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MOLECULAR PHYLOGENY AND COMPARATIVE BIOGEOGRAPHY OF OWLETS OF INDIA

A THESIS TO BE SUBMITTED TO
MANIPAL ACADEMY OF HIGHER EDUCATION
FOR FULFILLMENT OF THE REQUIREMENT FOR THE
AWARD OF THE DEGREE
OF
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BY
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UNDER THE GUIDANCE OF
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CERTIFICATE

This is to certify that the work incorporated in this thesis **"Molecular Phylogeny and Comparative Biogeography of Owlets of India"** submitted by **Mr. Pankaj Pramod Koparde** was carried out under my supervision. No part of this thesis has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged.

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ABSTRACT

Geographical ranges of species are a function of the interplay between ecology and evolutionary history. To understand range dynamics of co-distributed species, it is necessary to understand their evolutionary biogeography and ecology. The Endangered Forest Owlet (*Heteroglaux blewitti*) is a highly range-restricted species and is co-distributed with the widespread Spotted Owlet (*Athene brama*) and Jungle Owlet (*Glaucidium radiatum*) in India. The range of Spotted Owlet overlaps with the Eurasian Little Owl (*Athene noctua*). All four owlets show similar morphology and habits. To understand, processes underlying the nested pattern in the geographical distribution of the co-distributed owls, I used phylogenetic analysis to decipher their evolutionary biogeography, followed by past-projected Climatic Niche Models (CNMs) to understand the responses of the species to paleoclimate with respect to current time. I also modeled the ecological niche of Forest Owlet, incorporating remotely-sensed climate and vegetation data and topography, identified conservation priority areas, and future-projected the niche of Forest Owlet to 2050 to understand future threats to the species. I performed preliminary genetic analysis of a Forest Owlet population sampled from Madhya Pradesh. Results of the phylogenetic analysis showed that *H. blewitti* is not sister to *A. brama*, but nested within the *Athene* clade. *H. blewitti*, as well as other *Athene* members, diverged during Plio-Pleistocene boundary (3-5 Ma), possibly as a response to the changing climate. Past-projected CNMs showed that the suitable niche areas for all the owlets underwent cycles of expansion and reduction or a gradual expansion or reduction since the Last Interglacial (~120 Ka), and were nested in climatically stable areas. Forest Owlet niche models (ENMs) constructed using current climate, topography, and vegetation data, which were field-validated, resulted in identifying niche clusters for Forest Owlet in central India. When the ENMs were projected to future climate-change scenarios, reduction and shift in the niche extent were observed, indicating that future climate-change is going to impact the range of Forest Owlet severely. The genetic analysis of Forest Owlet individuals sampled from Madhya Pradesh population revealed low allelic diversity and high sharing of alleles. The results presented here underscore the need for basic research on endangered and co-distributed species to generate information that can aid conservation and form the basis of research recommendations such as deep phylogeny reconstruction, population connectivity and occupancy studies on the species.

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DECLARATION BY THE CANDIDATE

I, **Mr. Pankaj Pramod Koparde**, declare that this thesis, submitted for the degree of Doctor of Philosophy to the Manipal Academy of Higher Education, is my original work, conducted under the supervision of my guide **Dr. Shomita Mukherjee** (Principal Scientist, Division of Conservation Biology, Salim Ali Centre for Ornithology & Natural History). I also wish to inform that no part of the research has been submitted for a degree or examination at any university. References, help and material obtained from other sources have been duly acknowledged.

