases pockets of environmentally suitable areas exist in the other region and climatic niche models alone do not explain the observed distribution of the Phylloscopidae. This highlights the need for investigating the suitability of the habitats further in terms of other factors such as vegetation characteristics, distribution of resources, competitive interactions and niche conservatism in traits to explain the observed patterns in breeding distribution of the restricted species.

CHAPTER 5

Geographic variation in foraging ecology

5.1 INTRODUCTION

The latitudinal diversity gradient in species numbers is widely recognized but underlying causes are poorly understood (Hillebrand 2004; Mittelbach et al. 2007). Differences in the number of species in different places must ultimately reflect the history of speciation, extinction, and/or immigration, and recent advances have been made in estimating the relative contributions of these processes to both the marine (Goldberg et al. 2005; Jablonski et al. 2006) and terrestrial (Wiens et al. 2006, 2009; Weir and Schluter 2007) gradients. Less clear is how speciation, extinction and dispersal are themselves regulated. In one class of explanations, communities are not at equilibrium, and the greater age, area and/or stability of the tropics has resulted in greater net diversification in these regions. In this case, species numbers are generally increasing, but have been doing so at a greater rate or over a longer time in the tropics. Such non-equilibrium explanations have been applied over timescales of tens of millions of years (Wiens et al. 2006; Fine and Ree 2006), several million years (Weir and Schluter 2007) and the Pleistocene (Wallace 1878; Svenning and Skov 2007; Hortal et al. 2011; Normand et al. 2011).

In an alternative class of explanations, termed local determinism (Ricklefs 2006), local factors (e.g. competition, predation, resources, harsh climate) limit immigration into communities and ultimately speciation as well (Phillimore and Price 2009; Weir and Price 2011). Communities are considered close to saturated, so the past history of speciation, extinction and immigration in different regions is largely irrelevant what sets species richness (Ricklefs 2006; Rabosky 2009). In this case, the terrestrial latitudinal gradient arises because more niches are present in warm, wet, productive and climatically stable areas than in cooler, drier, less productive and seasonal areas (MacArthur 1969; Schoener 1971, reviewed in Evans et al. 2005; Ricklefs 2006). The number of niches idea has been difficult to test for two reasons. The first is empirical, and concerns how to compare niche diversity between regions whose resources differ both quantitatively and qualitatively. The second is that the theory of why niche diversity should increase with productivity or aseasonality is poorly developed (Currie et al. 2004; Evans et al. 2005). A simple idea is that higher productivity leads to more individuals, so rare species can persist in more productive areas, but not in less productive areas (MacArthur 1969; Rosenzweig and Abramsky 1993). However, Currie et al. (2004) found that productivity across regions is poorly correlated with number of individuals.

I label the nonequilibrial historical and the equilibrial (locally deterministic), alternatives as the "historical" and "ecological" hypotheses for simplicity. They are not mutually exclusive and both are likely to apply in most systems, but with respect to the latitudinal gradient the issue is whether temperate regions are further from any equilibrium (Ricklefs 2006). Components of one or other hypothesis have been examined, as in the productivity-> individuals-> species test described above. With respect to historical hypotheses "niche conservatism" is required to explain models that invoke history over very long timespans to explain why species in one region do not expand their ranges across climatic regimes (Wiens and Donoghue 2004; Wiens et al. 2006). In two specific case studies, niche conservatism has been rejected as an explanation for species richness gradients (Algar et al. 2009; Price et al. 2011), although it may apply to other groups and areas (Wiens et al. 2006; Harrison and Grace 2007). More recent historical effects may also apply, and reconstructions of Pleistocene climate have found that diversity in formerly glaciated areas is lower than expected from predictions based on current climate (Hawkins 2004; Hortal et al. 2011; Normand et al. 2011). In this chapter, I compare the ecological and historical models using a new approach that examines geographical variation across the range of species that extend from species-rich to species-poor locations.

Under the historical scenario, species diversity is lower in temperate regions because numbers are displaced further from any ecological carrying capacity. Thus, I predict that those species that straddle both regions should contain more generalist populations in species-poor regions, expanding their niches to fill ecological space, which is occupied by other species in species-rich regions. This prediction arises more formally from the theory of spatial models of character displacement (Case and Taper 2000; Goldberg and Lande 2006). Those models are based on the assumption that resource diversity is constant across space, which applies if history alone is responsible for variation in species numbers (Fig. 5.1). In the models, two species are introduced at different positions in space, and partially spread into each other's range, where niches contract. The history of introduction rather than resource diversity determines where the two species are sympatric and allopatric.

The historical model could be considered the null hypothesis, being based on the assumption of constant ecological conditions across regions (Fig. 5.1). It is rejected as the sole contributor to a decline in species diversity if geographical variation within species is associated with increased specialization in less diverse regions.

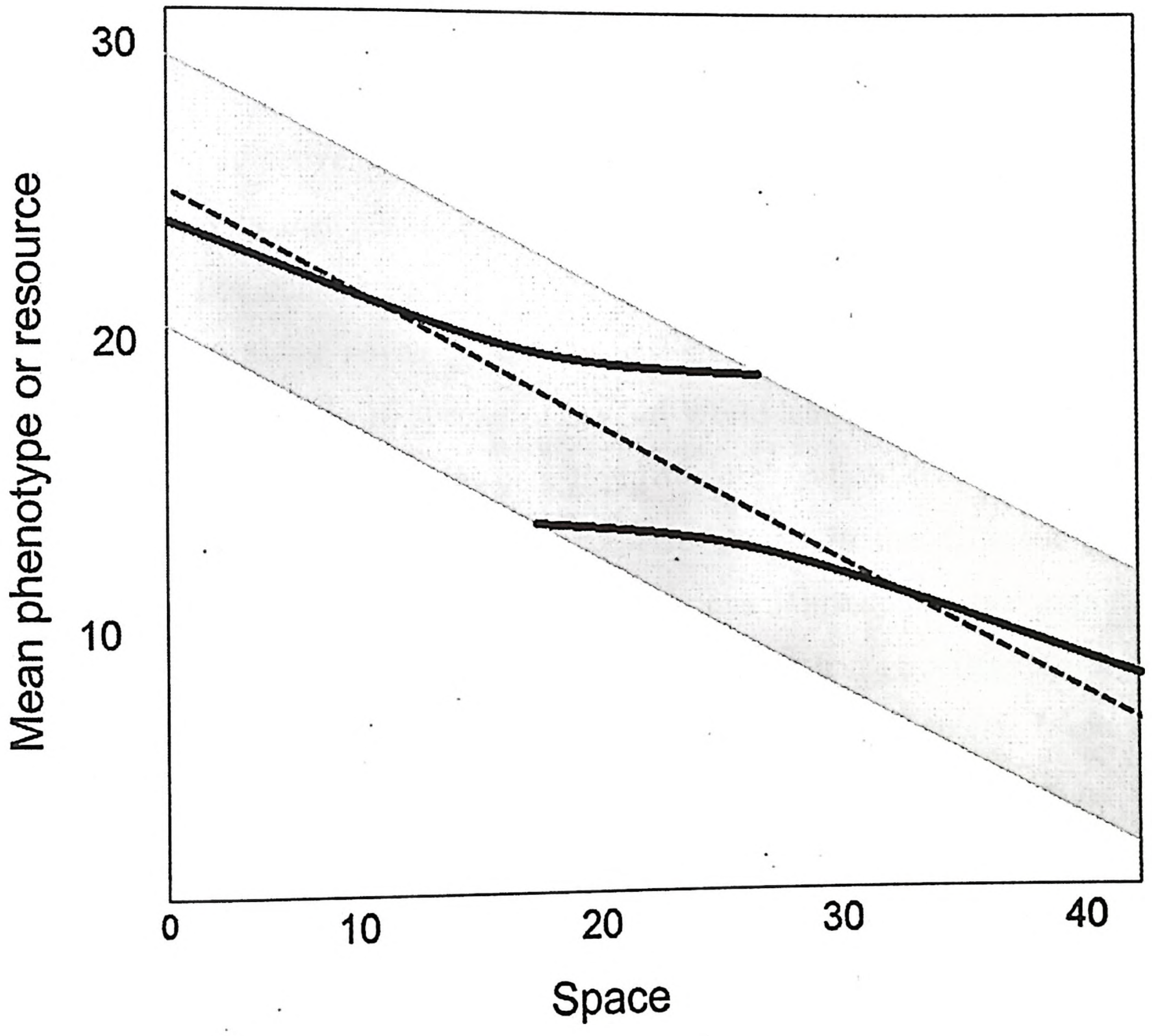


FIGURE 5.1. Mean phenotypes of two competing species along an environmental gradient, after the model of Case and Taper (2000). Mean phenotype tracks the distribution in the average value of some resource (e.g. size), but resource diversity is assumed constant, as indicated by the shaded area. In allopatry, species exploit the complete range of resources, whereas in sympatry, each is displaced to one side of the resource spectrum and specializes.

On the other hand, both expansions and contractions may be expected under the ecological model, depending on how underlying resources vary. Under the fewer niche idea, a decline in resource diversity drives the decline in species numbers, so it may also drive greater specialization in low diversity regions. However, the prediction depends on multiple factors, including both resource diversity and what competitors are present. Here I estimate resources and show that this is consistent with the prediction of increased specialization in the region of low species diversity. However, some ecological hypotheses predict generalization in more temperate regions in response to resource shortages and/or direct effects of variability in climate (Vázquez and Stevens 2004; McCain 2009). I consider the implications of these hypotheses further in the discussion.

As I noted above, a major difficulty with comparisons between temperate and tropical regions is that resource axes may not only differ quantitatively, but also qualitatively. The consequence is that any niche expansions in species-depauperate regions may be along novel, potentially unstudied, axes. In this chapter, I study geographical variation in 10 species of the Old World leaf warblers (Phylloscopidae) across the Himalayas. By focusing on a group of closely related species I can evaluate the extent to which ecological differences are similar in the different locations; similarity strengthens the case that the dimensions I investigate are important to coexistence. To do this, I compare ecological-morphological associations along three dimensions (prey size, feeding method, habitat occupied). Second, I can ask if species expand their niches in species-poor regions in the direction of missing related species. This is predicted under the historical models, because close relatives should be ecologically similar and hence their ecological niches most easily exploited by these relatives when they are absent.

I compared breeding communities of Old World leaf warblers, in the eastern and western Himalayas, ca. 900km separated (Fig. 2.1). Fourteen species breed along single elevational gradients in the eastern Himalayas, and up to 10 species in the western Himalayas. The 30% decline in species numbers from east to west is commensurate with the decline in total bird species numbers from the east of Nepal to the west of Nepal (Price et al. 2003; Price et al. 2011). As one proceeds further to the northwest in Kashmir, total bird species numbers decline further, although numbers of

Phylloscopidae remain roughly constant as two species drop out, but are replaced by two others (Price et al. 2011). I measured both resources and warbler community structure along this diversity gradient and studied geographical variation in foraging behaviour of the 10 species held in common between the western and eastern regions. By studying 10 species, I was able to use species as the replicate in tests for consistent patterns in geographical variation across regions.

5.2. ANALYTICAL METHODS

For all species, I found no significant difference in morphological measurements between east (defined as Nepal eastwards) and west (defined as west of Nepal, and including some specimens beyond the region of our field study, from Kashmir; see Table 1, Appendix 1). Therefore, I combined the measurements of specimens of each species from both regions to obtain species means. For all sixteen species in the study I extracted principal components from the correlation matrix of ln-transformed species mean values. Based on correlations with univariate measures, I interpret PC1 as body size and PC2 as tarsus length (Table 5.1). Unlike a study in Kashmir (Price 1991), PC3 is not readily interpretable as a measure of beak shape. Therefore, I used an alternative measure of beak shape as ln(beak length)-ln(beak width).

TABLE 5.1. Principal components (PCs) describing the morphological variables of the 16 warbler species using species means averaged over the Himalayas. The correlations (either positive or negative) for each morphological variable are listed.

Morphological variables	PC1	PC2
Beak length	0.92*	-0.18
Beak depth	0.90*	-0.39
Beak width	0.85*	-0.35
Tarsus length	0.30	0.92*
Wing length	0.84*	0.42
Tail length	0.94*	0.19
% Variation explained	67.7	22.9

* P < 0.01

To control for elevational variation I used ANCOVA to test for differences in arthropod abundance across regions. For sites (Khellong, Sessni, Sachen, Lama

Camp, Bompu, Kanchlakarakh), which were sampled for arthropods across two years (but at the same time of the year, see Table 2.1, Chapter 2), I found no significant inter-annual variation (t-tests based on bag as replicate, $P > 0.05$). Therefore, within each site, I averaged arthropod samples by combining the data from two sampling years to obtain an arthropod abundance value.

I obtained warbler densities by averaging detections across point count stations within 500m elevational bands for the west and the east. I used Pearson's correlation to test for association of warbler densities with arthropod prey abundance, which I likewise assigned (based on stations in Table 2.1, Chapter 2) to a 500 m elevational band at each site. When more than one site is present in a 500-m band, the arthropod values were averaged. To avoid pseudo-replication, I compared regions using site as replicate, rather than bag.

In order to compare altitudinal distributions of the species, mid-point of the elevational range, maximum and minimum elevation, and total range (maximum-minimum) were used. To test for geographical variation, paired t-tests were used comparing populations of each of the 10 species as the replicate. For statistical analysis of foraging data, all proportion values were arcsine-square root transformed. I used a linear mixed-effects model (LMM) to test for influence of region and foraging substrates on the use of standpick as a foraging manoeuvre using package lme4 (Bates et al. 2010) in R 2.12.1 (R Development Core Team 2010). In these analyses, species is included as a random factor to take into account the occurrence of species common to both regions (Pinheiro and Bates 2000). I used backward model selection to select the most parsimonious model. The significance of LMM fixed effects was obtained from 10,000 Markov chain Monte Carlo (MCMC) simulations, performed using the pvals.fnc function in the languageR package (Baayen 2008).

To compare species attributes, I used standard tests as well as corrections for phylogenetic non-independence (Felsenstein 1985). In the phylogenetic analyses, Iused the molecular-based ultrametric phylogeny published in Johansson et al. (2007). The tree was pruned to include only the species included in any specific analysis. Independent contrasts (PICs) were calculated using the package ape (Paradis et al. 2004) in R 2.12.1 (R Development Core Team 2010) and significance assessed via regressions and correlations forced through the origin. Because some of the dependent variables I studied were not normally distributed, being presence/absence data, I confirmed all results using general estimating equations in ape, specifying normal or binomial errors as appropriate. All significance values (measured against □ = 0.05) were unchanged and I present the independent contrast results in the text.

5.3 RESULTS

5.3.1 Habitat and resources

The climate is drier and more seasonal to the northwest (Fig. 2.2, Price et al. 2011) and the vegetation sparser with more coniferous trees (Table 5.2). In Figure 3.1, I show variation in prey abundance along the elevational gradients. Arthropod abundance is highest at intermediate elevations, and higher at lower elevations than higher elevations and higher in the east than the west (Fig. 3.1). The proportion of large arthropods is higher at lower rather than higher elevations and is highest at intermediate elevations (Fig. 3.2), but once elevation is in the model the proportion of large arthropods does not differ significantly between regions. This suggests that birds at similar elevations should encounter large prey at similar frequencies in the east and west.

TABLE 5.2. Vegetation characteristics from 34 5-ha grids at multiple sites along several elevational gradients in the east and the west. Standard errors are indicated in parentheses.

Region	Elevational range	Tree density	Foliage density	% Conifer*
East	< 2000 m	77.8 (5.06)	152.5 (21.5)	0.00
	> 2000 m	74.8 (17.93)	91.5 (20.76)	0.09 (0.03)
West	< 2000 m	56.4 (9.62)	82.2 (9.81)	0.37 (0.13)
	> 2000 m	31.7 (9.62)	49.8 (17.15)	0.38 (0.15)
ANCOVA	Site	$F_{2,31} = 7.4$, $P = 0.01$	$F_{2,31} = 10.9$, $P = 0.002$	$F_{2,22} = 6.0$, $P = 0.02$
	Elevation	$F_{2,31} = 1.9$, $P = 0.18$	$F_{2,31} = 11.9$, $P = 0.002$	$F_{2,22} = 1.0$, $P = 0.32$

* % conifer was not measured at every grid, hence the fewer error degrees of freedom.

5.3.2 Niche dimensions

As noted in the introduction, a general problem with assessment of niche diversity across regions is that resources are not *a priori* expected to be directly comparable. I evaluated this possibility in two ways. First, I asked if communities are structured in roughly similar ways in both locations. Second, I made predictions about how species should vary geographically under the historical model, based on the ecology of species restricted to just one region. I consider each in turn.

In order to compare community structure between the east and west, I studied covariation between ecological and morphological attributes (Price 1991; data from Tables 5.1, 5.3, 5.4 and Appendix 1). First, PC1 (body size) is highly correlated with proportion of large prey captures in both regions (Fig. 5.2a). The positive correlation of prey and body size is widely observed in nature (Vezina 1985) and presumably reflects differences among species in their efficiency in handling prey of different sizes (Krebs et al. 1977). Second, PC2 (tarsus length) is significantly correlated with breeding elevation in the east, and the association is also borderline significant in the west (Fig. 5.2b). Price and Gross (2005) showed that species with long tarsi hop more, with more hopping at higher elevations attributed to the more open vegetation. Finally, beak shape (ln (beak length/beak width)) is nearly significantly correlated with proportion of standpicking in both the east and west (Fig. 5.2c). When the P values from each site are combined using Fisher's combined probability test, $P = 0.03$ for the species values, while $P = 0.29$ for the phylogenetically corrected values. A wider beak is favored when prey are captured in flight (Price 1991). However, differences among species do not reflect a shift in the quantity of resting vs. flying prey (cf. Davies and Green 1976) because the majority of flying movements are used to snatch resting prey from leaves (Tables 5.3, 5.4). The best predictor of flying is broadleaf substrate (Fig. 5.3). Across all foraging events of all species combined, standpicking from broadleaves forms 35% of all foraging movements, with flying movements to take prey resting on leaves very frequent. In contrast standpicking from branches forms 78% of all observations, from twigs 71%, and from coniferous needles 52%.

The ecological-morphological correlations depicted in Figure 5.2 were observed in a previous study in Kashmir, on an overlapping set of species (Price

1991). They also appear to be present even among those four species in the east which are not present in the west (Fig. 5.2). I conclude that despite differences in vegetation and climate, patterns in niche segregation and variation among species remain broadly comparable across regions. Together, the ecological measures explain ~60% of the total measured morphological variation among species, based on the correlations reported in the legend to Figure 5.2 and online Table 5.1. This suggests that the three niche dimensions I have measured capture a large fraction of the adaptive differentiation in the foraging ecology of these species.

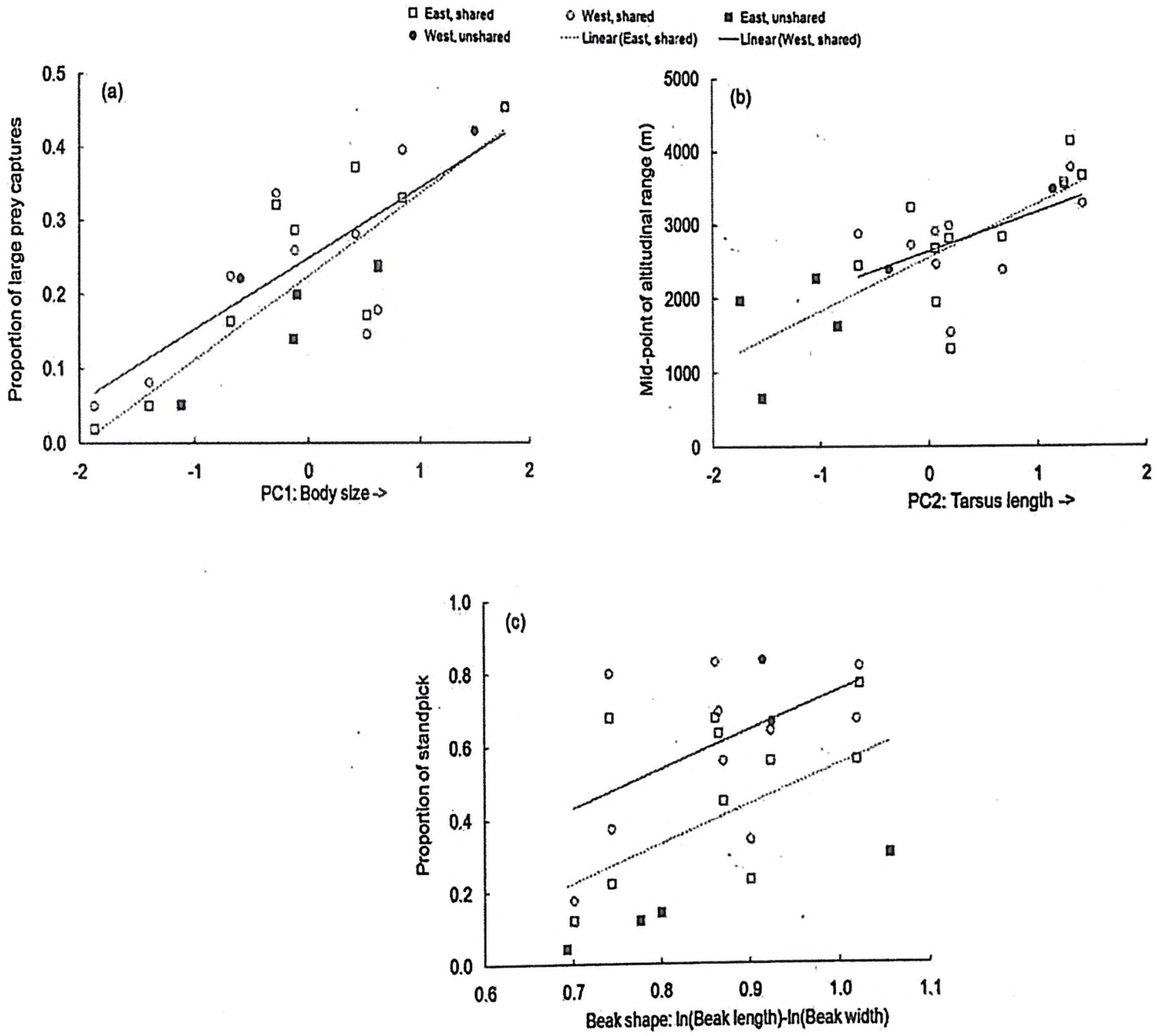


FIGURE 5.2. Ecomorphological associations among the species breeding in the east and west. (a) Body size (morphological PC1) is correlated to proportion of large prey captures across sites and west; (b) Tarsus length (morphological PC2) is positively correlated with mid-point of altitudinal range in the east and west. (c) Beak-shape is positively correlated to proportion use of standpick as a foraging method in the east and west.