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ABBREVIATIONS

Abbreviation	**Long Form**
AOO	Area of Occupancy
CNM	Climatic Niche Model
EDGE	Evolutionary Distinct and Globally Endangered
ENM	Ecological Niche Model
EOO	Extent of Occurrence
ESS	Effective Sample Size
GCM	Global Circulation Model
IUCN	International Union for Conservation of Nature
Ka	Thousand Years Ago
LGM	Last Glacial Maximum
LIG	Last Interglacial
Ma	Million Years Ago
MCMC	Markov Chain Monte Carlo
MDH	Mid-Holocene
RCP	Representative Concentration Pathway

CHAPTER 1: GENERAL INTRODUCTION

Geographical distributions of species are a result of interactions between evolutionary biogeography, ecology, species interactions, and interactions with their environments. Therefore, an understanding of evolutionary and ecological processes that underlie patterns in species geographical distributions is essential. Most species are non-randomly distributed (Gilpin & Diamond 1984), and specialists are usually severely range-restricted and at a higher extinction risk (McKinney 1997, Biesmeijer et al. 2006, Colles et al. 2009), owing to their narrow niche breadth. Many specialists are also often endemic and endangered, with a limited area of occupancy and small population size, and therefore, are of conservation priority (Julliard et al. 2004). Identifying the drivers of geographical distributions of endemic and endangered species is crucial to their conservation.

Birds are among the few taxa that have been studied in detail over the past two centuries. There are rich natural history and ecological data available on many groups of birds (Edwards et al. 2005a, 2005b). Yet, unresolved phylogenies (Jetz et al. 2014, Reddy 2014) and lack of ecological data on tropical endemic species (Cayuvela et al. 2009) present a significant hurdle in research in avian biology. For instance, there is a paucity of phylogenetic data on owls (Order: Strigiformes) (Fuchs et al. 2008; Wink et al. 2009; Wink 2014; Wood et al. 2016) with tropical owls being very poorly represented. Given their cryptic nature, little effort has been made to understand patterns and drivers of geographical distributions of owls.

The tropics provide good landscapes to study endemic and endangered species. Owing to the characteristic seasonality, with wet and dry climates, tropics host a variety of niches and habitats, which explain high bird diversity (Brown 2014). They also provide a template for co-distributed generalist species, to interact with and impact the ranges of endemic and endangered species. From a biogeographic perspective, the population histories of such co-distributed species could influence niches and ranges of each other. Apart from species interactions, climate (Walther et al. 2002, Dirnböck et al. 2011, Goetz et al. 2014), topographical features (Davies et al. 2007, Moura et al. 2016), vegetation (Goetz et al. 2014, Moura et al. 2016), other biotic interactions (Wisz et al. 2013), resource availability (Mac Nally & Timewell 2005), and land-use change

(Chace & Walsh 2006) have been discussed to be significant factors shaping species distributions. Researching endemicity in tropical areas, therefore, mandates an inquiry into evolutionary relationships and biogeography of severely range-restricted and other co-distributed species, and the effect of biotic and abiotic factors on ranges and niches of these species.

In this thesis, I aimed to infer processes underlying the nested pattern in the geographical distribution of three co-distributed small owls of similar morphology and ecology. The study species are Jungle Owlet *Glaucidium radiatum* (Tickell, 1833), Spotted Owlet *Athene brama* (Temminck 1821), and the Endangered Forest Owlet *Heteroglaux blewitti* (Hume 1873) (BirdLife International 2017). At the end of range-restriction among the study species is the Forest Owlet, which is distributed only through central India followed by the Jungle Owlet distributed through India and Sri Lanka, and the Spotted Owlet which is distributed across the Indian Subcontinent with the exception of Sri Lanka (Figure 1). I used molecular phylogeny to infer evolutionary biogeography and niche modeling to explore the effect of Quaternary climatic fluctuations on the ranges of the owlets. Further, I predicted effects of future climate change on the species range and identified landscape-wide drivers of geographical distribution and conservation priority areas for the Endangered Forest Owlet.

1.1. Endemic Species – Evolutionary History and Ecology

The state of endemicity is associated with the geographical distribution of the species. Endemicity is realized in terms of geographic limits on suitable niches and habitats of a species, which might be constrained by ecological interactions with other species, including humans. The evolutionary history of species is a significant contributor to its contemporary geographical distribution (Sechrest et al. 2002). The process of speciation involves the establishment of intrinsic barriers to gene flow, between closely related populations. The barriers can be geographical (allopatric and peripatric speciation) or ecological (sympatric and parapatric speciation) (Bush 1975).

Distribution patterns of species are primarily dependent on the availability of suitable habitats (Coulon et al. 2006). Due to the discontinuity in suitable habitats, most species occur patchily in all or some parts of their distribution range (Koopman et al. 2007). Although patchily distributed, dispersal may genetically connect spatially distant populations, reducing the effect of habitat fragmentation to some extent (Hanski 1999). High endemism and population fragmentation are of conservation concern. Fragmented populations suffer increased extinction probabilities mainly from demographic processes (Lande 1988; Woodroffe & Ginsberg 1998) and secondarily from gradual genetic processes, such as inbreeding depression (Hedrick & Kalinowski 2000). Anthropogenic and ecological factors may further affect fragmentation resulting in isolated populations. If populations are isolated and small, there is a higher probability of inbreeding depression (Frankham 1995a, 1995b) and risk of local extinction (Maruyama & Kimura 1980; Hanski 1998; Reinhardt et al. 2005).

Habitat specialist species are at high risk of fragmentation-related extinction (Turner 1996). In such systems, it is vital to understand the causes of their restricted range and endangerment, especially if the species are of high conservation importance.

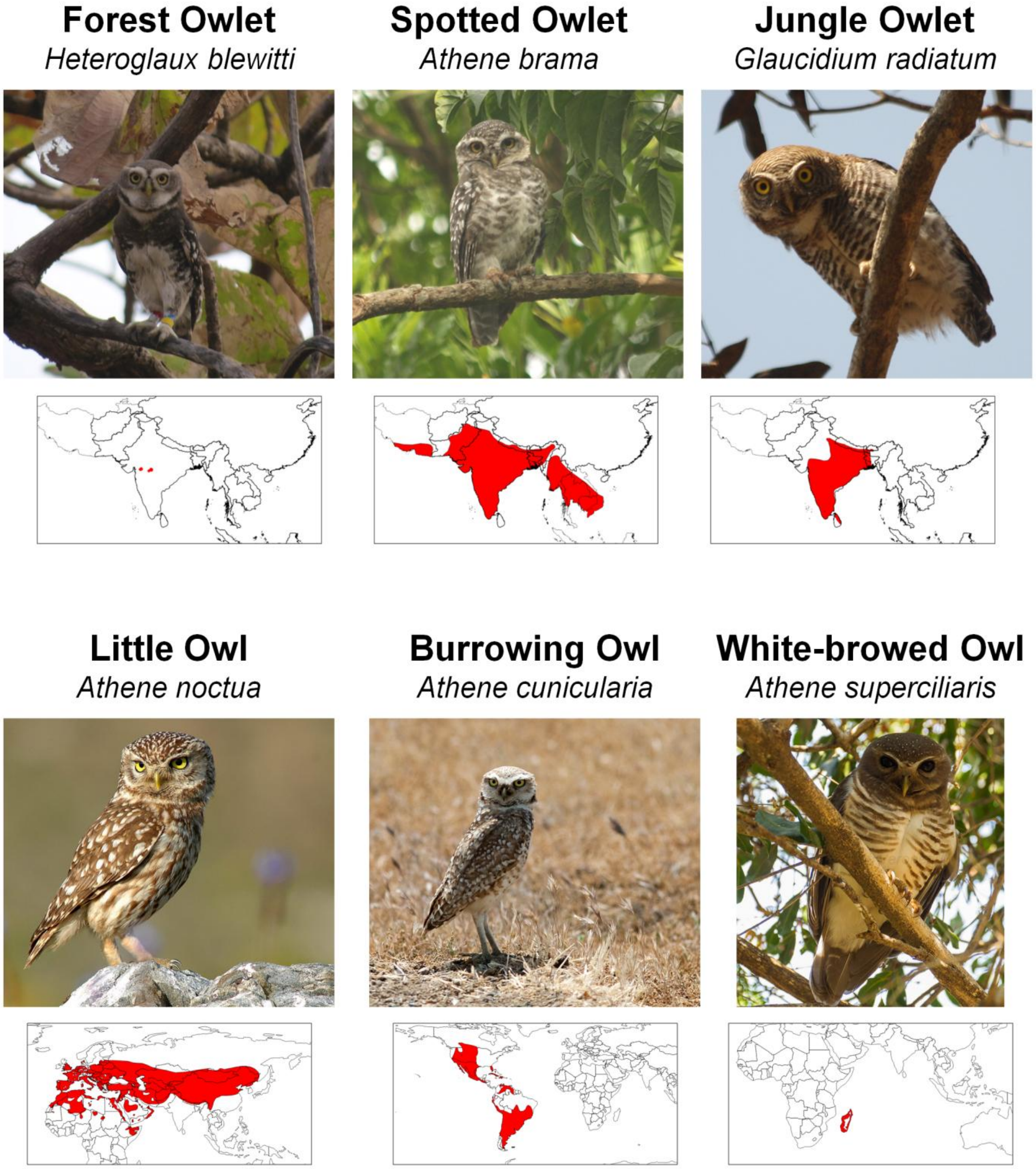

Figure 1. *Heteroglaux-Athene-Glaucidium* owls show similarity in morphology including plumage but differ in their spatial distribution. Forest Owlet, Spotted Owlet, and Jungle Owlet are co-distributed in India, Photo credits - Forest Owlet: Prachi Mehta, Spotted Owlet, and Jungle Owlet: Pankaj Koparde, Little Owl$^{\mathbf{WC}}$: Trebol-a, Burrowing Owl$^{\mathbf{WC}}$: Kevin Cole, and White-browed Owl$^{\mathbf{WC}}$: Francesco Veronesi. $^{\mathbf{WC}}$: Obtained through Wikimedia Commons for use.

1.2. Endemic Species – The Role of Paleoclimate