TABLE 5.3. Proportion of foraging manoeuvres, large prey intake and mean foraging heights for species breeding in the west and the east. Standard errors (on the untransformed data) are indicated. *N* indicates sample size.

	East						**West**					
Species	Standpick	Hoverpick	Flypick	Flycatch	Large prey	N	Standpick	Hoverpick	Flypick	Flycatch	Large prey	N
P. cantator	0.31 (0.06)	0.14 (0.05)	0.55 (0.07)	-	0.20 (0.05)	55	-	-	-	-	-	-
S. castaniceps	0.12 (0.04)	0.22 (0.05)	0.63 (0.06)	0.03 (0.02)	0.05 (0.03)	58	-	-	-	-	-	-
S. affinis	0.14 (0.05)	0.05 (0.03)	0.76 (0.06)	0.05 (0.03)	0.24 (0.06)	48	-	-	-	-	-	-
S. poliogenys	0.04 (0.02)	0.08 (0.03)	0.88 (0.03)	-	0.14 (0.04)	93	-	-	-	-	-	-
S. burkii	0.12 (0.04)	0.09 (0.04)	0.76 (0.06)	0.03 (0.02)	0.17 (0.05)	58	0.18 (0.05)	-	0.74 (0.06)	0.09 (0.04)	0.15 (0.06)	34
S. whistleri	0.22 (0.06)	0.08 (0.04)	0.70 (0.06)	-	0.24 (0.06)	54	0.38 (0.07)	0.02 (0.02)	0.60 (0.07)	-	0.08 (0.04)	48
P. chloronotus	0.23 (0.05)	0.52 (0.07)	0.25 (0.06)	-	0.05 (0.03)	60	0.34 (0.06)	0.48 (0.07)	0.18 (0.05)	-	0.08 (0.04)	61
P. xanthoschistos	0.56 (0.07)	0.07 (0.03)	0.37 (0.06)	-	0.29 (0.06)	59	0.64 (0.06)	0.07 (0.03)	0.24 (0.06)	0.06 (0.03)	0.26 (0.04)	123
P. pulcher	0.56 (0.07)	0.18 (0.05)	0.26 (0.06)	-	0.16 (0.05)	55	0.67 (0.06)	0.08 (0.04)	0.25 (0.06)	-	0.22 (0.05)	49
P. reguloides	0.68 (0.04)	0.04 (0.02)	0.28 (0.04)	-	0.38 (0.04)	136	0.83 (0.03)	0.06 (0.02)	0.11 (0.03)	-	0.28 (0.06)	53
P. maculipennis	0.68 (0.06)	0.09 (0.04)	0.23 (0.06)	-	0.02 (0.02)	53	0.80 (0.06)	0.08 (0.04)	0.12 (0.04)	-	0.11 (0.04)	65
P. trochiloides	0.63 (0.06)	0.1 (0.04)	0.27 (0.06)	-	0.33 (0.06)	63	0.69 (0.06)	0.06 (0.03)	0.24 (0.05)	0.01 (0.01)	0.4 (0.05)	85
P. affinis	0.77 (0.08)	0.06 (0.04)	0.17 (0.07)	-	0.35 (0.08)	31	0.82 (0.07)	0.04 (0.04)	0.14 (0.06)	-	0.34 (0.09)	31
P. magnirostris	0.45 (0..09)	0.11 (0.06)	0.38 (0.08)	0.06 (0.04)	0.46 (0.09)	33	0.56 (0.09)	0.08 (0.05)	0.32 (0.08)	0.04 (0.03)	0.46 (0.09)	35
P. humei	-	-		-	-	-	0.67 (0.04)	0.05 (0.02)	0.26 (0.04)	0.02 (0.01)	0.22 (0.04)	117
P.occipitalis	-	-		-	-	-	0.84 (0.05)	0.05 (0.03)	0.10 (0.04)	0.02 (0.01)	0.43 (0.06)	61

TABLE 5.4. Proportion of substrate use and mean foraging heights for species breeding in the west and the east. Standard errors (on the untransformed data) are indicated. *N* indicates sample size.

	East						West					
Species	Perch height (m)	Leaf	Branch	Twig	Needles	Air	Perch height (m)	Leaf	Branch	Twig	Needles	Air
P. cantator	10.02 (0.81)	0.65(0.06)	0.18(0.05)	0.16(0.05)	-	-	-	-	-	-	-	-
S. castaniceps	6.51 (0.47)	0.90(0.04)	0.03(0.02)	0.03(0.02)	-	0.03(0.02)	-	-	-	-	-	-
S. affinis	2.22 (0.19)	0.83(0.05)	0.02(0.02)	0.13(0.05)	-	0.02(0.02)	-	-	-	-	-	-
S. poliogenys	4.23 (0.24)	0.95(0.02)	0.01(0.01)	0.04(0.02)	-		-	-	-	-	-	-
S. burkii	2.05 (0.17)	0.79(0.05)	-	0.17(0.05)		0.03(0.02)	1.69 (0.16)	0.76(0.07)	0.03(0.03)	0.09(0.05)	0.03(0.03)	0.09(0.05)
S. whistleri	4.16 (0.38)	0.83(0.05)	0.09(0.04)	0.07(0.04)	-		3.19 (0.54)	0.73(0.06)	0.08(0.04)	0.15(0.05)	0.04(0.03)	-
P. chloronotus	9.02 (0.55)	0.52(0.06)	-	0.02(0.02)	0.46(0.06)	-	11.06 (0.88)	0.49(0.06)	-	0.05(0.03)	0.46(0.06)	-
P. xanthoschistos	10.61 (0.58)	0.58(0.06)	0.15(0.05)	0.27(0.06)		-	7.49 (0.45)	0.45(0.04)	0.04(0.02)	0.08(0.02)	0.37(0.04)	0.06(0.02)
P. pulcher	2.37 (0.21)	0.47(0.07)	0.04(0.03)	0.18(0.05)	0.31(0.06)	-	6.11 (0.73)	0.43(0.06)	0.20(0.05)	0.08(0.04)	0.29(0.06)	-
P. reguloides	8.61 (0.41)	0.68(0.04)	0.10(0.03)	0.21(0.04)	0.01(0.01)	-	10.69 (0.78)	0.57(0.07)	0.13(0.04)	0.23(0.06)	0.08(0.04)	-
P. maculipennis	5.56 (0.65)	0.72(0.06)	0.09(0.04)	0.13(0.05)	0.06(0.03)	-	9.03 (0.63)	0.49(0.06)	0.23(0.05)	0.26(0.05)	0.02(0.02)	-
P. trochiloides	2.71 (0.18)	0.52(0.06)	0.05(0.03)	0.11(0.04)	0.32(0.06)	-	4.5 (0.33)	0.45(0.05)	0.04(0.02)	0.15(0.04)	0.35(0.05)	0.01(0.01)
P. affinis	0.92 (0.11)	0.32(0.08)	0.10(0.05)	0.19(0.07)	0.39(0.09)	-	0.86 (0.09)	0.32(0.08)	0.10(0.05)	0.16(0.07)	0.42(0.09)	-
P. magnirostris	3.96 (0.64)	0.82(0.07)	0.03(0.03)	0.09(0.05)	-	0.06(0.04)	4.59 (0.52)	0.63(0.08)	0.03(0.03)	0.14(0.06)	0.09(0.05)	0.11(0.05)
P. humei	-	-	-	-	-	-	6.82 (0.38)	0.44(0.05)	0.18(0.04)	0.09(0.03)	0.27(0.04)	0.02(0.01)
P.occipitalis	-	-	-	-	-	-	9.55 (0.65)	0.52(0.06)	0.11(0.04)	0.13(0.04)	0.21(0.05)	0.02(0.02)

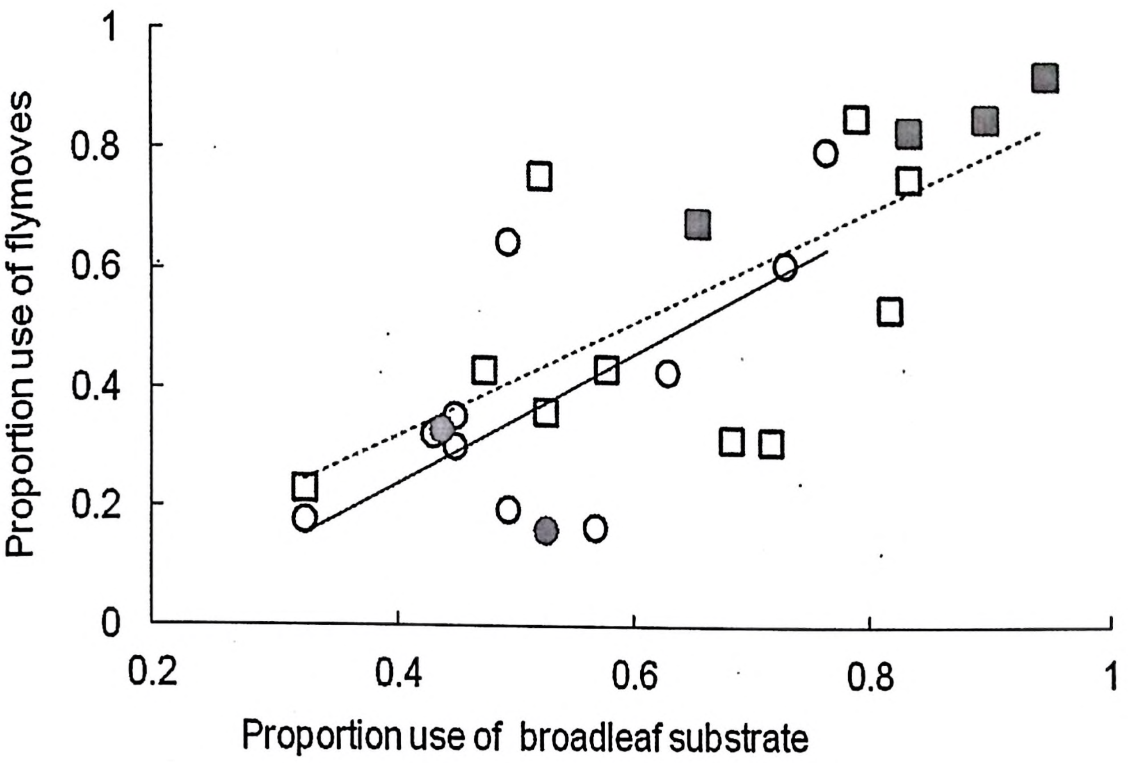


FIGURE 5.3. Relationship between use of flymoves as a foraging method and use of broadleaf as a foraging substrate for the species in the east (squares, r = 0.75, N = 14, P = 0.002; correlations of independent contrasts: r = 0.54, N = 13, P = 0.046) and the west (circles, r = 0.68, N = 12, P = 0.015; correlations of independent contrasts: r = 0.60, N = 11, P = 0.04).

5.3.3 Geographical variation

Under the historical non-equilibrium hypothesis species should generalize in species-poor communities. Given the similarity in community structure between regions, which implies that much of niche space is qualitatively similar in the two regions, I can refine the prediction of the historical hypothesis, based on the ecological characteristics of those close relatives which are missing from the species poor region. Four species are confined to the east, whereas 10 eastern species extend west. Under the historical hypothesis, therefore, these 10 species should expand their niches in the direction of the absent species (Fig. 5.1). In the next sections, I evaluate geographical variation in each of the three identified niche dimensions:

Prey size.- The proportion of large prey captures does not vary geographically within species (paired t-test using species as replicate, $t_9 = 0.71$, $P = 0.94$). This is consistent with both the historical (competitor based) and ecological (resource based) models. First, with respect to missing congeners, the average body size (PC1) and prey size of species which are restricted to the east is similar to those species that extend their range to the west (see Fig. 5.2a: body size: two sample t-test $t_{12} = 0.28$, $P = 0.78$, phylogenetic correction using independent contrasts, $P = 0.24$; proportion of large prey in diet: $t_{12} = 0.9$, $P = 0.38$, phylogenetic correction, $P = 0.15$). Second, with respect to the ecological hypothesis the proportion of large arthropods does not differ significantly between regions (Fig. 3.2).

Altitudinal distribution.- The four species restricted to the east occur at relatively low elevations (Fig. 5.4; two sample t-test: maximum elevation: $t_{12} = 3.46$, $P = 0.005$, phylogenetic correction, $P = 0.008$; mid-point elevation: $t_{12} = 2.82$, $P = 0.02$, phylogenetic correction, $P = 0.02$), so I predicted that under the historical hypothesis, those species held in common between regions should expand altitudinal ranges downwards in the west. In fact altitudinal ranges contract to the west (Fig. 5.5, paired t-test: $t_9 = 3.37$, $P = 0.01$). Such range contractions are consistent with the ecological hypothesis, because high prey abundances are found over a smaller altitudinal band in the west (Fig. 3.2).

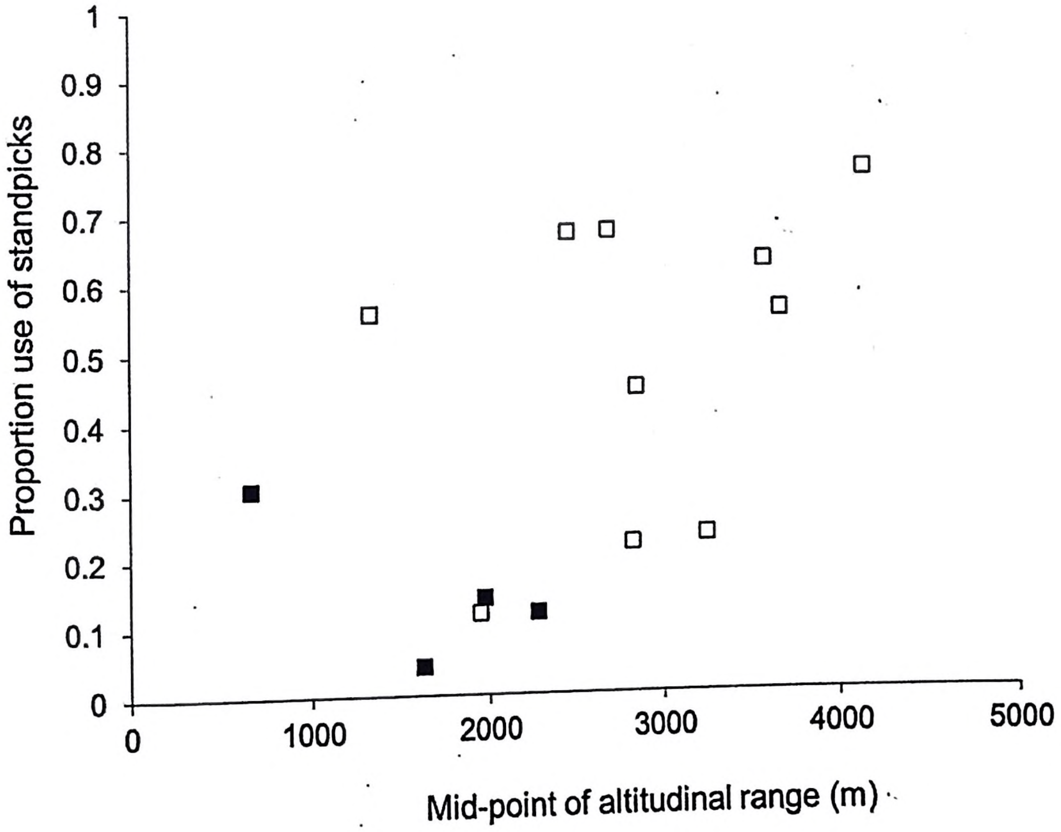


FIGURE 5.4. Scatterplot of proportion use of standpick as a foraging method against mid-point of altitudinal range for all observations in the east, redrawn from Fig. 5.2. Filled symbols are for those species absent from the west.

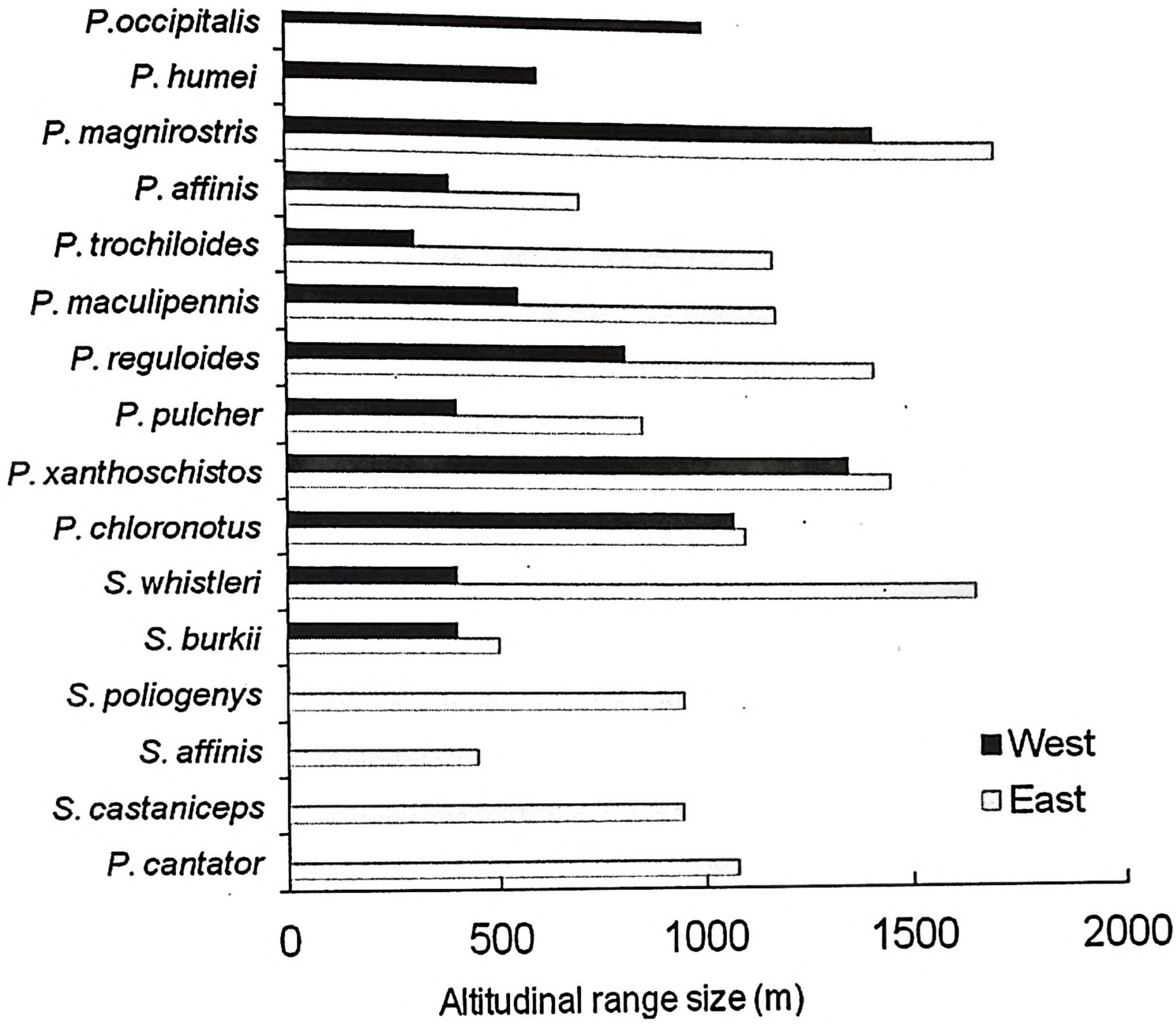


FIGURE 5.5. Altitudinal range sizes (in metres) in the east and the west.

Feeding method. - The four species restricted to the east capture prey exceptionally often in flight (Fig. 5.4; two sample t-test: $t_{12} = 3.28$, $P = 0.01$, phylogenetic correction, $P = 0.02$). Therefore, under the historical hypothesis, I expect species with large ranges to have a higher fraction of flying movements in the west, exploiting niches vacated by the eastern species. In fact, species used less flying movements in the west than in the east (Fig. 5.6, paired t-test on arcsine square root transformed data: $t_9 = 2.84$, $P = 0.02$).

The use of fewer flying movements in the west is consistent with responses to resource distributions. While broadleaf was the primary substrate used in both regions, the use of broadleaf was significantly lower in the west as compared to the east (paired t-test comparing proportions of observations on broadleaf, $t_9 = 4.01$, $P = 0.003$), and as shown in Fig. 5.3 broadleaf is a significant predictor of foraging technique within regions. In order to partition contributions of region and substrate (broadleaf, needle, twig, branch and air) to foraging habit in the paired test, I used the mixed-effects model in the package lme4 in R (Bates et al. 2010) with the 10 species as a random effect (Pinheiro and Bates 2000). Significance of the fixed effects was obtained from 10,000 Markov chain Monte Carlo simulations, performed using the pvals.fnc function in the languageR package (Baayen 2008). I found that while use of broadleaved substrates remained significantly different between regions (MCMC interval: -1.49 to -0.63, P = 0.0001) but the difference in foraging techniques disappears once substrate is controlled for (MCMC interval: -0.10 to 0.21, P = 0.48). Thus differences in foraging method across regions are explained as a response to differences in foraging substrates.