The role of climate change in shaping species distributions has been discussed in detail (Walther et al. 2002, Parmesan & Yohe 2003). Specialist species, occupying narrow climatic niches, are more prone to changes in climate; the change sometimes severely reducing populations of such species (Jansson 2003, Dirnbock et al. 2011). Climate change may affect geographical distributions, ranges, population sizes, demographic factors and could have long-term impacts altering responses of species to natural selection (Crick 2004). The evidence for the role of climate change in bird distributions comes from bird fossils, ecological data, phylogeny and phylogeography studies, and explicit past-projected Climatic Niche Models (CNMs) (Gibbons & Wotton 1996, Hilbert et al. 2004, Robin et al. 2010, Zhao et al. 2012, Smith et al. 2013, Ramchandran et al. 2017).

Phylogenies coupled with molecular dating and ancestral area reconstructions provide the best means to reconstruct evolutionary biogeography of species. Such analyses provide testable hypotheses on evolutionary relationships among species suggesting possible processes behind speciation and a divergence date estimate to decipher the evolutionary biogeography of the species concerned. Therefore, dated phylogenies provide the first line of evidence indicating whether the paleoclimate, geological changes or other secondary processes caused speciation. With this first line of evidence, the effect of historical climate change can be tested in a statistical framework. With an easy access to the current and historical climate databases and species presence data generated through crowd-sourcing and the rise of easy-to-use algorithms for constructing niche models, recently, several studies (Gibbons & Wotton 1996, Hilbert et al. 2004, Robin et al. 2010, Zhao et al. 2012, Smith et al. 2013, Ramachandran et al. 2017) have used past- and future-projected niche models, to highlight the role of paleoclimate and future climate in shaping species distributions.