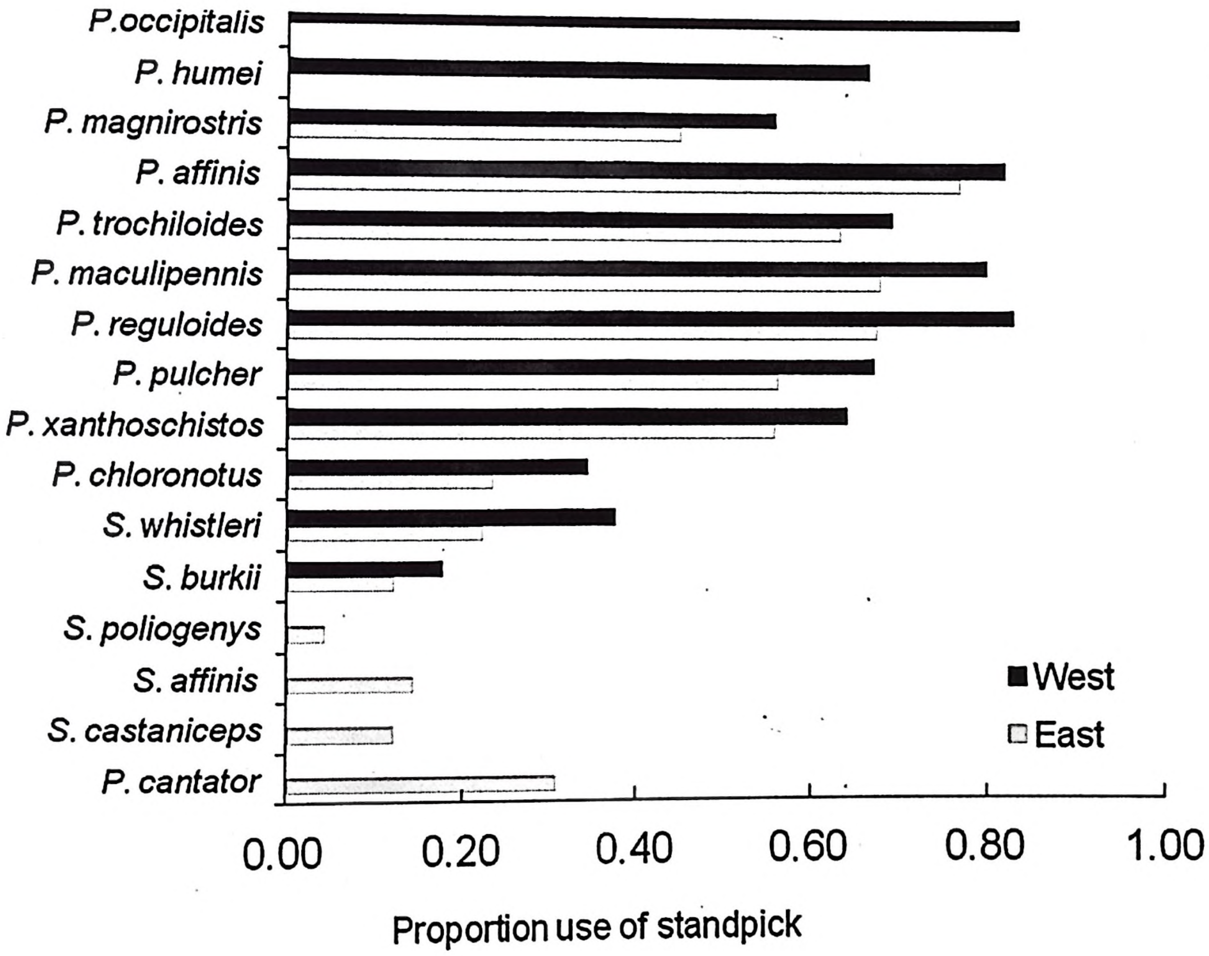


FIGURE 5.6. Proportion use of standpick as a foraging method by species in the east and the west.

5.3.4 Resource limitation

Evidence so far implicates underlying resource distributions as drivers of geographic variation in foraging behaviour. These findings are strengthened by strong correlates between arthropod and species abundance along the elevational gradients in both the east (r = 0.94, N = 8, P = 0.0004) and the west (r = 0.81, N = 7, P = 0.03), as well as between regions (Fig. 5.7). Such strong correlations imply that as resources decrease, population sizes decrease, and finally decline to zero at the range limit.

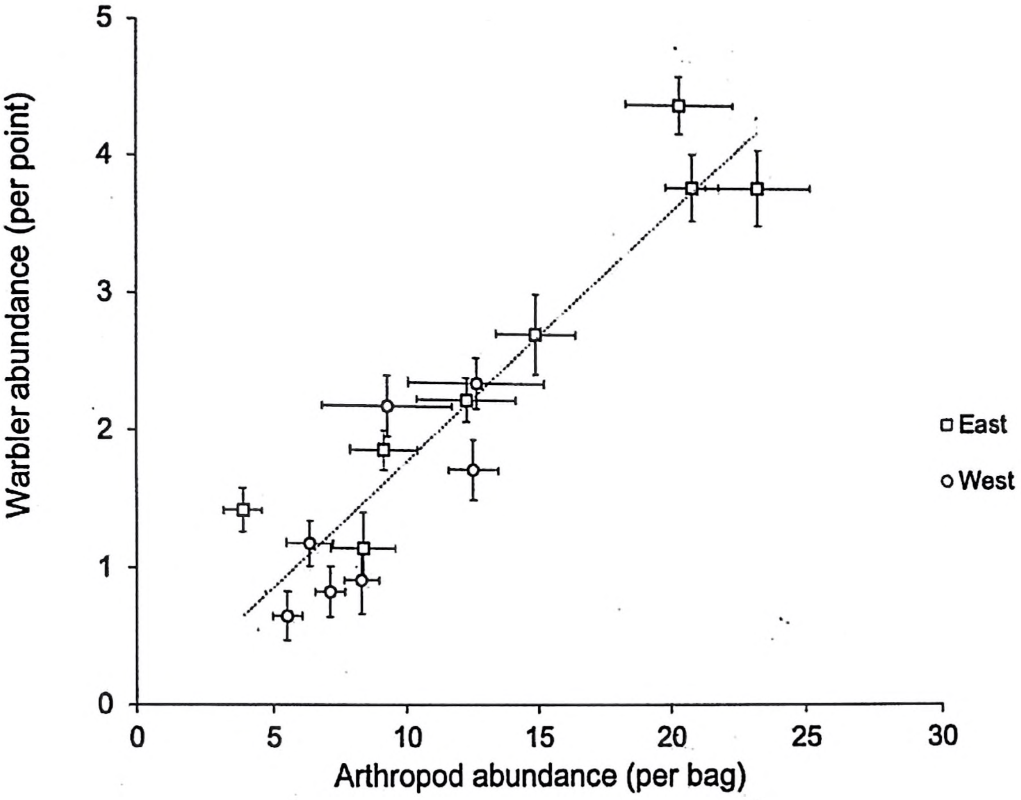


FIGURE 5.7. Relationship between average warbler abundance (per point count station) and arthropod abundance (per bag) over 500m elevational bands combined across sites (r = 0.89, N = 15, P = 0.0001) in the east and the west. Standard errors on warbler abundance and arthropod abundance are based on points and bags, respectively.

5.4 DISCUSSION

Several historical non-equilibrial explanations for the latitudinal diversity gradient have been proposed, all of which assume that temperate regions are further below any possible carrying capacity than tropical regions (Mittelbach et al. 2007). A historical explanation for a reduction in species diversity from east to west along the Himalayas is plausible, especially as it relates to Pleistocene climate change (Price et al. 2011). The western Himalayas were apparently treeless at multiple periods during the Pleistocene (Ray and Adams 2001), during which time forest species may have withdrawn to the east. The implication is that colonization of the west has been relatively recent, and plausibly, many species have failed to become established over the last 18,000 years since the last glacial maximum.

In many bird groups as shown here for the Phylloscopidae, those eastern species present at higher elevations are most likely to have ranges extending west (Price et al. 2011). Several explanations for this include (1) a greater effect of river barriers at lower elevations and (2) climate tracking: higher elevations in the east experience similar climates to higher elevations in the west, whereas climates at lower elevations in the east and west are more different (Price et al. 2011). In these scenarios, it is the higher elevation species, which have preferentially re-colonized the west from the east. Then, if history alone accounts for the lack of species in the west, the high elevation species should expand their foraging niches to consume resources of the absent lower elevation species. The prediction appears robust to effects from competitors outside the group I studied, because the decline in species richness is pervasive across many groups, and in many of these groups it is the lower elevation species which fail to extend their ranges west (Price et al. 2011).

In the Phylloscopidae I found no evidence in support of this hypothesis. Species which occur in both the east and west do not have broader elevational ranges when they are in the west, nor do they use flying manoeuvres more when in the west, as would be expected if they were expanding into the niches of the missing eastern Phylloscopidae. Instead they have narrower elevational ranges and flypick less. I attribute these patterns to be a direct response to shifting resources. In particular, a lower proportion of broadleaf and greater proportion of conifer in the west (Table 5.2) favors increased standpicking. Further, the generally drier and cooler conditions, with lower foliage density (Table 5.2) and lower prey abundances (Fig. 3.1) reduce the elevational range over which any given species persists. Finally, strong correlations of abundance with resources (Fig. 5.7) lead to the expectation that as resources decline still further to the west, species drop out.

I made predictions about competitive effects based on what species in the west should do in the absence of several eastern confamilials, because that is the direction over which total species richness declines. Nevertheless, two Phylloscopus species in my study are restricted to the west, and not found in the east, so the predictions could also be developed using a west to east focus. These two species (Phylloscopus humei, P. occipitalis) forage with a high proportion of standpicking (Table 5.3), which is consistent with the general shift in the widespread species towards more standpicking in the west and inconsistent with the historical hypothesis.

Species become more specialized in the more temperate part of their range. This contradicts an impression in comparisons across species, which is that species are more generalized in temperate regions in response to fluctuating resources (Vázquez and Stevens 2004; Valentine et al. 2008). Indeed, some ecological models, where communities are saturated, predict increased generalization in temperate regions. First, if resources fluctuate wildly a specialist species will be unable to persist (MacArthur 1972; Vázquez and Stevens 2004; Valentine et al. 2008). Second, climatic variability may drive a broader physiological tolerance resulting in a species ability to expand range across climatic regimes and hence habitats. This idea has been specifically applied to elevational gradients (Kozak and Wiens 2007; McCain 2009, reviewed by Ghalambor et al. 2006). Some comparative cross-species comparisons do find elevational ranges to be generally broader in the temperate region than in the tropics (Ghalambor et al. 2006; Kozak and Wiens 2007; McCain 2009), but others have not (Cadena et al. 2012). Here I have found narrower elevational ranges within species in more temperate regions, and related this to declining resource diversity, rather than any direct impact of climatic variability.

A pattern of increased generalization in the temperate across several niche dimensions apart from elevation gradients has been hard to demonstrate (Vázquez and Stevens 2004). Where and if it is present, generalization may reflect reduced competition during the time of year when food resources are abundant and niche breadth often measured (Price et al. 2011). Such a high ratio of resources to individuals at high continental latitudes may go some way towards explaining the finding of Ricklefs (2011) that the make-up of breeding bird communities across North America has little compelling pattern. In this regard, Irwin (2000) found that along a latitudinal gradient into Siberia food abundance increased but warbler abundance decreased. The decline in warblers was attributed to distance from the wintering grounds in India and associated costs of migration. By contrast in my low latitude study, warbler abundances and food abundance are positively correlated (Fig. 5.7). Thus one value of the Himalayan system is that food resources in the breeding season are more strongly limiting, resulting in the expectation of ecologically driven patterns.

My findings have consequences for empirical tests of character displacement. The quantitative genetic models of Case and Taper (2000), and Goldberg and Lande

(2006) consider that the optimal phenotype changes linearly across space, thereby tracking a shift in the average dimensions of some resource, but the width of the (Gaussian) resource distribution remains constant (Fig. 5.1). Goldberg and Lande (2006) showed that, despite competitive interactions driving divergence, species often show greater differences in allopatry in response to different positions of the resource optima than in sympatry, where each species is selected towards the same optimum (Fig. 5.1). These models have led to novel approaches in testing for character displacement (Goldberg and Lande 2006; Meiri et al. 2011), which, following Grant (1972) rely on extrapolating patterns in allopatry into sympatry. However, they do depend on simple assumptions about resource distributions (Goldberg and Lande 2006).

Here I have directly measured resources, and in Figure 5.8 I illustrate how resource distributions may often be complex, making inferences about character displacement misleading. To make the comparison with theory (Fig. 5.1) as close as possible, I map the most closely related pair of sister species in our dataset *(Phylloscopus occiptalis* and *P. reguloides),* which also have largely parapatric ranges, across a single resource dimension, elevational distribution (Fig. 5.8). Despite apparent character release, with both species having broader elevational ranges and habitat utlilization in allopatry than sympatry, extrapolations from allopatry to sympatry lead to convergence in sympatry, presumably reflecting common responses to a changing resource base (Fig. 5.8) and other related competitors (notably *P. xanthoschistos,* which breeds at lower elevations). Meiri et al. (2011) also inferred a predominant role for resources in shaping geographical variation in a recent study of weasels. However, in their study, resources were not measured, but rather were inferred to vary linearly from allopatry into sympatry. Because resources may often vary in unexpected ways and have strong influences on trait evolution (Fig. 5.8), it seems necessary to measure and control for them if character displacement is to be assessed (Schluter et al. 1985). For example, Pfennig et al. (2006) found that two species of spadefoot toad only coexist when resources are diverse (i.e., in accord with the ecological rather than the historical model), but were able to infer character displacement from experimental manipulations of both congeners and resources.

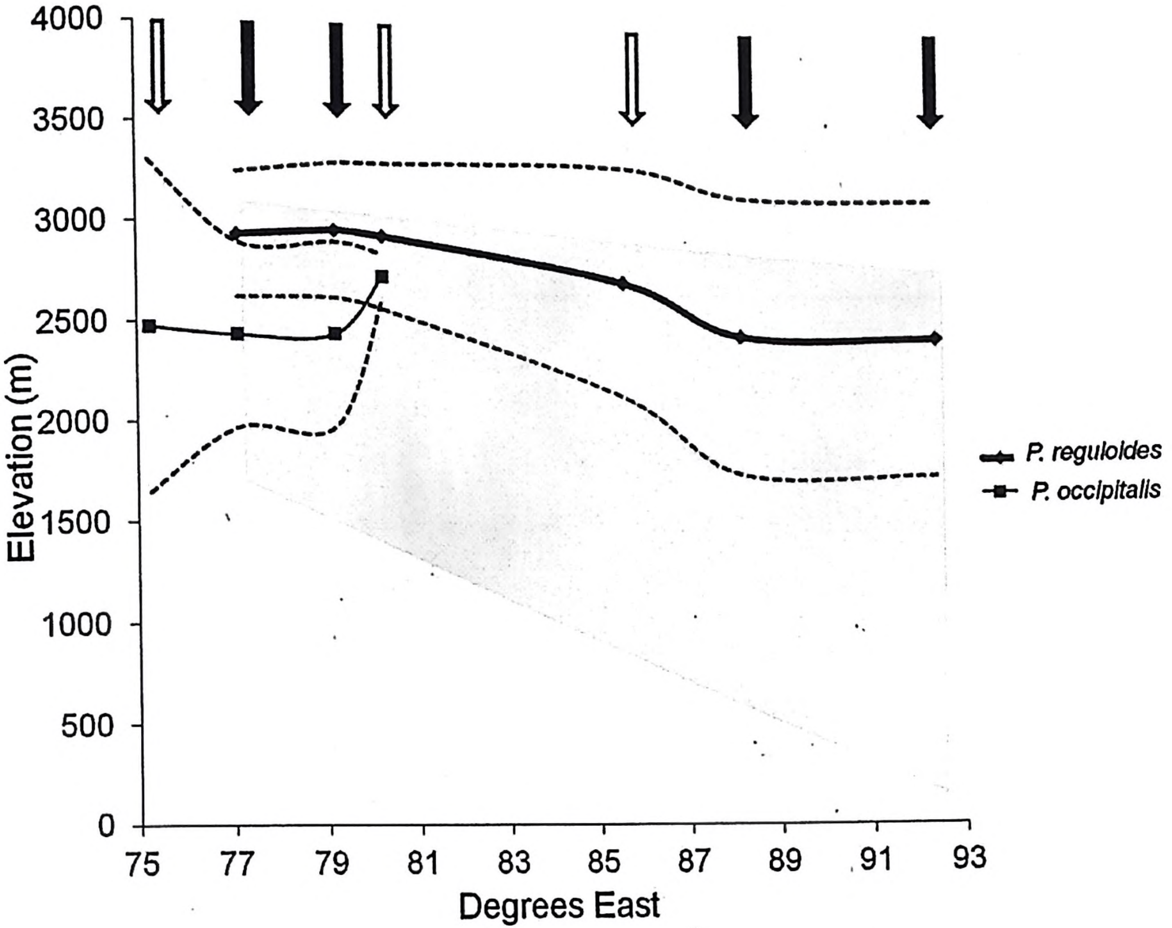


FIGURE 5.8. Altitudinal distributions of *Phylloscopus occipitalis* and *P. reguloides* across the Himalayas based on extrapolation from locations indicated by the arrows. Filled arrows indicate points from this study, where both birds and arthropods were studied. Open arrows are for birds only and taken from Price et al. (2003) and Price (unpublished observations). Dashed lines indicate the upper and lower limits of breeding distributions and solid line the midpoint. The shaded region indicates the altitudinal range within which abundance of large arthropod prey (> 4mm in body length) is greater than one per bag. No prey abundance measures are available west of 77°E. The western limit of *P. reguloides* and eastern limit of *P. occipitalis,* as drawn are very close to the actual limits.

In summary, the results imply that species diversity is lower in the west not for historical reasons such as the impact of Pleistocene climate, but because resources are less diverse in the contemporary temperate climate. These conclusions apply specifically to the Phylloscopidae, which are migratory. They are a group likely to have high dispersal capabilities and rather easily cross barriers and colonize new areas. Plausibly, other less dispersive groups would show a greater imprint of history, and I predict that in these groups, species straddling the region will show niche expansions in the species-poor northwest.

CHAPTER 6

Phylogenetic and ecomorphological community structure

6.1 INTRODUCTION

Determining the processes shaping community assembly has been a central theme in ecology (Cody and Diamond 1975; Brown 1995; Ricklefs 2006). Ecological differences between co-occurring species within a community are an outcome of diverse ecological processes acting on a common ancestor (Webbe et al. 2002). Mechanisms including climatic tolerances ("environmental filtering", Weiher and Keddy 1995; de Bello et al. 2006), competition for resources (Tilman 1982), negative density-dependence (Janzen 1970; Connell 1971), dispersal limitation and demographic stochasticity (Hubbell 2001), may therefore, be inferred from relationship between the observed phylogenetic and ecological distribution of functional traits (Webb et al. 2002; Cavender-Bares et al. 2004; Kraft et al. 2007).

In recent years, the availability of well-supported phylogenies has greatly facilitated attaining a better understanding of the ecological and evolutionary processes that underlie spatial variation in community composition (Stevens 2006; Emerson and Gillespie 2008; Graham and Fine 2008; Algar et al. 2009; Cavender-Bares et al. 2009; Vamosi et al. 2009). This modern framework integrates traditional nomenclatural approach based on taxonomic similarities (Elton 1946) with information on the phylogenetic relatedness between species constituting the communities, towards elucidating the relative contributions of niche-based and neutral processes in shaping communities (Webb et al. 2002; Kraft et al. 2008; Kembel 2009; Swenson and Enquist 2009). The assessment of the phylogenetic structure of each community is followed by comparison with the patterns expected under some null model of community assembly, to infer whether the community is significantly 'clustered' or 'over-dispersed' (Webb et al. 2002). In general, in communities where competition is the driving force, species tend to be distant relatives (over-dispersion), though trait convergence could lead to similar pattern (Kraft et al. 2007). Alternatively, Webb et al. (2002) argued that phylogenetic clustering could result due to environmental filtering on traits showing phylogenetic signal, or could be a consequence of ecological divergence of closely-related species to facilitate co-existence. Therefore, interpretation of mechanisms shaping the phylogenetic structure of communities is not possible without examining the phylogenetic distribution of relevant ecological traits for the species concerned (Losos 2008; Pearman et al. 2008; Machac et al. 2011). Given recent analytical advances, equivalent measures of functional-trait based indices of community structure can be quantified and correlated to the observed phylogenetic structure (Kraft and Ackerly 2010; Graham et al. 2012), which allow us to attain greater insights into the processes that structure communities than can be uncovered using either of the approaches alone (Swenson and Enquist 2009).

While comparison of empirical and null assemblages enables detection of assemblage structures that deviate from random expectations, the direction of such deviations, especially along spatial and environmental gradients, gives insights into the processes governing species assembly (Kluge and Kessler 2011). Given that species diversity and composition often vary systematically along elevational gradients corresponding to changes in various environmental and biotic factors (e.g. competition) over small distances, studies using community phylogenetic approaches to uncover processes driving species diversity patterns along elevational gradients are gaining popularity (Bryant et al. 2008; Graham et al. 2009; Machac et al. 2011; Parra et al. 2011). Although elevation is merely a surrogate for a suite of regulators and resources that limit species distributions (Rahbek 2005), these studies treat elevation *per se* as a covariate influencing variation in phylogenetic community structure. Given that the relationship between these covarying factors and elevation is complex and often context-dependent, identifying ecologically meaningful causal factors is essential in order to explain variation in species richness along elevational gradients.

Here, in an effort to assess the factors structuring elevational diversity patterns, I examine the patterns of phylogenetic structure of Old World leaf warbler communities along six elevation gradients distributed in the eastern and western regions of the Himalayas. The Old World leaf warblers belonging to the *Phylloscopus* and *Seicercus* clade are dominant components of warbler communities in most parts of Asia and are represented by 21 species in the Himalayas (Johansson et al. 2007; Price 2010). These warblers breed along the elevational gradients and range across the Himalayan bioclimatic gradient from the wetter, species-rich east to the drier, relatively species-poor west (Price et al. 2011). Phylogenetic analyses of Phylloscopidae suggest that the Himalayan species assemblage is predominantly composed of immigrants from mountainous regions of Central China and tropical/subtropical areas of South-east Asia (Johansson et al. 2007). Elevational position (correlated to tarsus length), prey size (correlated to body size) and feeding method (correlated to beak shape) are the principal axes along which species segregate during the breeding season (Price 1991), giving rise to distinct species communities as we move along the mountain slopes.

In this study, I examined the phylogenetic community structure and dispersion metrics of three ecomorphological traits (body size, beak shape and tarsus length) of leaf warbler communities distributed along elevational gradients in the east and west Himalayas. While tarsus length is known to vary along the elevational gradient, variation in traits across the larger precipitation gradient is yet to be explored. Furthermore, in contrast to earlier studies examining processes shaping the phylogenetic structure of much larger assemblages using only species occurrences and remotely-sensed climatic variables, I focused on a smaller assemblage (16 species) using field-collected measures of assemblages, resource abundances (Chapter 3) and foraging behaviour (Chapter 5) to examine similar associations. By combining information on historical origin of species, phylogenetic structure of communities, phylogenetic distribution of relevant ecological traits as well as variation in ecological dispersion metrics of functional traits among assemblages across the Himalayan bioclimatic gradient, the processes structuring the community are drawn.

6.2 ANALYTICAL METHODS

6.2.1 Species assemblages

To accurately determine site-specific species assemblages, I established altitudinal transects following available forest trails on each of these sites. For each site, I derived the species assemblage and relative abundances using fixed-radius point counts conducted within 100m altitudinal stretches of the transects above and below the site (i.e. within 200m altitudinal belts). At every 25m (measured with an altimeter) along the transects, I counted all breeding birds seen or heard within ~ 25m radius for 5 minutes. For every site data from two trails or 16 point count stations were used to ensure that each site received the same sampling effort. I walked each transect twice and conducted the census during the first four hours in the morning (0600-1000 hrs). The accuracy (Price and Jamdar 1991) and repeatability (Price et al. 2003) of this census method makes it very appropriate for obtaining species occurrences and reliable estimates of relative abundances of species.

6.2.2 Climatic variables

I extracted climatic data for each of the sites using ArcMap 10 from the WorldClim database with 30-s spatial resolution (<www.worldclim.org>; Hijmans et al. 2005) to examine the relationship between climate and the phylogenetic community structure of breeding leaf warblers. WorldClim data are associated with considerable uncertainty, particularly in the Himalayas, owing to existence of few climate stations (Hijmans et al. 2005) and possibility of considerable variation in climatic conditions within 1-km^2. To check for possible bias, I correlated long-term climate data from eight Indian Meteorological Department weather stations (http://www.imd.gov.in/) with WorldClim data and found them to be significantly correlated ($r > 0.9$, $P < 0.05$). Therefore, I focussed on four Bioclim variables (annual precipitation, precipitation seasonality, maximum temperature and temperature seasonality) which have been used to adequately represent the climate of the study area and describe its influence on range limits of Himalayan birds (Price et al. 2011).

6.2.3 Ecomorphological traits

In studies on breeding communities, strong correlations between aspects of their foraging ecology and morphology have been identified which facilitate ecological segregation (Price 1991; Forstmeier and Kessler 2001; Fig. 5.2). These ecomorphological associations are (1) body size (morphological PC1, based on principal component analysis using species means for six morphological variables, see Table 5.1) strongly correlated with prey size, (2) tarsus length (morphological PC2), which is strongly correlated with breeding elevation/habitat associations, and (3) the beak shape {ln (beak length)-ln (beak width)}, correlated to feeding method, notably the proportion of prey captured while in flight.

6.2.4 Tests for niche conservatism

For phylogenetic analyses, I used the molecular-based ultrametric phylogeny published in Johansson et al. (2007). The tree was pruned to include only the 16 species found breeding in sites sampled in this study (Fig. 6.1). Since the assumption of phylogenetic niche conservatism is pivotal to the community phylogenetic approach (Losos 2008; Wiens et al. 2010), prior to assessing the phylogenetic structures of local communities, I computed Blomberg et al.'s (2003) *K* statistic independently for all the three morphological niche axes (PC1, PC2 and beak shape) as a measure of phylogenetic signal. The significance of the measure was assessed by randomizing the data across the tips (Blomberg et al. 2003). While K = 1 for rates of trait evolution consistent with Brownian motion, K < 1 indicates more evolution at the tips so that that closely related species are less similar than distantly related species owing to character displacement or trait convergence (Ackerly and Donogue 1998; Cavender-Bares et al. 2004). Conversely, K > 1 implies niche conservatism suggesting that phylogenetic similarity is a strong predictor of similarity in the ecomorphological axes (Losos 2008), especially at present.

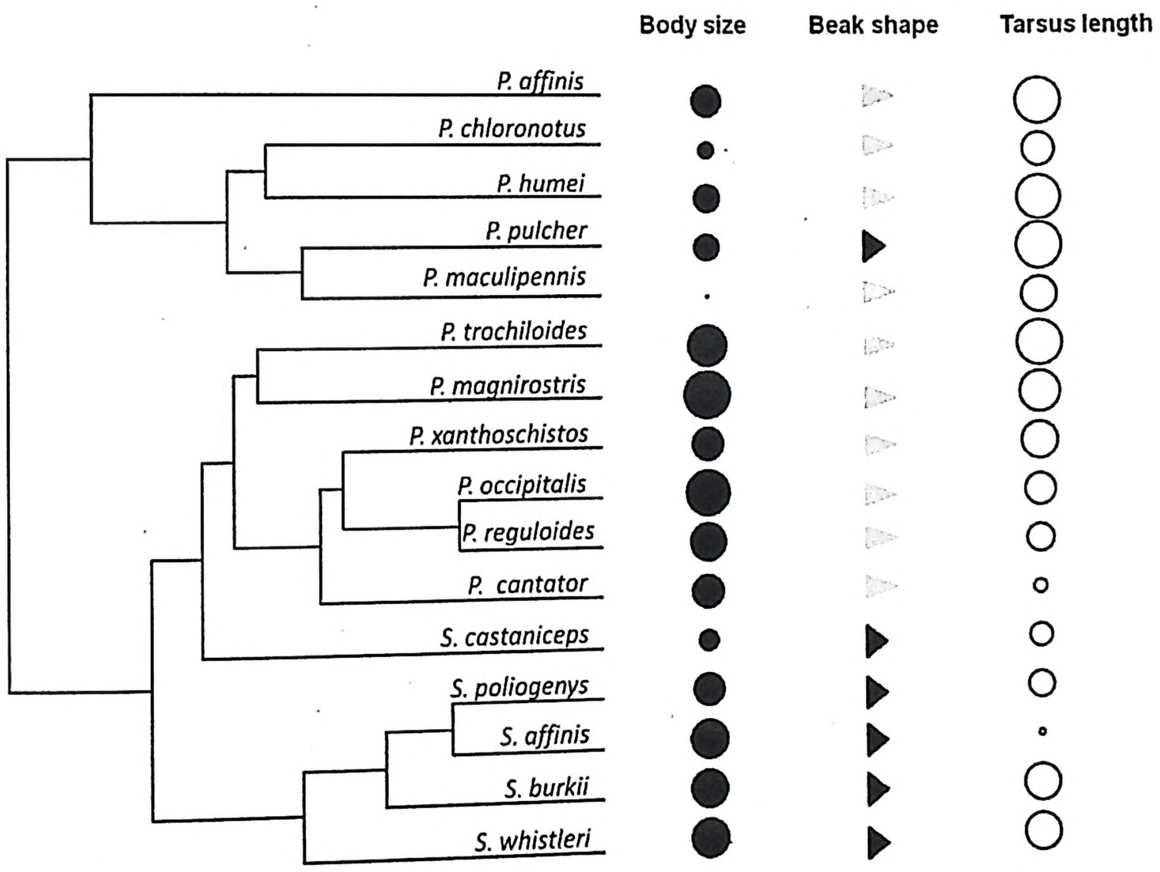


FIGURE 6.1 Phylogeny of the Himalayan leaf warbler species. The three functional traits are represented next to the tips of the phylogeny. The sizes of the bubbles for body size (morphological PC1) and tarsus length (morphological PC2) are based on PC scores (see Figs. 5.1, Fig 1, Appendix 1). The beak size is either slender (grey) or wide (black) based on beak shape scores (see Fig. 1, Appendix 1).

6.2.5 Phylogenetic structure

To describe the phylogenetic structure of local assemblages from the sixteen sites, I calculated mean pair-wise distance (MPD) (Webb 2000; Webb et al. 2002). MPD presents an estimate of the mean phylogenetic distance among all pair-wise species combinations present in a community within each site. I subsequently calculated net relatedness index (NRI), which describes the difference between the mean pair-wise phylogenetic distance (MPD) among all pair-wise combinations of species within a local community to the MPD of samples of the same size drawn from randomly generated null communities, standardized by the standard deviation of the null communities (Webb et al. 2002, 2008) as follows:

$$NRI = -1 \times (MPD_{obs}-MPD_{null})/SD\ (MPD_{null})$$

where, MPD_{obs} refers to the MPD estimated from the sample, MPD_{null} represents the MPD calculated for 999 null communities and SD refers to the standard deviation. I assessed the significance of the observed values of NRI for each community by comparing them to NRI values of null communities generated by Gotelli's swap algorithm (Gotelli 2000), which randomizes the species occurrence matrix while keeping the number of species per sample and species' occurrence frequencies across samples constant. Negative values of NRI indicate phylogenetic overdispersion, while a positive NRI suggests phylogenetic clustering of taxa. All analyses were carried out using *picante* in R 2.14.0 (Kembel et al. 2010). I calculated both abundance-weighted and unweighted measures for NRI. Abundance-weighted NRI measures represent phylogenetic distances between individuals of constituent species and therefore, enable us to infer whether abundances are phylogenetically clustered so that few clades dominate, or are evenly distributed across the phylogenetic tree.

6.2.6 Correlates of species richness and phylogenetic structure of communities

To examine the relationship between species richness as well as NRI and environmental variables, I used linear mixed-effects models. Prior to modelling, correlated variables were identified and the variables less relevant to warbler distribution were removed. Since arthropod abundance was strongly correlated to annual precipitation ($r = 0.75$, $P = 0.0009$, $N = 16$) and temperature range ($r = -0.71$, $P = 0.003$, $N = 16$), we retained only arthropod abundance as it is tightly correlated to warbler abundances (Fig. 5.7). In the model, I treated the identity of the elevational transects as a random effect since often multiple sites were located along a single transect, while maximum temperature, precipitation seasonality and arthropod abundance along with all their combinations were the explanatory variables. Estimates were generated using maximum likelihood procedures using the lme4 package (Bates et al. 2010) run in the R statistical environment (R Development Core Team 2010). For each model, Akaike's information criterion adjusted for small sample size (AIC_c) was calculated from the ML deviance (deviance*2Log-Likelihood), and used to compare the relative fit of the models (Burnham and Anderson 2002).

6.2.7 Ecomorphological spacing metrics

For all three ecomorphological traits (body size, tarsus length and beak shape), I calculated dispersion metrics using the R script provided in Kraft and Ackerly (2010). I quantified the range and variance (VAR) for the trait values to examine the role of environmental filtering in communities. Given the strong correlation between these two measures (body size, $r = 0.89$, $P = 0.00004$; tarsus length, $r= 0.94$, $P = 0.00001$; beak shape, $r = 0.89$, $P = 0.00004$), I retained only VAR in subsequent analyses. I computed two indices of spacing among traits, standard deviation of nearest neighbour distances normalized to range (SDNNr) and standard deviation of neighbour distances normalized to range (SDNDr) to denote trait similarity and even spacing, respectively. The observed ecomorphological dispersion metric as well as mean and standard deviation for the metric for each community were quantified based on 999 communities randomly assembled by sampling species with equal probability from the regional species pool, composed of 16 species present in the study system. I calculated the effect size of an observed metric (analogous to phylogenetic community structure metrics) for each community as the difference between the observed and mean value of the metric divided by the standard deviation of the simulated community. Environmental filtering is indicated by negative effect size for VAR, while negative values for SDNNr and SDNDr suggest that species exhibit limiting similarity and evenly spaced ecomorphological traits, respectively. In order to examine the univariate relationships between phylogenetic and ecomorphological dispersion metrics of communities, I conducted Pearson's correlation analyses between NRI and the ecomorphological spacing and mean metrics. Since ecomorphological dispersion metrics could not be computed for communities with less than four species (Khellong, Mandal and Patwadangar) which reduced the sample size further, influence of climatic variables was not investigated.

6.3 RESULTS

6.3.1 Species richness patterns

Sixteen species of warblers were found to breed in the sites sampled in this study. The maximum species richness was recorded at Manali (3100 m) and Tungnath (3600 m), where eight species co-occurred (Table 2.1). Sites at the lowest elevations in the west (Patwadangar: 1350) and the east (Khellong: 700m) had just a pair of species breeding. However, species richness was not significantly correlated with elevation ($r = 0.3$, $N= 16$, $P = 0.25$). Maximum temperature and arthropod abundance emerged to be the best predictors of species richness (Table 6.1), suggesting that while species richness was positively influenced by resource abundance, warmer sites had fewer species. The next best models was also plausible (with $\Delta AIC_c < 2$), and included the influence of all three covariates. The predictor weights were similar for both maximum temperature (0.95) and arthropod abundance (0.8), followed by precipitation seasonality (0.28).

TABLE 6.1. Models of species richness. The most parsimonious model was identified using Akaike Information Criteria adjusted for small sample size (AIC_c). The abbreviations refer to maximum temperature (Tmax), precipitation seasonality (Pcv) and Mean arthropod abundance (Ar_{ab}).

Models	K	ML Deviance	AIC_c	ΔAIC_c	Akaike weight
$Ar_{ab}+T_{max}$	5	47.82	67.69	0.00	0.53
$P_{cv}+T_{max}+Ar_{ab}$	6	47.79	69.13	1.44	0.26
T_{max}	4	58.61	70.25	2.56	0.15
Null	3	65.43	73.43	5.75	0.03
$P_{cv}+T_{max}$	5	58.44	74.44	6.76	0.02
Ar_{ab}	4	63.96	75.60	7.91	0.01
P_{cv}	4	55.79	76.79	9.11	0.01
$P_{cv}+Ar_{ab}$	5	63.00	79.00	11.32	0.00

6.3.2. Tests for niche conservatism

For two of the three morphological axes, test statistics were more phylogenetically conserved than would be predicted by a random association between phylogeny and traits (Table 6.2). Closely related species were more similar than expected in morphological axes related to their foraging ecology (PC1 and beak shape), indicating that within Phylloscopidae, there appears to have been little evolution in foraging traits at the tips of the trees relative to the rate of diversification deeper in the tree. The third morphological axis, PC2 (correlated to mid-point of breeding altitudinal range) does not show significant phylogenetic signal ($P > 0.05$).

TABLE 6.2 Tests of niche conservatism.

Trait	**Correlated to**	**K**	***P***
PC1 (body size)	Prey size	1.13	0.01
PC2 (tarsus length)	Elevational position	0.96	0.06
Beak shape	Feeding method	1.02	0.02

6.3.3 Phylogenetic community structure

Across sites, measures of both abundance-weighted and unweighted NRI (based on species presence-absence) were negatively correlated with elevation (abundance weighted: $r = -0.86$, $N = 16$, $P = 0.0001$; unweighted: $r = -0.84$, $N = 16$, $P = 0.0001$). Six sites at lower elevations showed significant phylogenetic clustering (Fig. 6.2a, b). In contrast, three of high-elevation communities were significantly over-dispersed (based on species presence-absence), while only one community remained significantly over-dispersed once species abundances were accounted for (Fig. 6.2b). No significant correlation is evident between species richness and NRI (abundance weighted: $r = -0.47$, $N = 16$, $P = 0.07$; unweighted: $r = -0.25$, $N = 16$, $P = 0.34$).

Since the two measures of NRI were significantly correlated ($r = 0.92$, $N = 16$, $P = 0001$), we built models using occurrence-based NRI. In terms of environmental factors, maximum temperature ($\beta = 0.025$, $P = 0.0004$) and arthropod abundance ($\beta = 0.112$, $P = 0.005$) were the best predictors of NRI (Table 6.3), so that communities occurring in warmer areas with more resources were more clustered. The second best model also included precipitation seasonality, although it was not significant (β = 0.022, P = 0.09). Predictor weights for maximum temperature, arthropod abundance and precipitation seasonality were 0.96, 0.88 and 0.23, respectively.

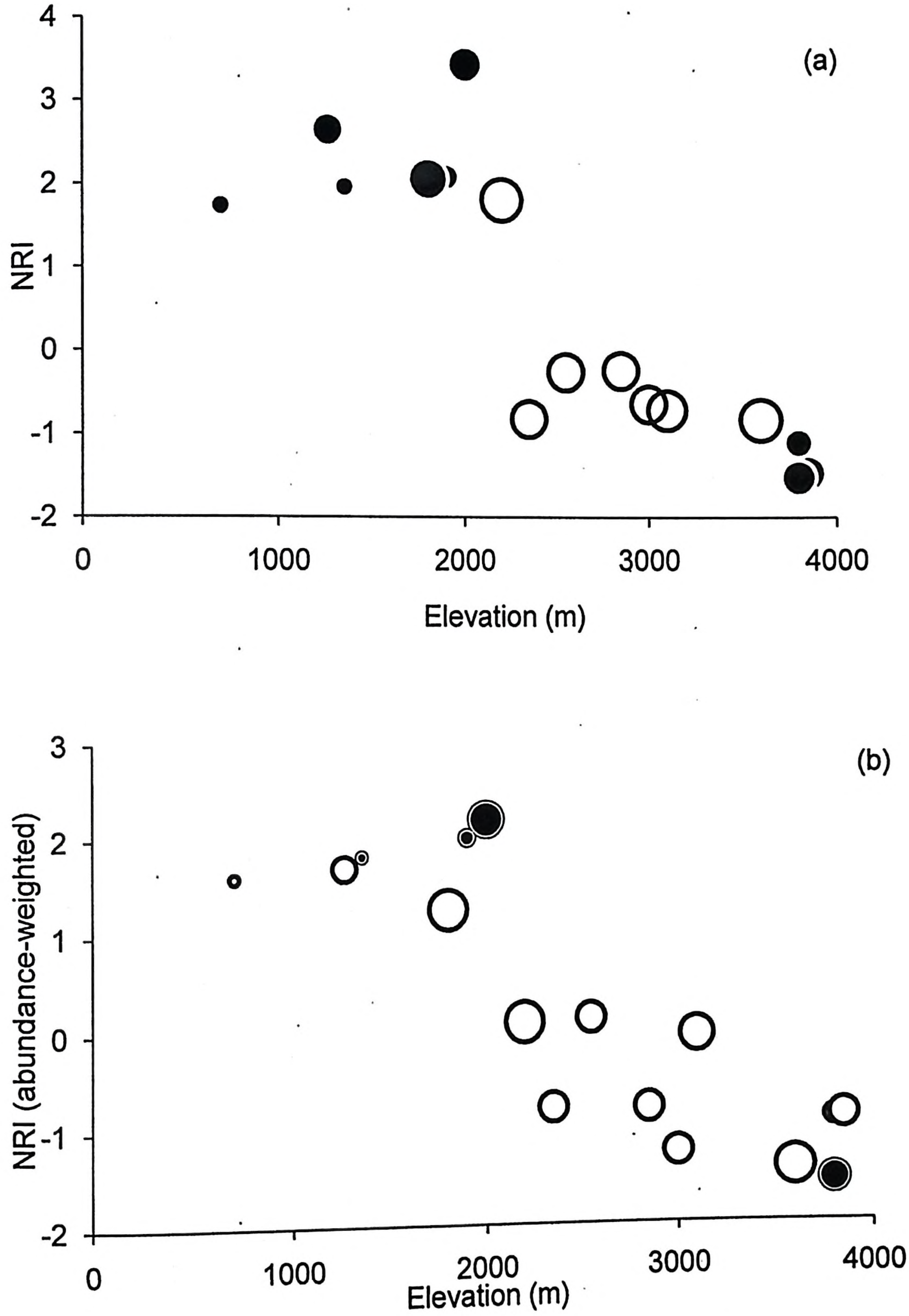


FIGURE 6.2. Net relatedness index (NRI) for communities plotted against elevation using species presences (a) and weighted by species abundances (b). The size of the circles is proportional of the number of species in the community and black circles indicate significantly clustered (high NRI values) or over-dispersed communities (low NRI values).

TABLE 6.3. Models of Net Relatedness Index (NRI). The most parsimonious model was identified using Akaike Information Criteria adjusted for small sample size (AIC_c). The abbreviations refer to maximum temperature (Tmax), precipitation seasonality (Pcv) and Mean arthropod abundance (Ar_{ab}).

Models	K	ML Deviance	AIC_c	ΔAIC_c	Akaike weight
$Ar_{ab}+T_{max}$	5	30.76	54.97	0.00	0.66
$P_{cv}+T_{max}+Ar_{ab}$	6	30.22	57.41	2.45	0.19
T_{max}	4	32.02	58.88	3.92	0.09
$P_{cv}+T_{max}$	5	31.75	61.74	6.77	0.02
Ar_{ab}	4	48.89	61.96	6.99	0.02
$P_{cv}+Ar_{ab}$	5	47.19	62.42	7.45	0.02
P_{cv}	4	50.70	67.43	12.46	0.00
Null	3	53.70	69.01	14.04	0.00

6.3.4 Ecomorphological spacing metrics

Of the three ecomorphological traits, VAR in body size within communities was negatively correlated to NRI indicating that phylogenetically clustered communities (positive NRI) show increased filtering. On the other hand, SDNDr was positively correlated to NRI suggesting that co-occurring species in phylogenetically overdispersed communities (negative NRI) have more evenly spaced trait values (Fig. 6.3a). For tarsus length, which does not show significant phylogenetic signal, mean values were negatively correlated to NRI so that phylogenetically clustered communities had shorter tarsi and it increased as communities become more overdispersed. However, no significant correlation between any of the other ecomorphological trait metrics and NRI was evident (Table 6.4). In case of beak shape, species in clustered communities had wider beaks while species co-occurring in overdispersed communities had more slender beaks as indicated by the negative correlation between mean values and NRI. Further, SDNDr was negatively correlated to NRI suggesting more constant spacing among trait values as communities become clustered (Fig. 6.3b).