Most of these studies include three distinct historical time periods, namely, the Last Interglacial (LIG, ~1,20,000-1,40,000 years ago), Last Glacial Maximum (LGM, ~18000-22000 years ago), and Mid Holocene (MDH, ~6000 years ago). During the LIG, warmer climate, relative to LGM, prevailed and there was an increase in global sea levels (Otto-Bliesner et al. 2006). Evidence suggests that during the LIG much warmer summers occurred in the Arctic than during the LGM and current time-period. During LIG, tropics exhibited a warmer and wetter climate. There is evidence for large tracts of moist rainforest across most of the tropics during the LIG (Van der Hammen 1974, Kershaw 1994, Sukumar et al. 1995, Prabhu et al. 2004). The LGM characterized the most recent driest period on earth. During this time, most of the northern parts of earth were covered by large ice sheets with low average temperatures, causing an increase in aridity and a drop in sea levels. This led to a change in climate and topography, and climate-associated change in vegetation (Anhuf et al. 2006), probably changing ranges of many bird species as a response. Vegetation changed from moist rainforests to dry forests in the tropics during the LGM (Van der Hammen 1974, Sukumar et al. 1995, Ray and Adams 2001, Prabhu et al. 2004, Bird et al. 2005, Anhuf et al. 2006). During the MDH, there was an increase in temperature and moisture with vegetative cover similar to that in the LIG. However, regional studies (Randhawa 1945, Sukumar et al. 1993, Chauhan 2002, Gupta et al. 2003, Shin et al. 2003, Mayle & Power 2008, Prado et al. 2013, Dallmeyer et al. 2017) indicate that the effect of warming and establishment of seasonality was not uniform throughout the tropics, with certain areas experiencing a different regional climate than the others (Karanth 2003).

Such fluctuations in climate, caused by Milankovitch oscillations (Webb & Bartlein 1992), are known to impact ranges of species, with areas that experienced lower variation in climate retaining more range-restricted or endemic species (Figure 2, Dynesius & Jansson 2000). This hypothesis was tested with a global multi-taxa dataset using spatially explicit niche models (Jansson 2003) supported by regional studies on South American and African birds (Fjeldsa 1994, 1995). These studies showed that paleoendemic and neoendemic species peaked in areas with high climatic stability.

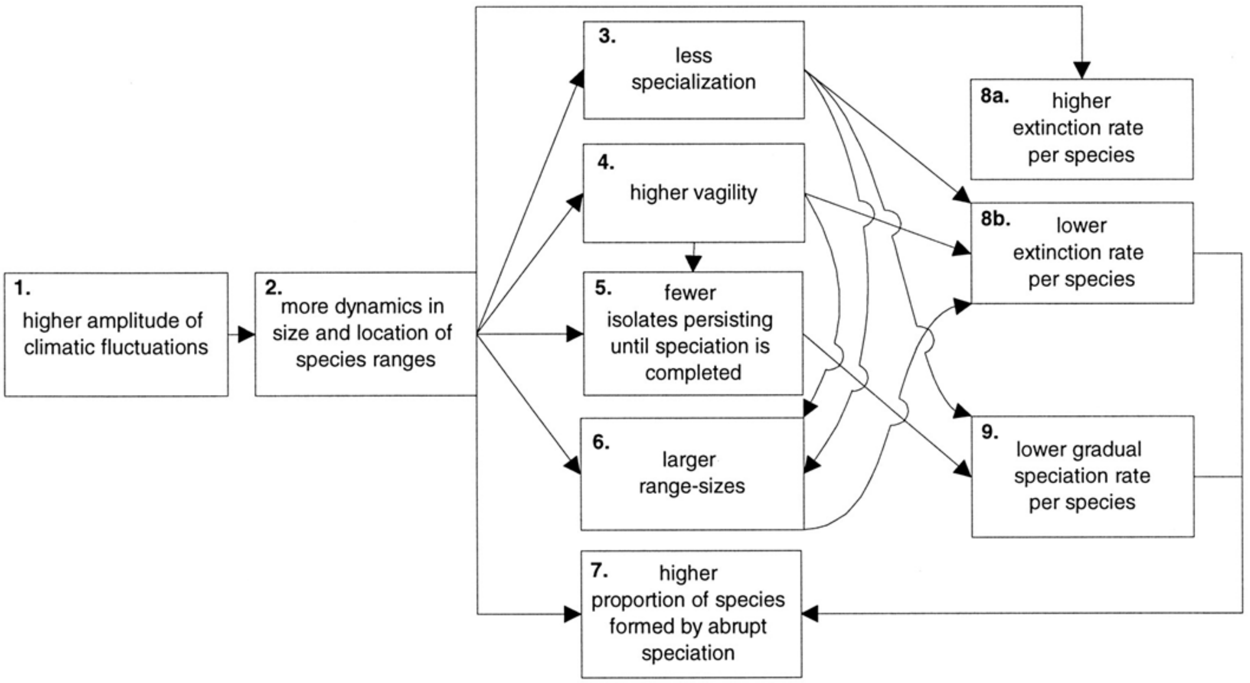

Figure 2. Milankovitch oscillations affect species ranges (*reproduced from* Dynesius & Jansson 2000).