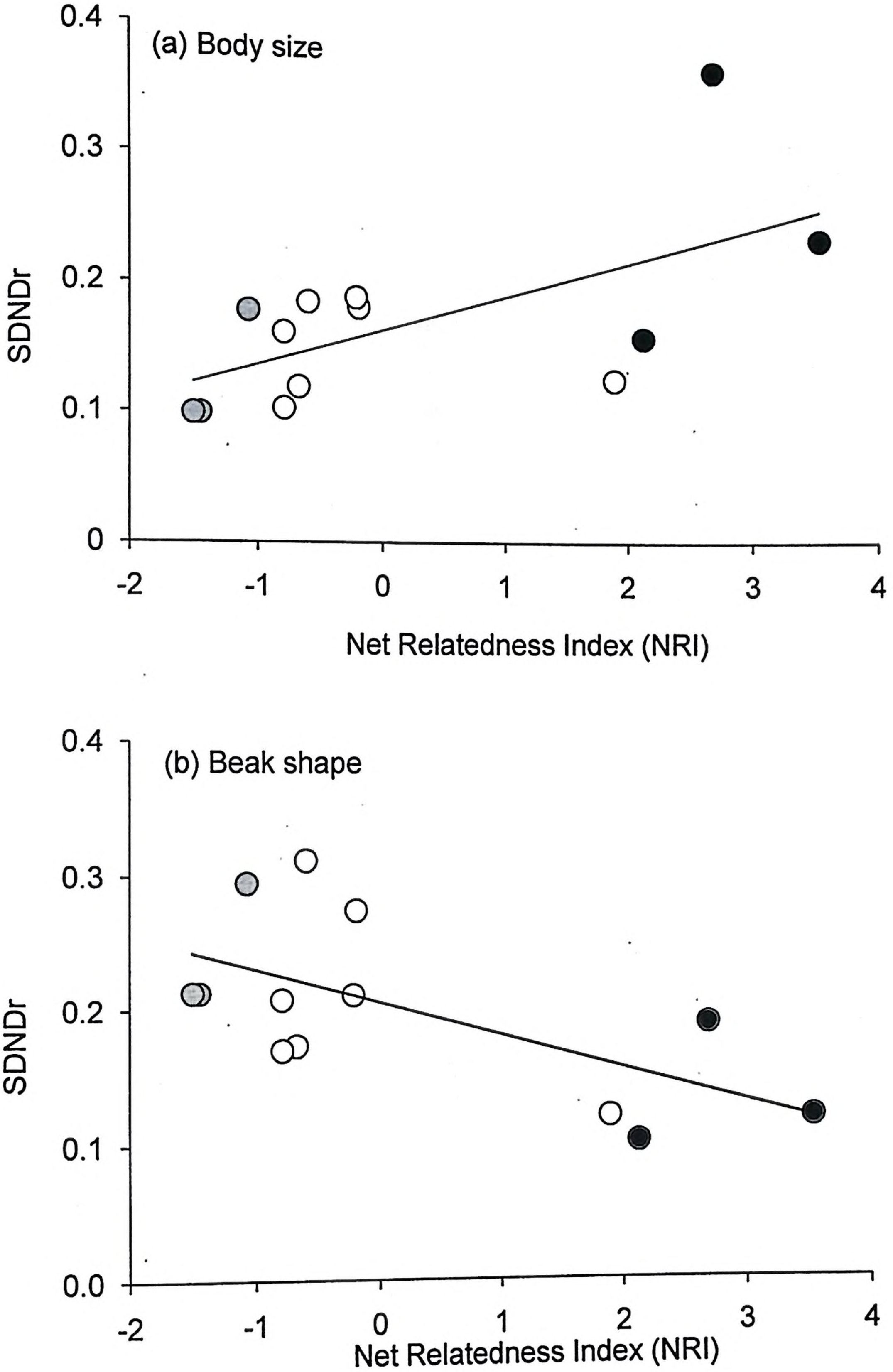


FIGURE 6.3. The relationship between standard deviation of neighbour distances normalized to range (SDNDr) and net relatedness index (NRI) for body size (r = 0.78, p = 0.001, N = 16) and beak shape (r = 0.78, p = 0.001, N = 16). The black and grey circles indicate significantly clustered (high NRI values) and over-dispersed communities (low NRI values), respectively.

TABLE 6.4 The relationship between ecomorphological trait metrics and net relatedness index (NRI) as well as species richness across 13 leaf warbler communities* across elevational gradients in the Himalayas.

Ecomorphological metric	NRI		Species richness	
	r	*P*	r	*P*
Body size (PC1)				
Mean	0.01	0.96	-0.63	0.02
VAR	-0.68	0.01	0.09	0.77
SDNNr	0.49	0.09	-0.02	0.96
SDNDr	0.64	0.02	-0.49	0.09
Tarsus length (PC2)				
Mean	-0.87	0.0001	-0.31	0.31
VAR	0.43	0.14	0.70	0.01
SDNNr	-0.09	0.76	-0.69	0.01
SDNDr	0.03	0.92	-0.67	0.01
Beak shape				
Mean	-0.77	0.002	-0.49	0.09
VAR	0.13	0.67	-0.26	0.39
SDNNr	-0.25	0.41	-0.56	0.04
SDNDr	-0.64	0.02	-0.67	0.01

*No ecomorphological metrics could be computed for three communities owing to these communities being composed of < 4 species.

Overall, body size-related ecomorphological metrics varied as expected suggesting environmental filtering (negative VAR) in clustered, low-elevation communities and more evenly spaced (negative SDNNr and SDNDr) at overdispersed high-elevation communities (Table 6.5). For beak shape which determines the foraging method, ecomorphological metrics were indicative of more constant spacing among trait values (negative SDNDr) in clustered communities. However, positive values of SDNNr and SDNDr in overdispersed communities demonstrated the lack of evenness in beak shape trait values (Table 6.5). For both beak shape and tarsus length, values for VAR were negative across all communities.

TABLE 6.5. Effect sizes for the phylogenetically overdispersed (N = 3) and clustered (N =3) and random communities for each ecomorphological metric.

Phylogenetic structure*	Sites	Body size (PC1)			Tarsus length (PC2)			Beak shape		
		VAR	SDNNr	SDNDr	VAR	SDNNr	SDNDr	VAR	SDNNr	SDNDr
Overdispersed	Mooling	0.33	-0.37	-0.54	-1.61	1.12	0.95	-1.05	0.81	0.32
	Dzongri	0.79	-0.78	-1.17	-1.45	-0.03	-0.32	-0.4	0.82	1
	Dirang	0.77	-0.78	-1.14	-1.43	-0.04	-0.31	-0.36	0.87	1.03
Clustered	Thosum	-1.16	1.89	1.79	-1.21	0.01	0	-1.83	-0.07	-1.03
	Bompu	-0.49	1.15	1.69	-1.61	1.17	1.3	-1.69	0.52	-0.92
	Sessni	-1.7	-1.16	2.54	-1.09	-0.11	-0.16	1.74	-0.16	-0.16
Random	Lama Camp	2.29	-0.51	0.19	-1.55	-0.58	-1.31	-1.65	-0.68	0.94
	Manali	1.54	-0.09	-0.31	-1.3	-0.62	-1.57	-0.71	0.36	0.89
	Tungnath	1.54	-0.55	-0.44	-1.5	-0.14	-0.98	-1.24	0.77	1.71
	Shokharakh	2.81	-1.9	0.64	-2	-0.32	-1.1	-1.39	-1.7	2.17
	Kanchulakharakh	2.68	-1.6	0.76	-2	0.99	0.13	-1.01	-0.99	1.04
	Tsokha	2.09	-1.03	0.75	-1.42	-0.22	-1.1	-1.59	-1	3.14
	Sachen	0.81	0.68	0.45	-1.19	0.52	0.08	-2.16	-1.16	-0.21

*Based on NRI; while 5 communities are phylogenetically clustered, no ecomorphological metrics could be computed owing to these communities being composed of < 4 species.

6.4 DISCUSSION

Among the Himalayan Phylloscopidae, phylogenetic community structure varied along the elevational gradient. The 16 communities composed of two to eight species ran the entire spectrum of significance in terms of their phylogenetic structure, resulting in many clustered communities at low elevations and few over-dispersed communities at higher elevations. Maximum temperature and resource abundance determined the variation in net relatedness indices so that warmer, low to mid-elevation sites with more resources had species more closely related than expected by chance while cooler, relatively resource-poor sites at higher elevations had species from more diverse lineages (Table 6.2, Fig. 6.2). In general, species richness did not correlate with elevation, although variation in species richness was explained by maximum temperature and abundance of arthropod resources so that temperate habitats at mid-elevations tended to be more species-rich than warmer sites at lower elevations (Table 6.1). In terms of ecomorphological traits, body size-related metrics varied as expected suggesting environmental filtering in clustered, low-elevation communities and heightened competitive interactions at overdispersed high-elevation communities. However, the beak shape metrics of co-occurring species in clustered communities were unexpectedly even indicating likely competition for resources.

The observed pattern of variation in phylogenetic community structure of Phylloscopidae along the elevation gradient is consistent with previous studies on few clades of hummingbirds in the Andes (Parra et al. 20011) and among plant communities in the Rocky Mountains (Byrant et al. 2008). However, along montane systems, phylogenetic clustering has been more commonly documented to increase at higher elevations as shown by studies involving the broader Andean hummingbird communities (Graham et al. 2009) and ants across three temperate montane systems (Machac et al. 2011) in response to the environmental stress imposed by low temperatures. Phylogenetic clustering could be attributed to environmental filtering or ecological divergence depending on the phylogenetic distribution of relevant ecological traits (Webb et al. 2002; Losos 2008; Cavender-Bares et al. 2009). In case of Phylloscopidae, ecomorphological traits which structure the ecological communities (prey size, foraging method) are niche conserved ($K > 1$, $P < 0.05$), which implies that maximum temperature and resource abundance act as an environmental filter for this group at lower elevation habitats so that species belonging to only a few lineages have to ability to persist in these sites. In contrast, the communities at higher elevations tended towards over-dispersion (one was significantly over-dispersed), thereby implying heightened inter-specific competition. Inter-specific competition has been held to play the most critical role in structuring the distribution of leaf warbler species in the breeding season based on a study along a single elevational gradient in Kashmir (Price 1991). However, the study was restricted to habitats above 2000m, elevations at which influence of competitive interactions appears to increase. Thus, these results imply that degree of over-dispersion, and thereby the strength of inter-specific interactions, varies along environmental gradients and appear to be more of an exception than a rule among Phylloscopidae as has been seen among the rodents of Mojave (Stevens et al. 2012). The communities showing no significant departure from random phylogenetic structure were in the mid-elevation mixed-conifer forests (2600-3300m), which incidentally show the highest abundance of arthropod prey. This subalpine zone also represents a transition from the Southeast Asian and Palaearctic fauna and has a mix of both elements (Packert et al. 2012; Wikramanayake et al. 2001), leading to highest species richness.

Ancestral reconstructions indicate that lower elevation (< 2600m) species (*P. cantator, P. xanthoschistos, P. reguloides, P. occipitalis* and *Seicercus spp.*) have a sub (tropical) South-east Asian origin and represent relatively old splits from their closest relatives, some dating back to early Miocene (Packert et al. 2012). This period is associated with a large ecological diversification in body size and beak shape among Phylloscopidae (Price 2010). In contrast, the high elevation species from the subalpine and temperate belts (*P. magnirostris*, *P. maculipennis*, *P. pulcher*, *P. trochiloides*, *P. humei* and *P. affinis*) which represent more recent splits dating back to the Pleistocene or Pliocene/Pleistocene boundary have a boreal origin. Therefore, immigration of the boreal species from the north-east Palearctic region to occupy the high-elevation habitats above the sub (tropical) species lower down resulted in the extant parapatric distribution of the Himalayan Phylloscopidae along the elevation gradient. The elevational separation has been facilitated by more recent divergence in tarsus length (PC2: correlated to mid-point of breeding altitudinal range; Richman and Price 1992; Price 2010), the only trait examined here which did not show evidence of significant niche conservatism (Table 6.2). Given the limiting influence of maximum temperature on the phylogenetic structure of the assemblage, while the sub (tropical) species have been able to range to cooler elevations higher up, the boreal species have been unable to range lower down to warmer climes. The resulting accumulation of multiple species at higher elevation of both boreal and sub (tropical) origins has resulted in an increasingly over-dispersed phylogenetic structure of communities.

On examining the ecomorphological spacing metrics, it was evident that not always could the trait spacing be predicted from the observed phylogenetic structure. In clustered assemblages, body size-related metrics agreed with the predictions of environmental filtering as suggested by narrow range and low variance (VAR). However, while tarsus length and beak shape also had low variance in clustered communities, so did communities with random or overdispersed phylogenetic structure (Table 6.3). Finally, the negative correlation between species richness and evenness (SDNDr) and limiting similarity (SDNNr) metrics for PC2 and beak shape implies that the increase in richness is facilitated by accumulation of ecologically segregated co-occurring species (Table 6.4). This contrasts with rodents in the Mojave Desert, where packing of ecologically similar species leads to increased number of species in more diverse communities (Stevens et al. 2012).

In summary, while the mechanistic basis of origin and assembly of species into communities is increasingly being investigated owing to a surge in the use of molecular genetics and phylogenetic reconstructions (Cavender-Bares et al. 2009; Kembel 2009; Stevens et al. 2012), very few studies simultaneously examine phylogenetic and ecological community structure to differentiate between contrasting processes which may give rise to clustered or over-dispersed community structures (Losos 2008; Machac et al. 2011). In this study, by incorporating field-based measures of resources and species abundances, the relative contribution of resources and environmental factors in determining the phylogenetic community structure was ascertained. By considering the ancestral areas of the boreal and sub (tropical) clades of Phylloscopidae and phylogenetic distribution of ecological traits, it was possible to evaluate how the limiting influence of maximum temperature shaped the phylogenetic structure of the Himalayan Phylloscopidae communities along the elevational gradient.

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APPENDIX 1

Morphological measurements and ecomorphological distribution of species

TABLE 1. Mean morphological measurements in mm with standard errors (SE) as measured from museum specimens.

	Beak length		Beak depth		Beak width		Tarsus length		Wing length		Tail length		*Beak shape	N
East	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE		
P. cantator (Pca)	6.86	0.10	2.51	0.10	2.42	0.09	17.09	0.55	54.10	0.55	39.60	0.43	1.04	10
S. castaniceps (Sca)	4.97	0.09	2.10	0.03	2.34	0.08	17.13	0.57	50.90	0.57	39.00	0.42	0.75	10
S. affinis (Saf)	6.70	0.42	2.80	0.14	2.80	0.14	16.95	0.85	56.75	0.75	45.00	0.72	0.87	2
S. poliogenys (Spo)	5.58	0.09	2.44	0.07	2.75	0.06	18.23	0.46	51.91	0.46	43.00	0.56	0.71	12
S. burkii (Sbu)	6.07	0.02	2.50	0.05	3.05	0.03	18.92	0.67	54.83	0.67	41.67	0.51	0.69	12
S. whistleri (Swh)	6.02	0.11	2.42	0.08	2.79	0.07	19.39	0.62	57.30	0.62	47.70	0.79	0.77	10
P. chloronotus (Pch)	4.86	0.06	1.90	0.03	2.06	0.02	17.63	0.80	51.70	0.80	37.10	0.63	0.86	13
P. xanthoschistos (Pxa)	5.98	0.05	2.37	0.07	2.35	0.05	**19.04**	0.48	54.90	0.48	41.10	0.62	0.93	10
P. pulcher (Ppu)	5.68	0.09	1.99	0.02	2.04	0.02	19.75	0.62	58.10	0.62	40.60	0.55	1.02	14
P. reguloides (Pre)	6.37	0.12	2.57	0.10	2.65	0.07	18.07	1.11	57.40	1.11	42.10	0.89	0.88	10
P. maculipennis (Pmc)	4.16	0.04	1.93	0.02	2.03	0.02	**18.20**	0.52	**48.30**	0.52	**32.60**	0.51	0.72	17
P. trochiloides (Ptr)	6.37	0.11	2.52	0.09	2.69	0.09	**20.92**	0.47	62.80	0.47	**50.40**	0.45	0.86	10
P. affinis (Paf)	5.99	0.10	2.07	0.02	2.09	0.02	19.72	0.65	57.60	0.65	44.70	0.71	1.02	15
P. magnirostris (Pmg)	7.10	0.13	2.99	0.07	2.92	0.05	20.07	0.71	69.00	0.71	51.00	0.46	0.89	12
West														
S. burkii (Sbu)	6.45	0.26	2.33	0.16	2.93	0.08	20.21	0.20	58.25	0.60	47.75	1.38	0.79	4
S. whistleri (Swh)	6.28	0.12	2.51	0.08	2.89	0.06	19.38	0.14	58.44	0.69	46.89	0.95	0.78	9

P. chloronotus (Pch)	5.19	0.11	2.00	0.02	2.03	0.07	18.10	0.16	53.10	0.52	37.10	0.51	0.94	10
P. xanthoschistos (Pxa)	6.08	0.19	2.42	0.08	2.39	0.09	**19.64**	0.06	55.40	0.40	41.50	0.69	0.93	10
P. pulcher (Ppu)	5.36	0.08	1.95	0.02	2.04	0.02	20.18	0.10	57.40	0.54	40.30	0.67	0.97	11
P. reguloides (Pre)	6.40	0.12	2.64	0.08	2.74	0.07	18.38	0.17	59.70	0.94	43.10	0.50	0.85	10
P. maculipennis (Pmc)	4.49	0.09	1.99	0.03	2.09	0.02	**18.78**	0.18	**52.40**	0.73	**34.90**	0.48	0.76	10
P. trochiloides (Ptr)	6.16	0.08	2.32	0.08	2.62	0.09	**20.03**	0.23	63.00	0.49	**46.60**	0.65	0.85	10
P. affinis (Paf)	5.86	0.07	2.08	0.02	2.07	0.02	19.99	0.11	58.60	0.50	43.80	0.52	1.04	17
P. magnirostris (Pmg)	7.00	0.11	2.93	0.03	2.96	0.05	19.90	0.13	68.70	0.88	50.60	0.56	0.86	10
P. humei (Phu)	5.29	0.11	2.05	0.02	2.07	0.02	19.42	0.14	58.80	0.29	41.50	0.48	0.94	10
P. occipitalis (Poc)	7.46	0.13	2.84	0.04	3.00	0.03	18.63	0.12	65.10	0.85	48.20	0.55	0.91	10

Notes: Measurements were made as in Price (1991).
In order to obtain sufficient sample sizes, locations beyond the field study area were included.
East includes measurements from Nepal eastwards. West includes measurements from Kashmir, Himachal Pradesh and Uttar Pradesh.
Bold values indicate significant differences ($\alpha = 0.05$) between measurements from eastern and western populations using t-tests with Bonferroni correction for multiple comparisons
*Beak shape = ln(beak width/beak length)

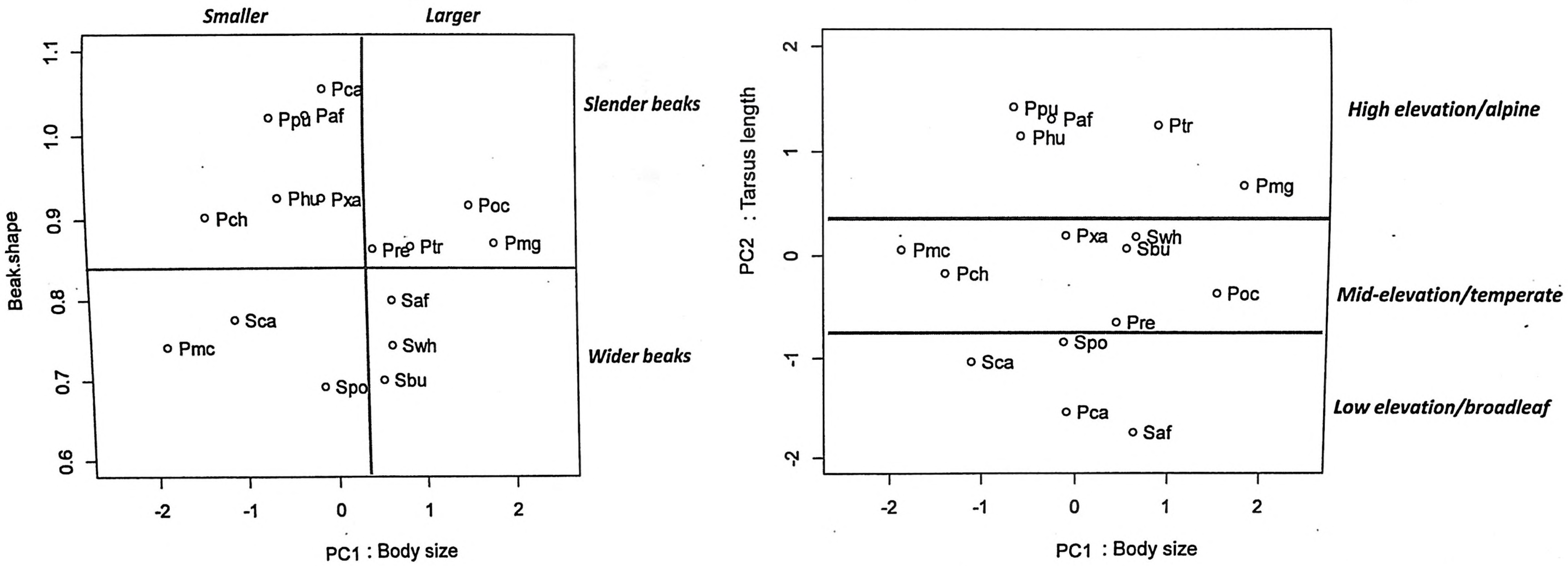


FIGURE 1: Mean morphologies for 16 Himalayan species projected onto two principal component axes (see Table 5.1): PC1 (correlated to prey size), PC2 (correlated to elevational position) and beak shape (correlated to foraging method). For species abbreviations, please refer to Table 1 above. Left: Beak shape *versus* PC1; Right: PC2 *versus* PC1.

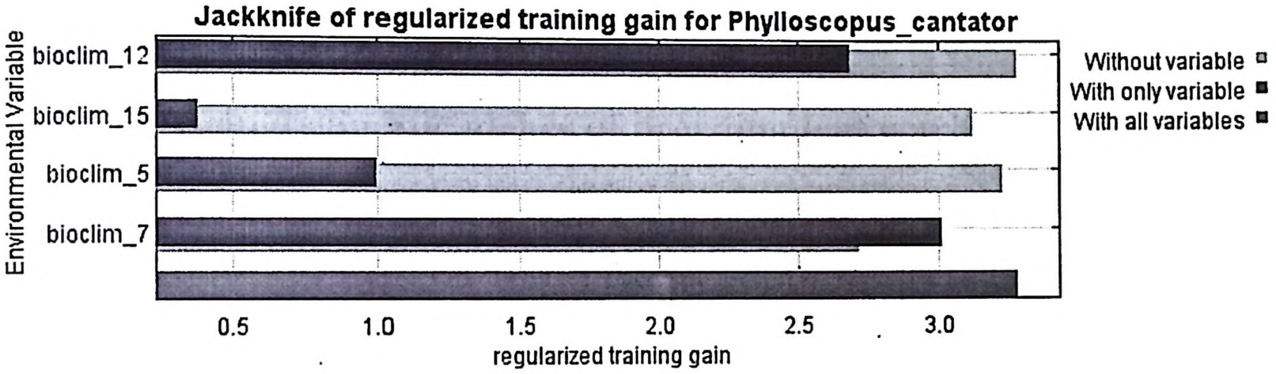
APPENDIX 2

Predicted climatic niches of breeding leaf warbler species

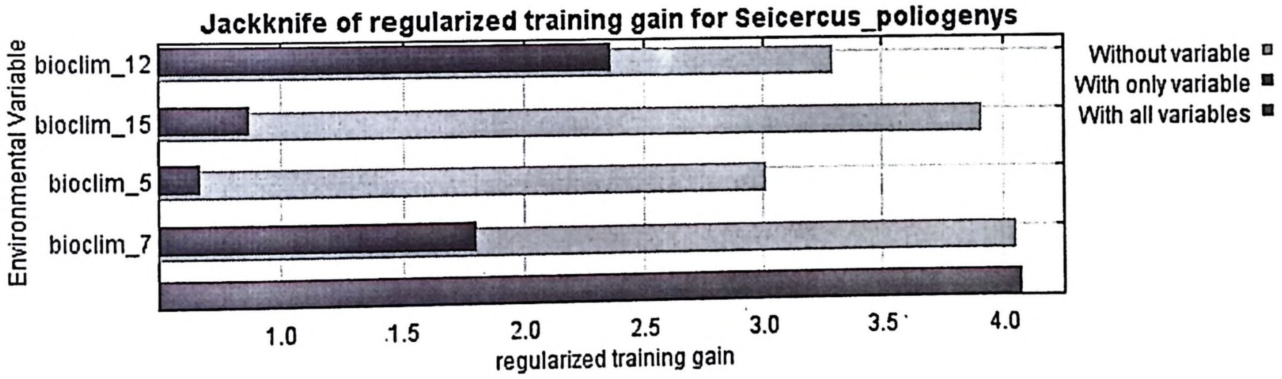
A. RELATIVE CONTRIBUTION OF THE FOUR ENVIRONMENTAL VARIABLES IN DETERMINING THE PREDICTED CLIMATIC NICHE OF SPECIES RESTRICTED TO THE EAST OR WEST

NOTE: Bio_5: maximum temperature of the warmest month (°C*10); Bio_12: Annual precipitation (mm), Bio_15: temperature annual range; Bio_17: precipitation seasonality expressed as coefficient of variation in annual precipitation

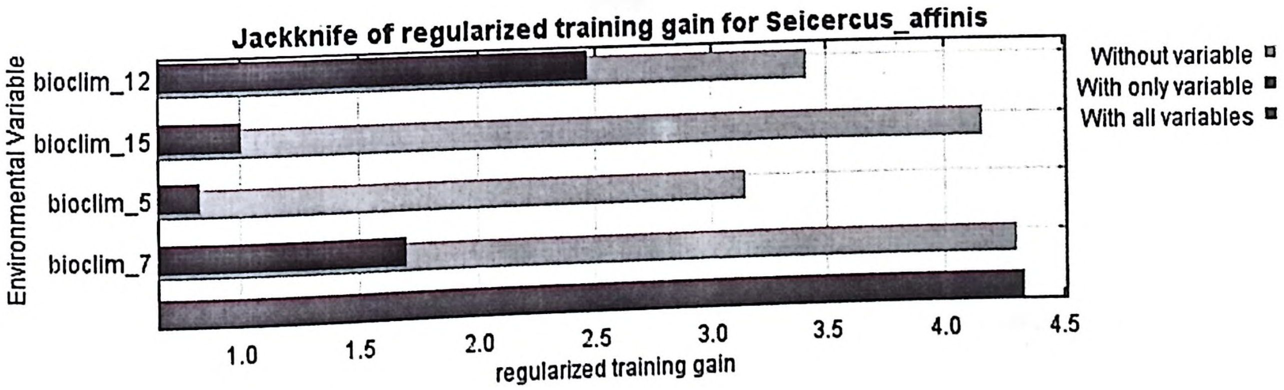
(a) ***Phylloscopus cantator***



(b) ***Seicercus poliogenys***



(c) ***Seicercus affinis***



(d) *Seicercus castaniceps*

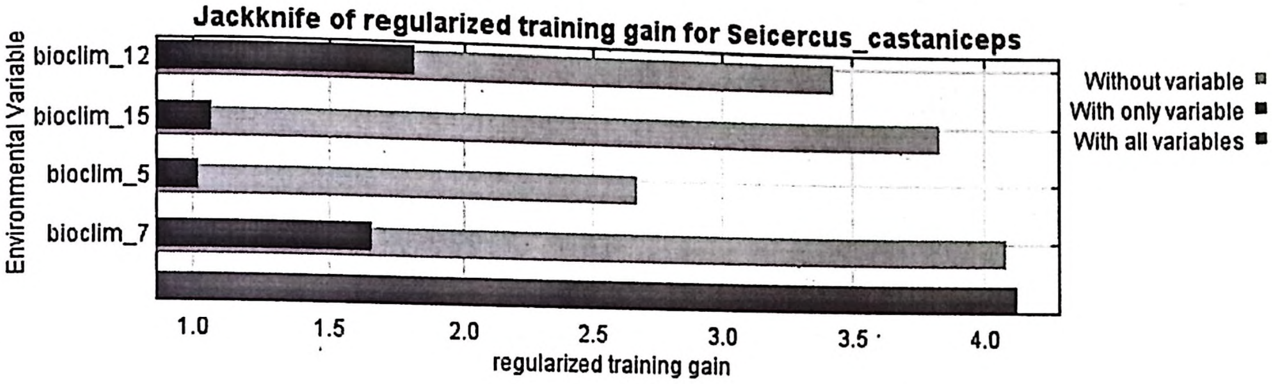
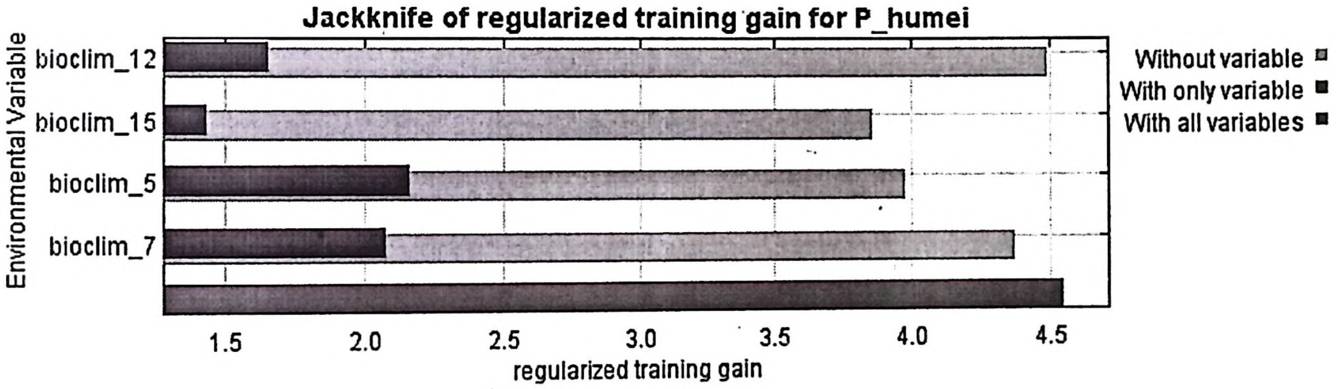


Figure 1. Results of jackknife test of variable importance for the four east-restricted species. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

(a) *Phylloscopus humei*



(b) *Phylloscopus occipitalis*

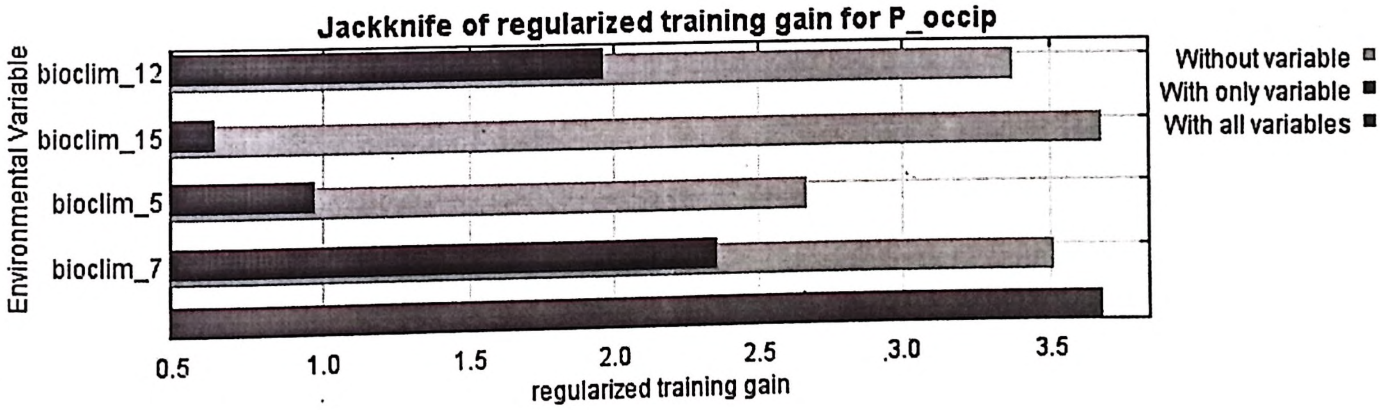


Figure 2. Results of jackknife test of variable importance for the two west-restricted species. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

B. SPECIES DISTRIBUTION MODELS OF SPECIES COMMON TO EAST AND WEST BASED ON LOCATIONS IN THE EAST

1. *Phylloscopus affinis*

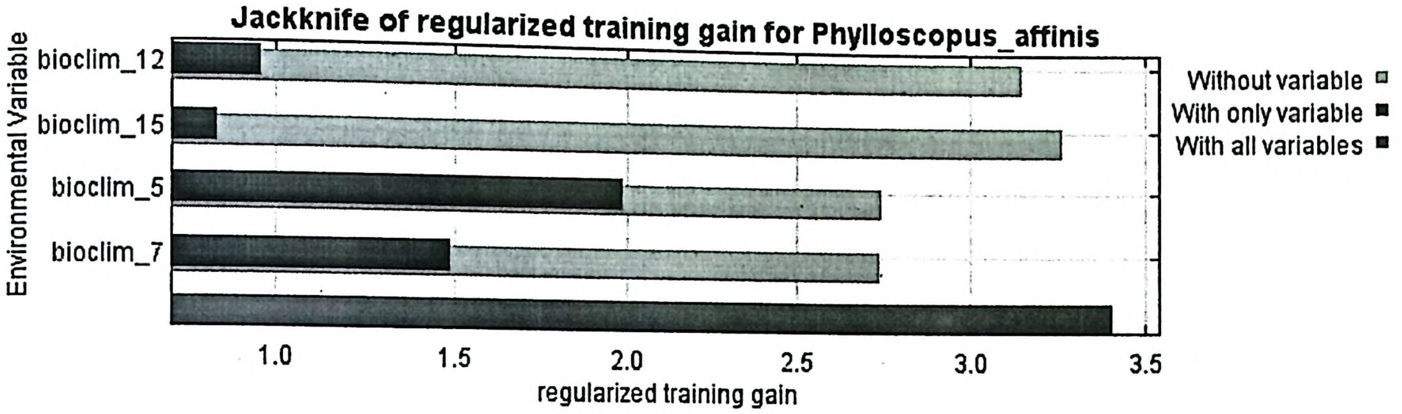


Figure 3a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

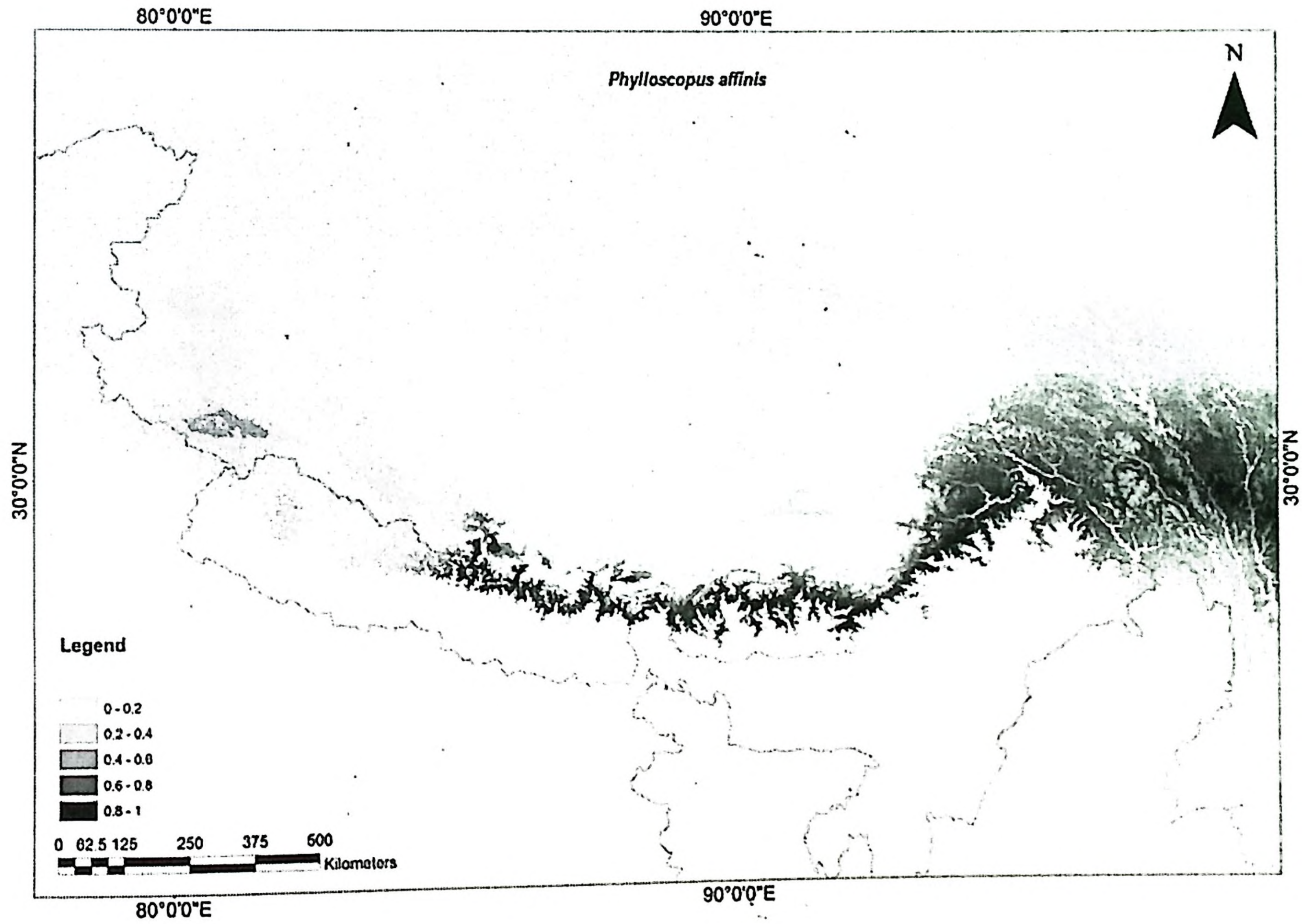


Figure 3b. Predicted geographic distribution of Tickell's Leaf Warbler (*Phylloscopus affinis*) across the Himalayas using occurrence locations from its breeding range in the east.

2. *Phylloscopus chloronotus*

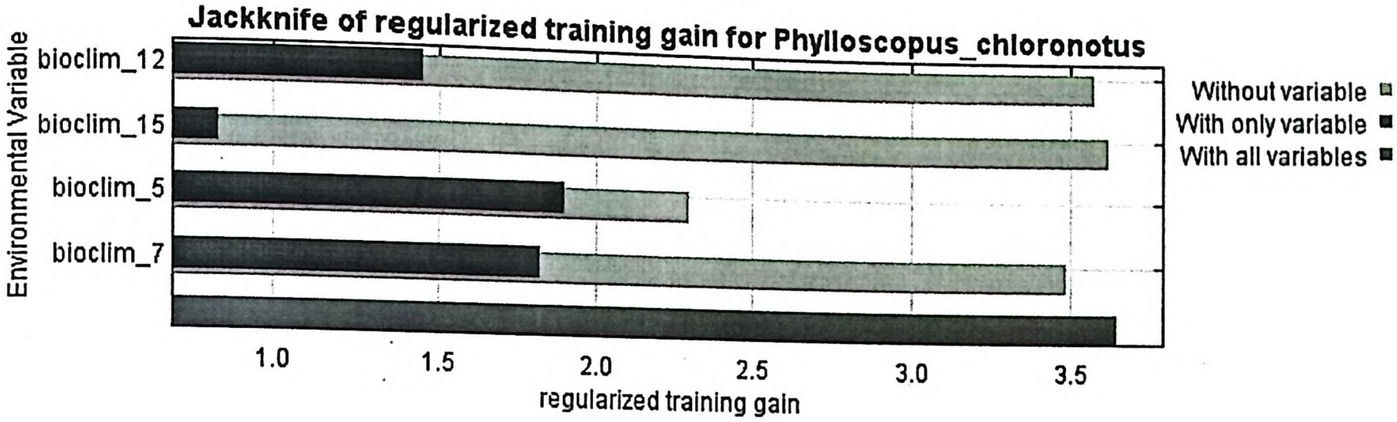


Figure 4a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

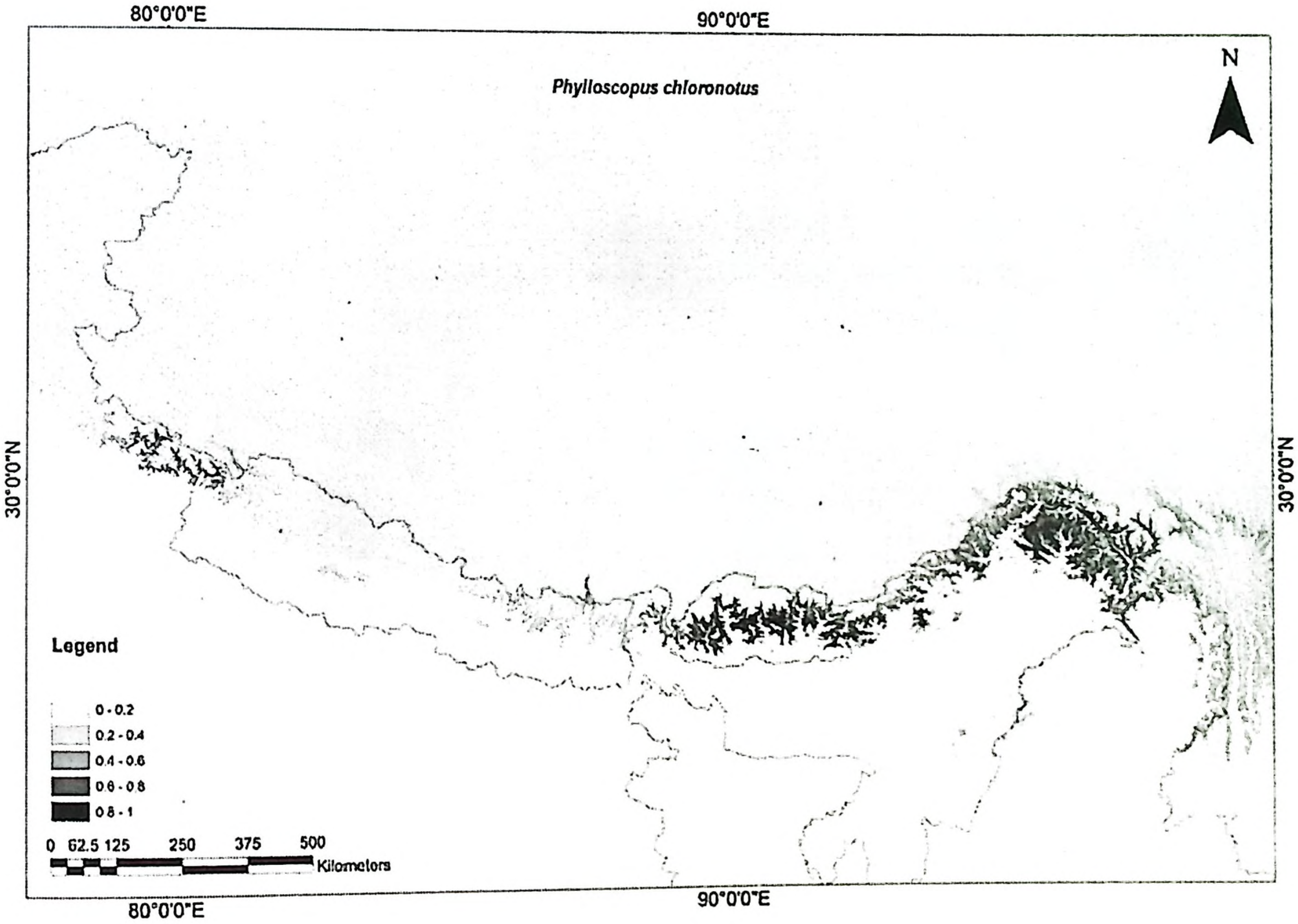


Figure 4b. Predicted geographic distribution of Lemon-rumped Warbler (*Phylloscopus chloronotus*) across the Himalayas using occurrence locations from its breeding range in the east.

3. *Phylloscopus maculipennis*

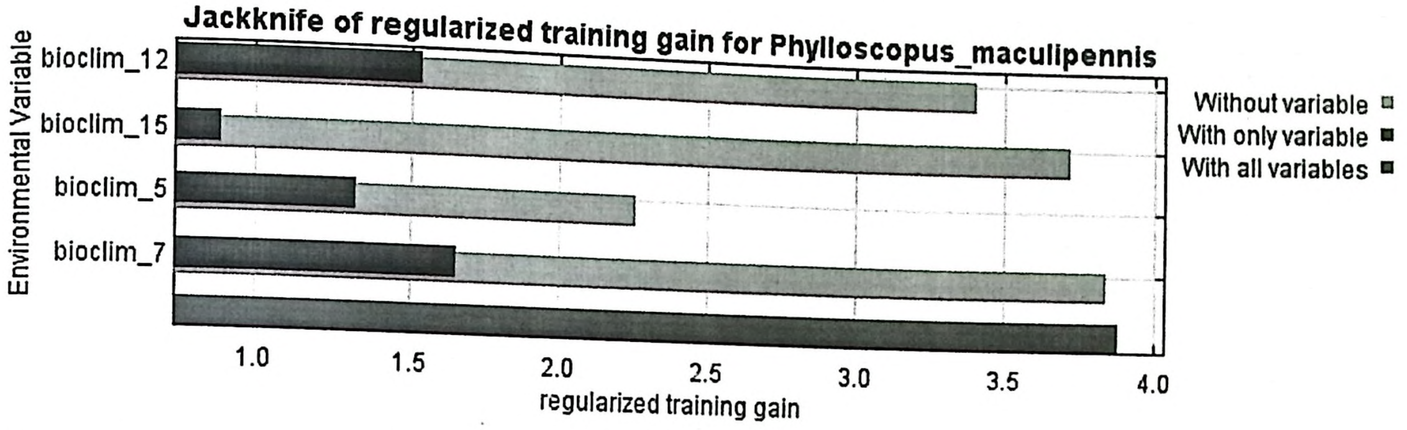


Figure 5a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

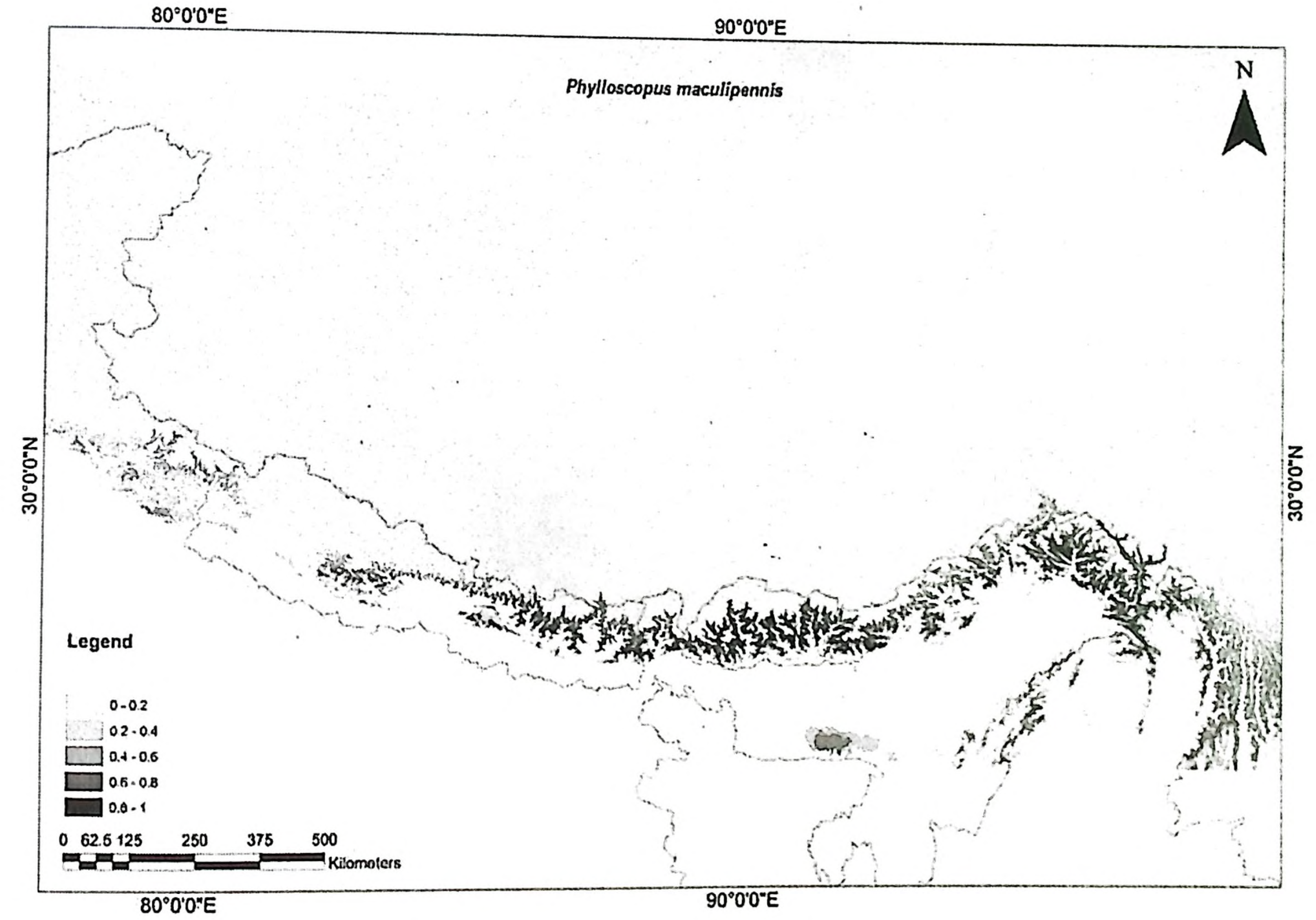


Figure 5b. Predicted geographic distribution of Ashy-throated Leaf Warbler (*Phylloscopus maculipennis*) across the Himalayas using occurrence locations from its breeding range in the east.

4. *Phylloscopus reguloides*

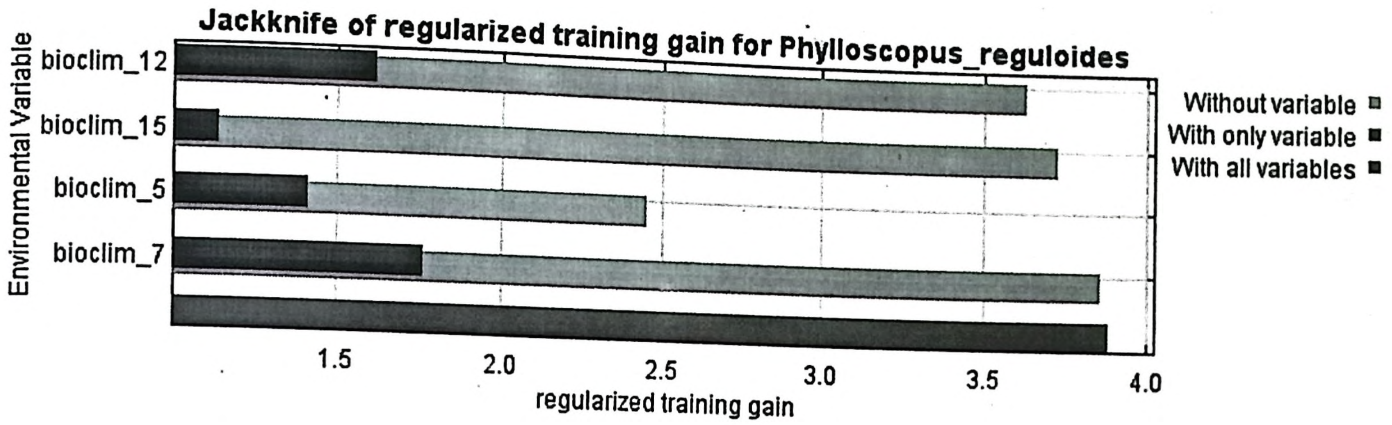


Figure 6a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

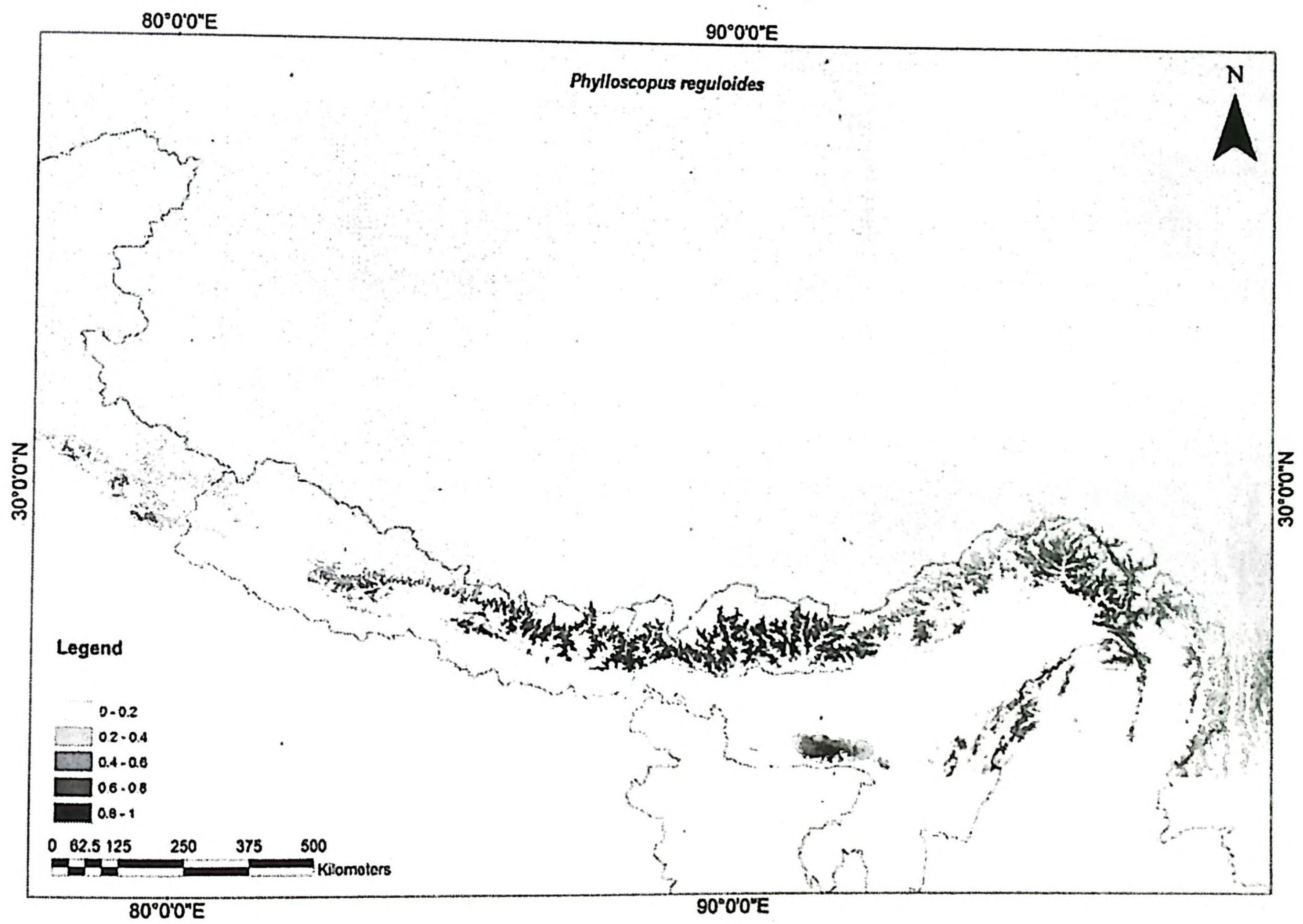


Figure 6b. Predicted geographic distribution of Ashy-throated Leaf Warbler (*Phylloscopus maculipennis*) across the Himalayas using occurrence locations from its breeding range in the east.

5. *Phylloscopus magnirostris*

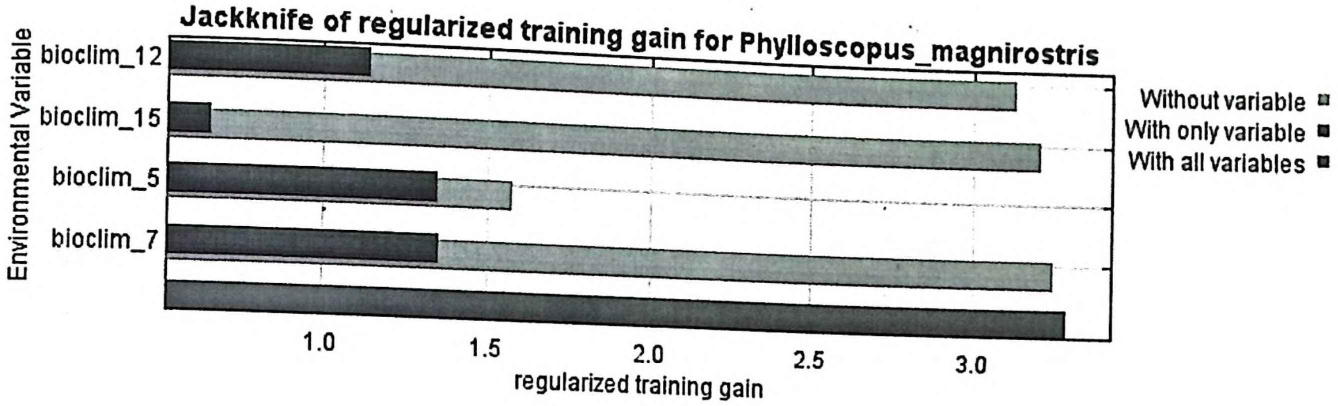


Figure 7a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

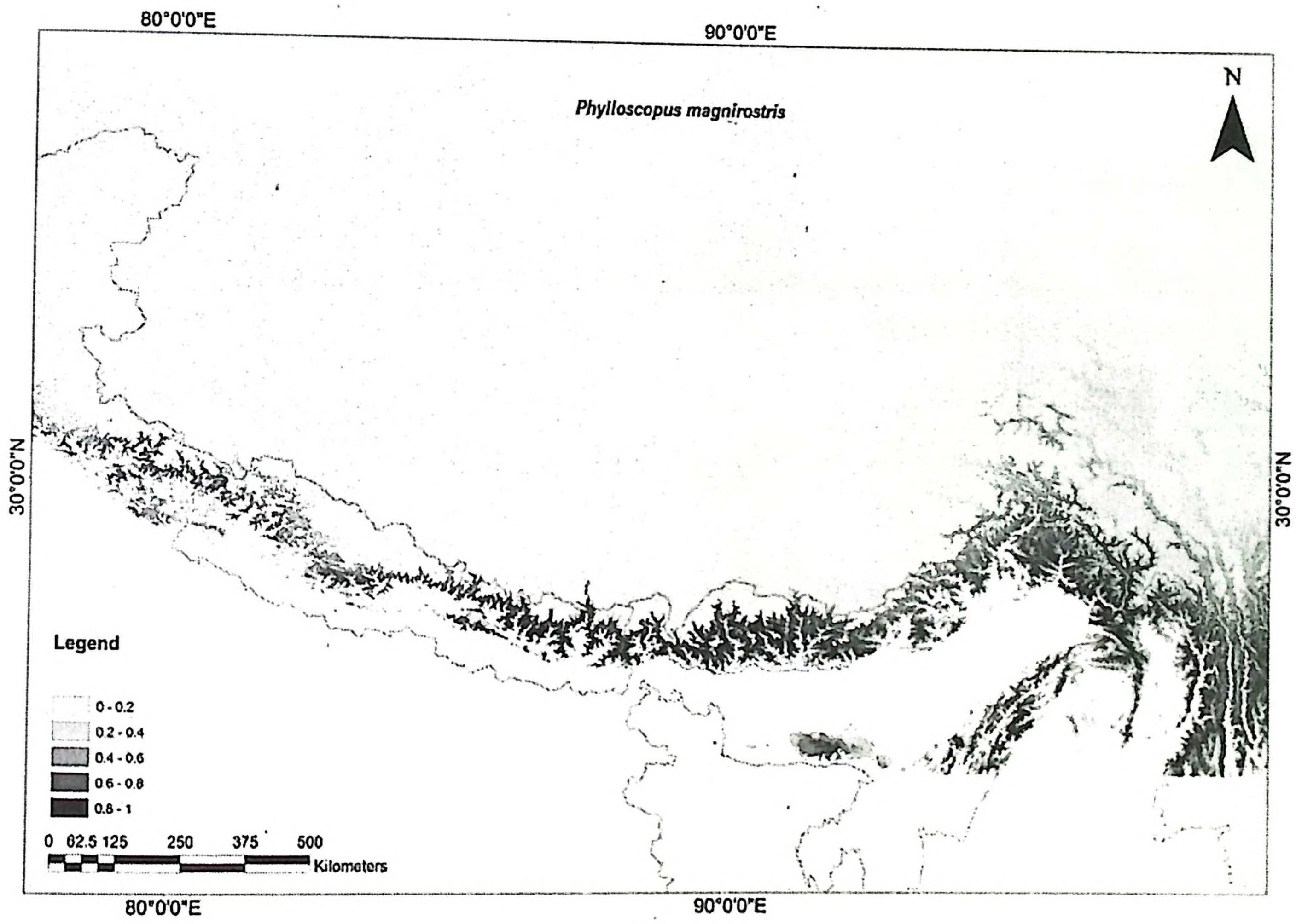


Figure 7b. Predicted geographic distribution of Large-billed Leaf Warbler (*Phylloscopus magnirostris*) across the Himalayas using occurrence locations from its breeding range in the east.

6. *Phylloscopus pulcher*

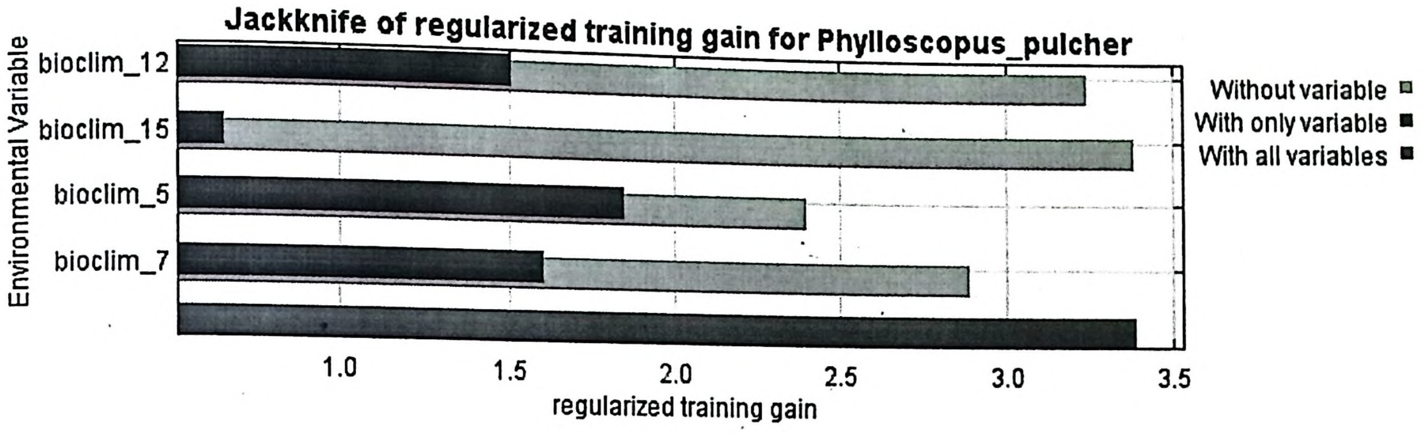


Figure 8a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

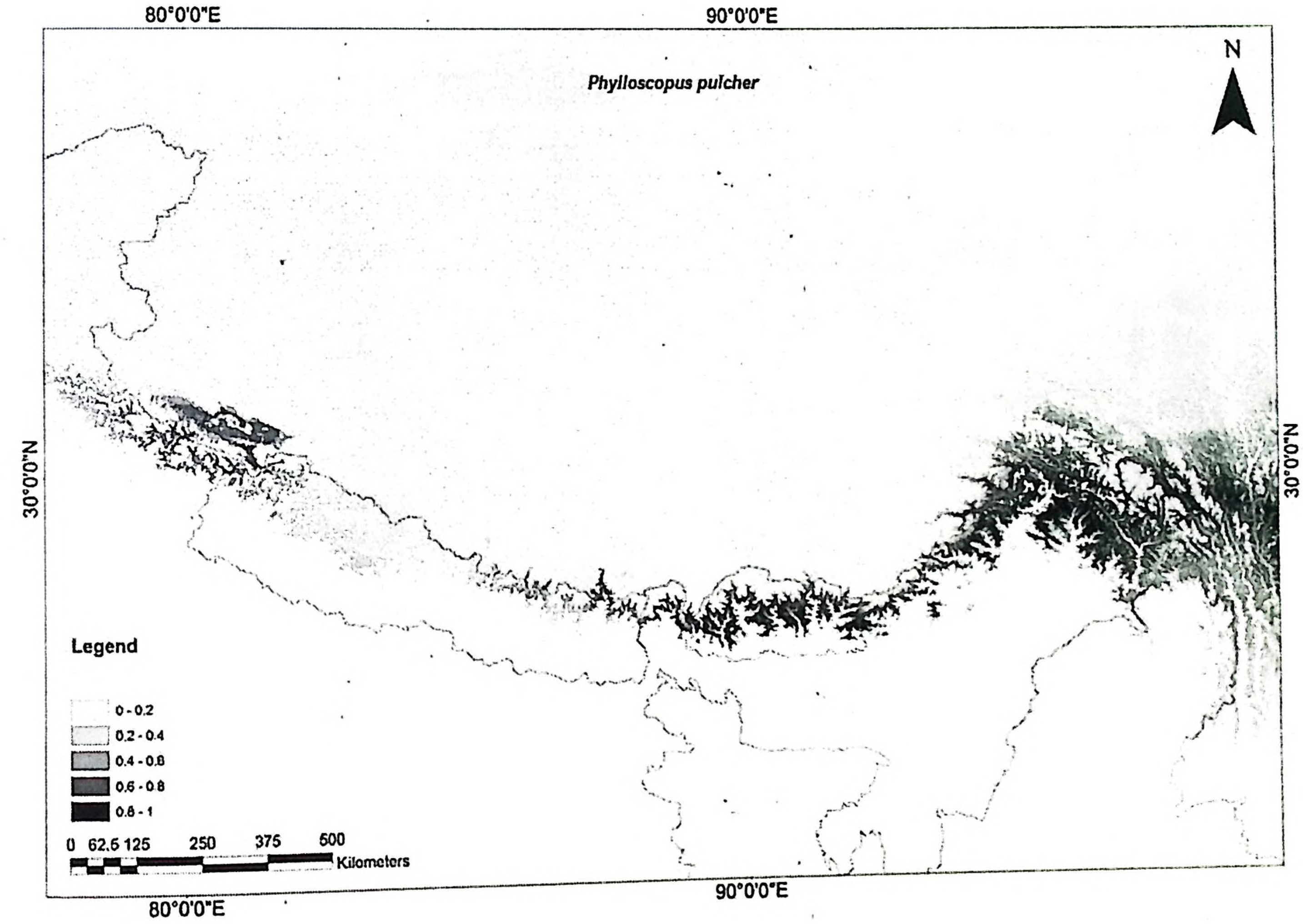


Figure 8b. Predicted geographic distribution of Buff-barred Leaf Warbler (*Phylloscopus pulcher*) across the Himalayas using occurrence locations from its breeding range in the east.

7. *Phylloscopus trochiloides*

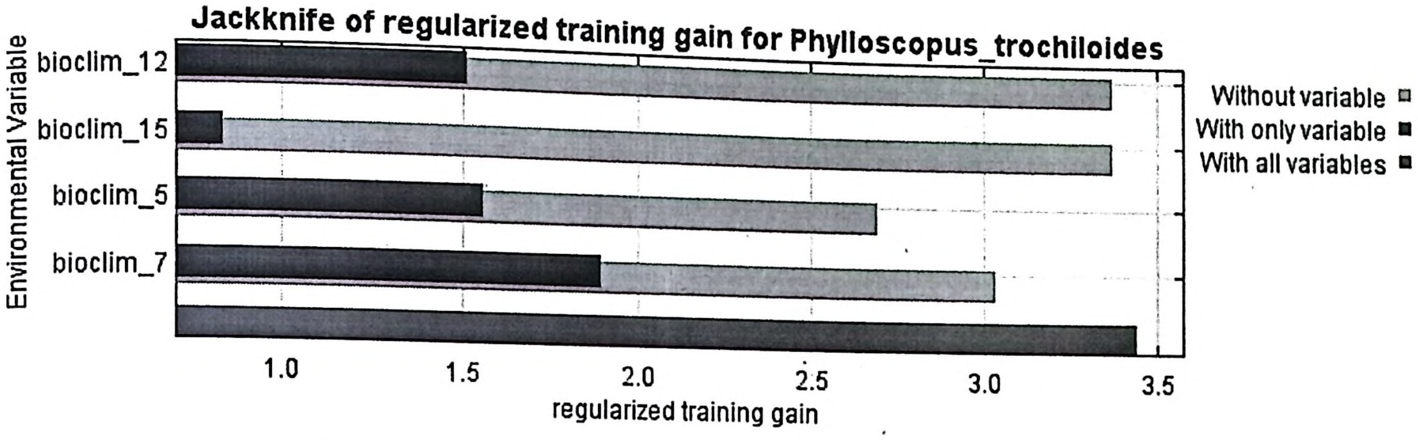


Figure 9a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

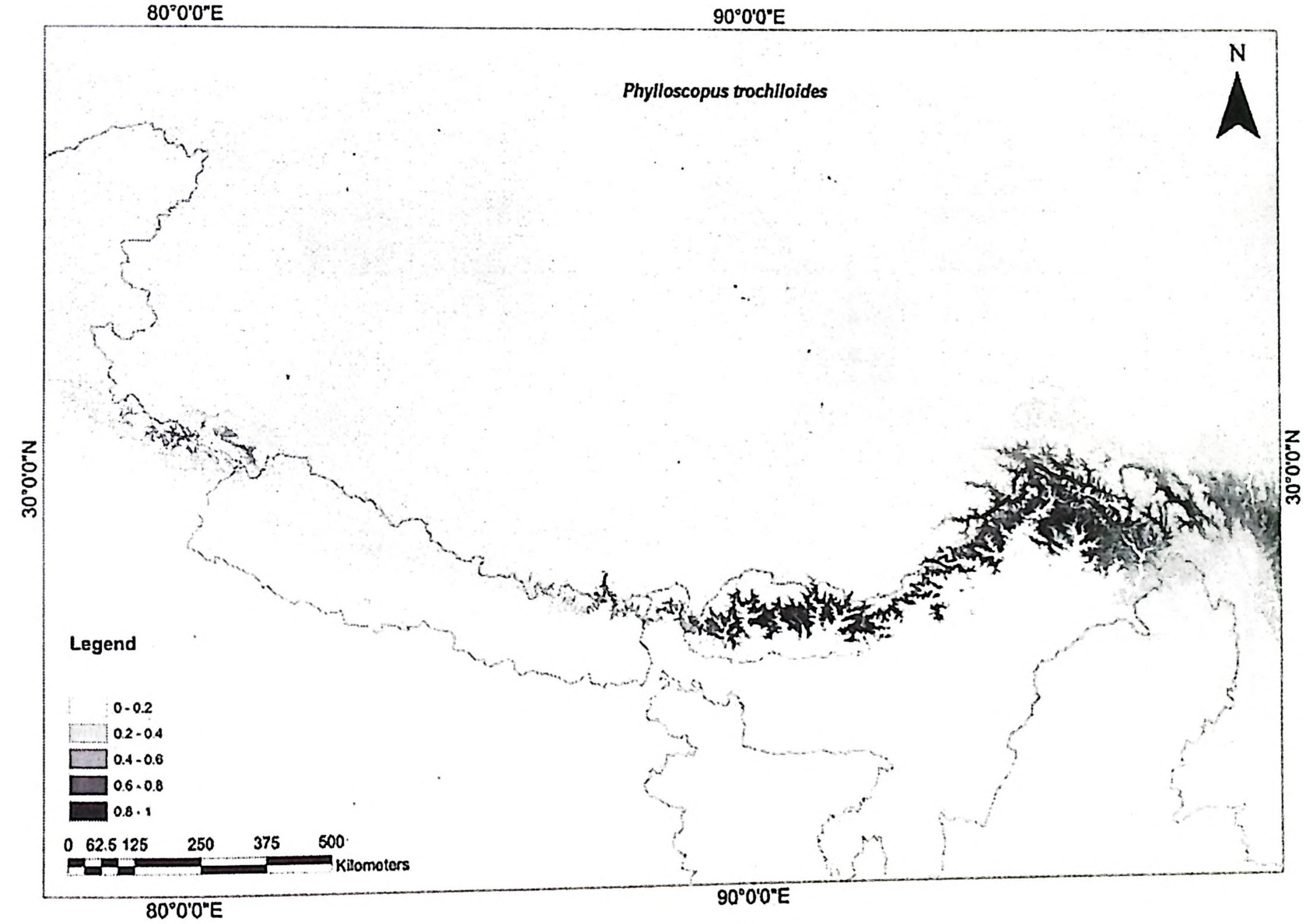


Figure 9b. Predicted geographic distribution of Greenish Warbler (*Phylloscopus trochiloides*) across the Himalayas using occurrence locations from its breeding range in the east.

8. *Phylloscopus xanthoschistos*

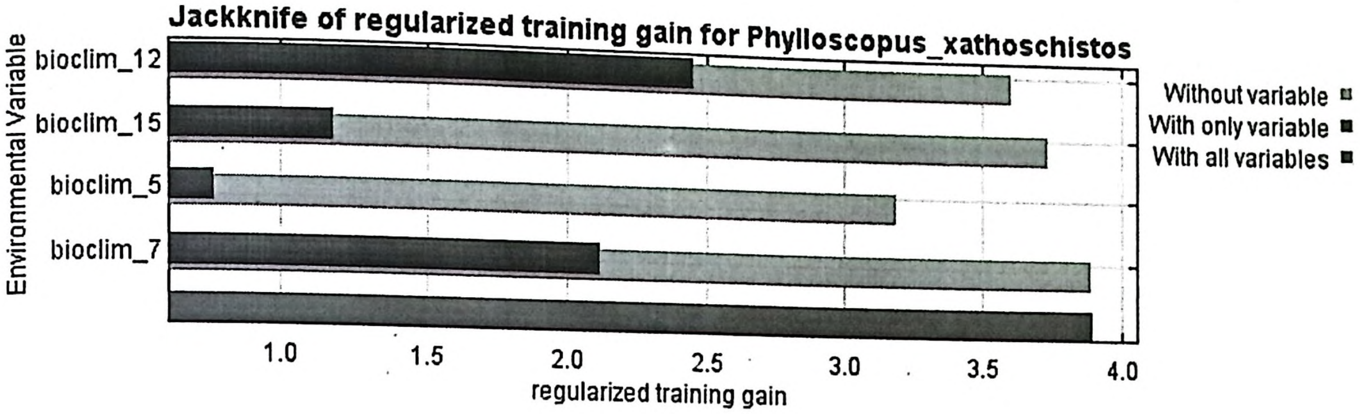


Figure 10a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

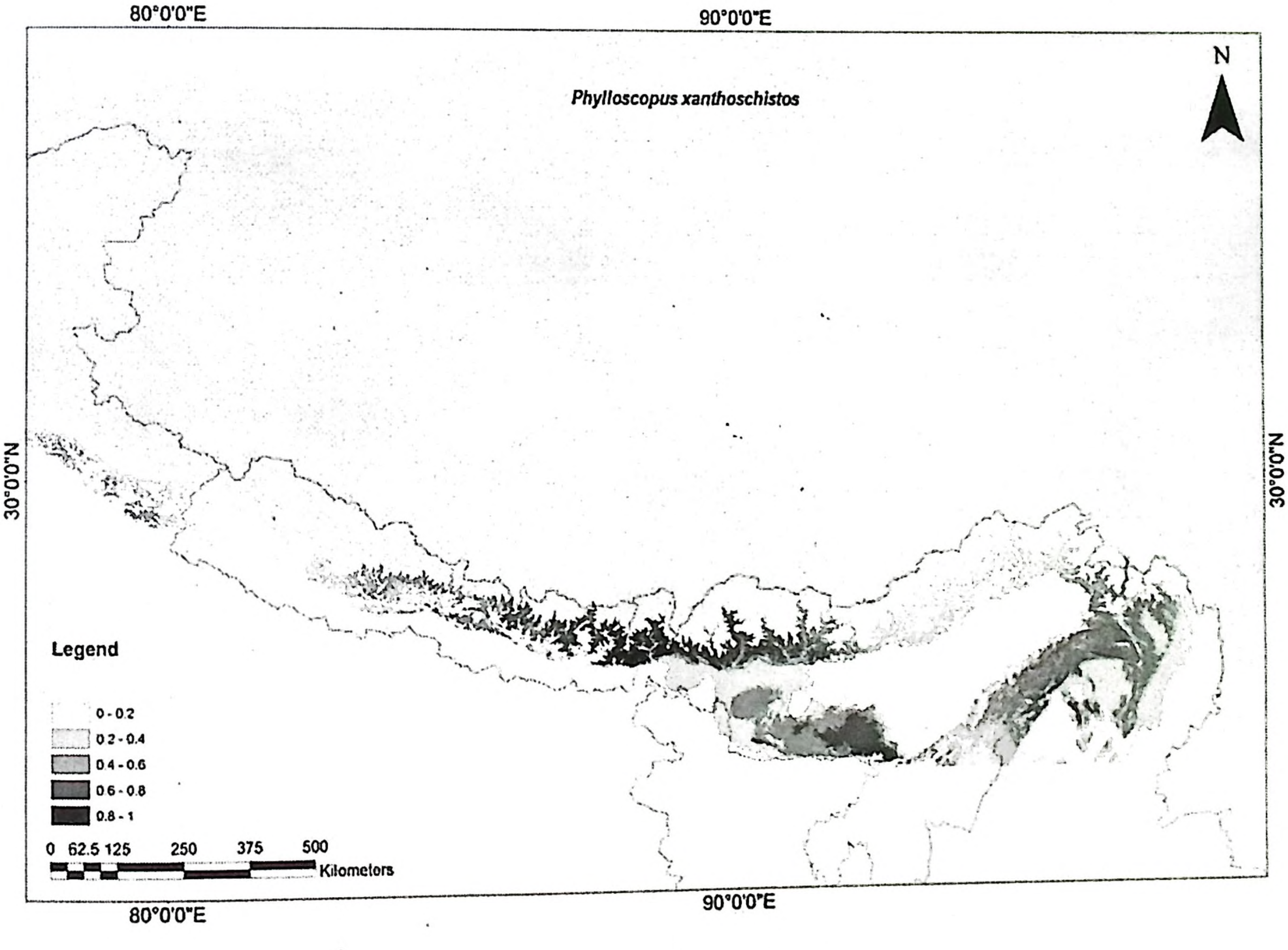


Figure 10b. Predicted geographic distribution of Grey-hooded Warbler (*Phylloscopus xanthoschistos*) across the Himalayas using occurrence locations from its breeding range in the east.

9. *Seicercus whistleri*

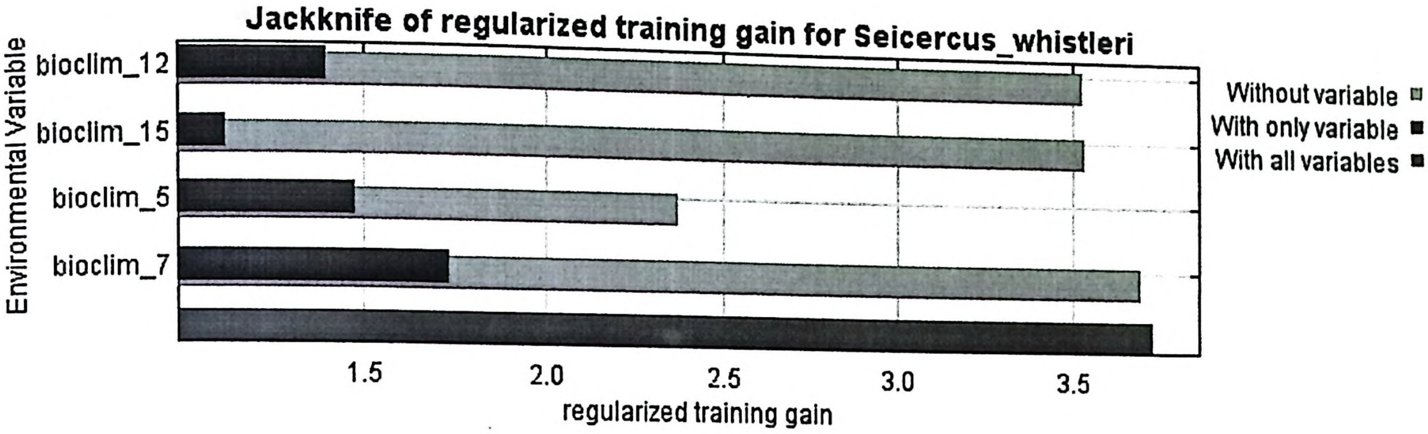


Figure 11a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

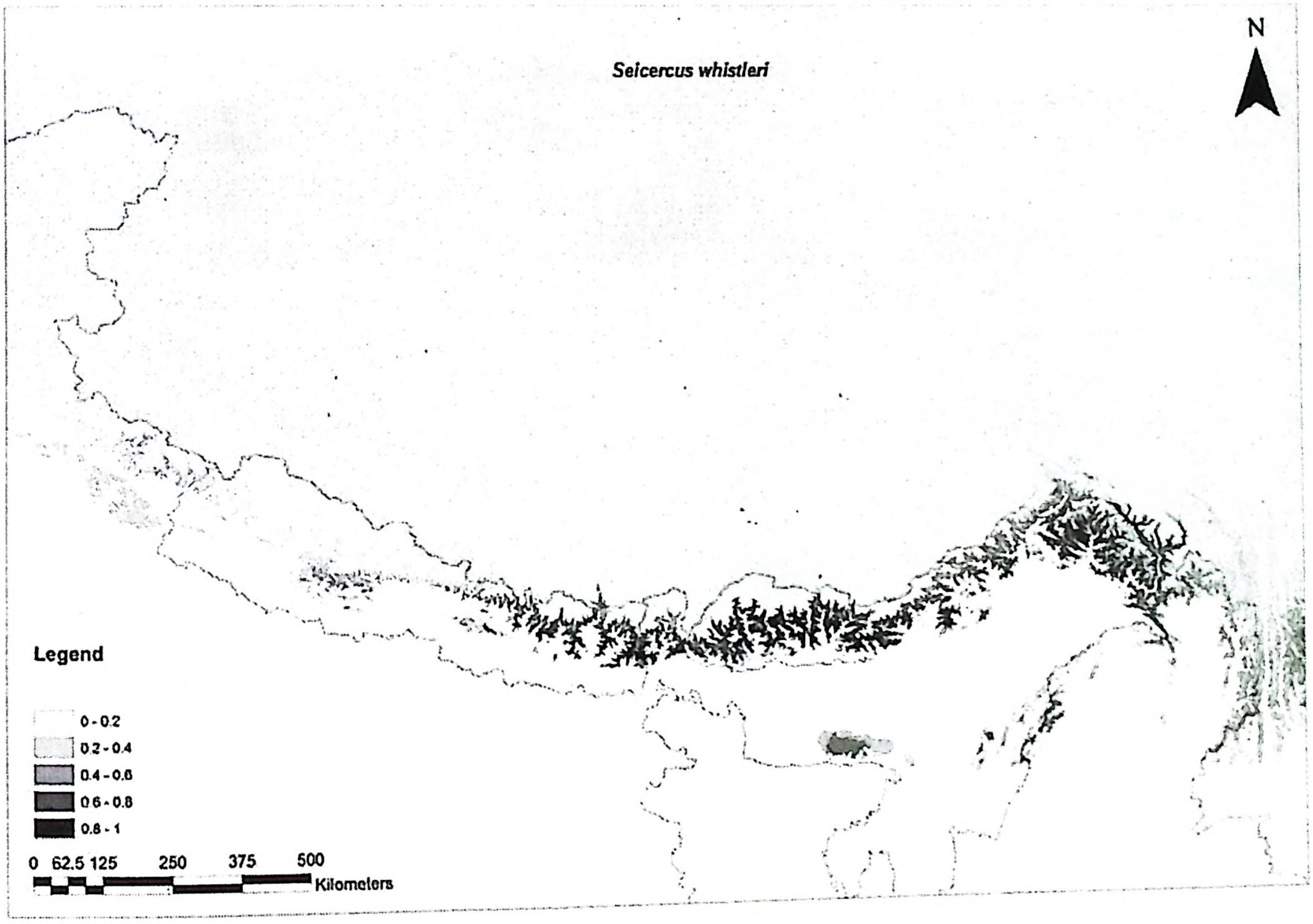


Figure 11b. Predicted geographic distribution of Whistler's Warbler (*Seicercus whistleri*) across the Himalayas using occurrence locations from its breeding range in the east.

10. Seicercus burkii

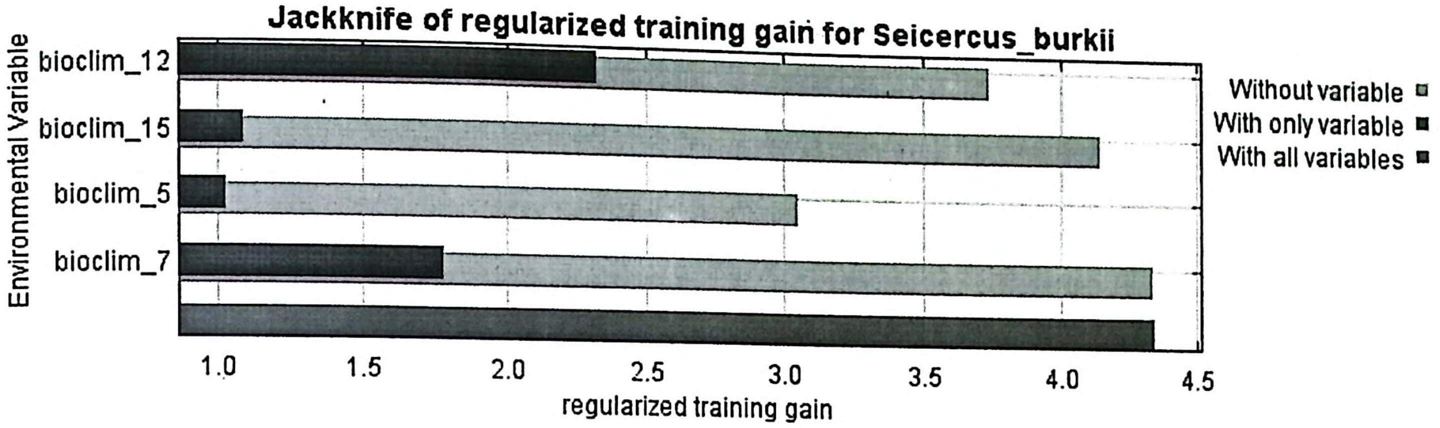


Figure 12a. Results of jackknife test of variable importance. The environmental variable with the highest gain when used in isolation has the most useful information by itself.

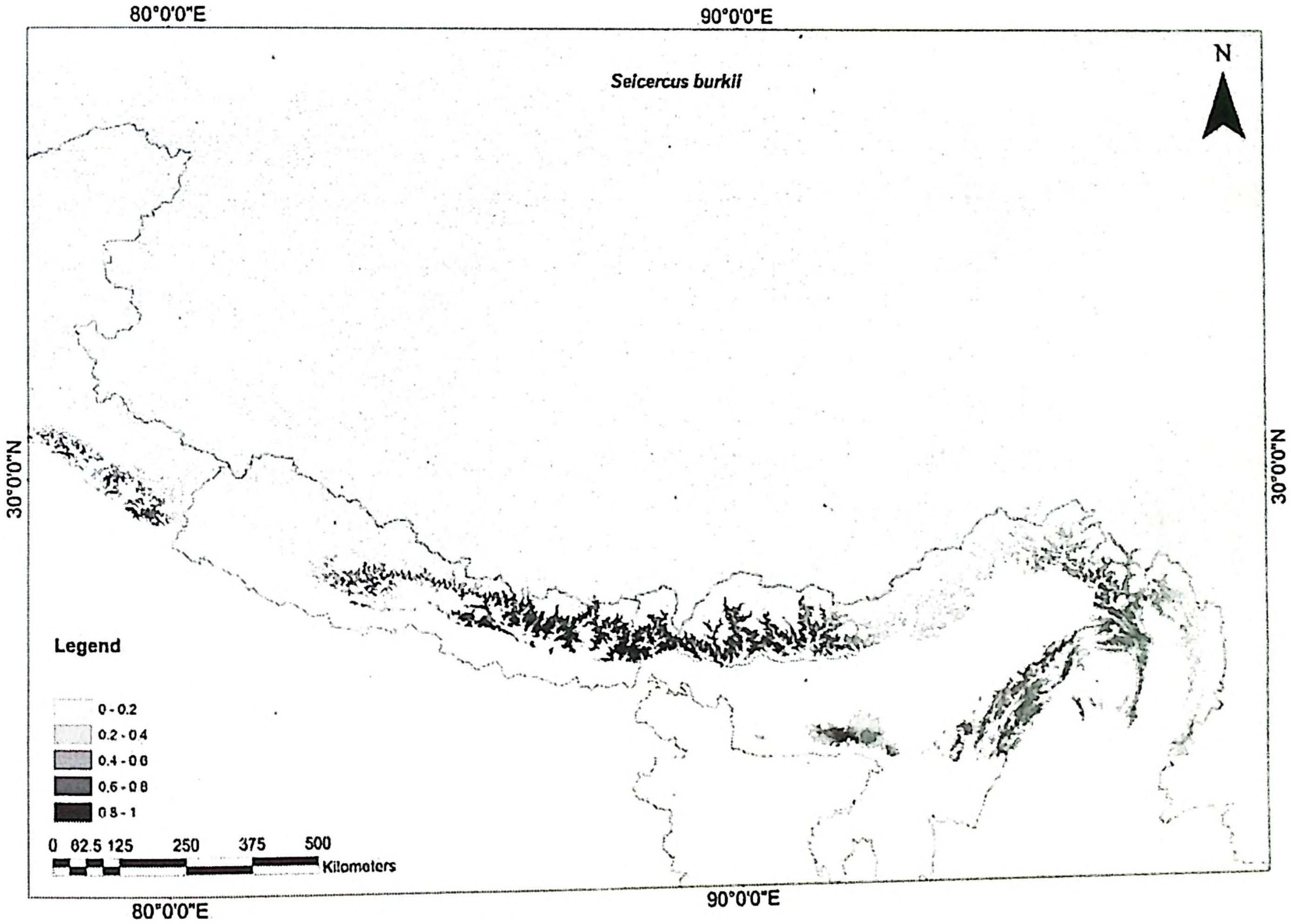


Figure 12b. Predicted geographic distribution of Green-crowned Warbler (*Seicercus burkii*) across the Himalayas using occurrence locations from its breeding range in the east.