1.3. Endemic Species – Future Climate Change and Conservation

The Anthropocene, an era dominated by human activities, has been discussed to be the period of accelerated species extinction caused mainly due to modern human-induced disturbances (Barnosky et al. 2011, Pievani 2014, Ceballos et al. 2017). The current rate of species extinction is many-folds higher than the background rate, suggesting that the earth is entering into the sixth mass extinction (Barnosky et al. 2011). Human-induced activities leading to habitat degradation and loss, conversion of land-use and over-exploitation of natural resources are some factors responsible for the acceleration in loss of biodiversity. Based on historical species extinctions, Pimm & Jenkins (2011) propose rarity of the species to be the most powerful predictor of its extinction risk, apart from their small geographic range size and low density (Pimm et al. 2014).

Anthropogenic climate change is mainly due to the emission of heat-trapping gases through industrial and domestic pollution and changing land-use leading to an increase in surface temperatures. Based on current greenhouse gas emission rates and historical climate change, the Intergovernmental Panel on Climate Change (IPCC) has come up with emission scenarios. Based on these scenarios the future climate has been constructed (Bernstein et al. 2008). The general trends in future climate are a rise in temperature, sea levels, and a shift in high precipitation areas (Walsh et al. 2016), leading to changes in biotic and abiotic elements. Climate change has been implicated as the sole trigger in extinction risks for multiple taxa (Pounds et al. 1999, Thomas et al. 2004). This necessitates assessing the effects of climate change on rare and endangered species to plan their conservation, keeping future changes in the species distribution in mind, to minimize their extinction risk.

Conserving endangered species primarily depends on identification of factors causing their endangerment, followed by implementing strategies which will effectively safeguard such species from future habitat loss, population reduction, reduction in population viability, ensuring long-term survival of the species even when the external conservation action stops (Soulé 1985). International conservation listings such as IUCN, Evolutionary Distinct and Globally Endangered (EDGE), and Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) use a variety of criteria to assign threat status to assessed species. IUCN uses Extent of Occurrence (EOO), Area of Occurrence (AOO), population size, and trend in population size as their major criteria (IUCN 2001). EDGE uses phylogenetic information providing an Evolutionary Distinctness (ED) score coupled with IUCN information. CITES refers to endangerment along with trade value of a species to assign a threat status. This makes it clear that international conservation listings rely not only on ecology but also evolutionary biology and socio-economic valuation of species. Therefore, before realizing conservation requirements of a species, generating data on its ecology and evolutionary biology, as well as socio-economic importance is a must. This could be achieved by sampling the species for phylogeny, phylogeography, population genetics, functional connectivity, habitat and niche ecology, behavioral ecology, demography, and finally identifying population hotspots and providing legal protection to the populations making sure that dispersal is not hampered across a regime of protected and non-protected areas. Such long-term conservation planning has produced a handful of success stories in tropical countries.

In this thesis, I generated baseline data on the Endangered Forest Owlet using a combination of methods including phylogeny (Chapter 2), paleoclimatic niche modeling (Chapter 3), forward-time climatic niche modeling and identification of conservation hotspots (Chapter 4 and 5), and population genetics (Chapter 4). Results from the present study provide directions for future conservation research and action.

The terms ‘niche’ and ‘niche extent’ used throughout the thesis refer to the modeled niche using MaxEnt program and geographical area covering the suitable niche respectively. The term ‘climatic niche’ (chapter 3, 4, and 5) refers to niche as a function of temperature and precipitation variables, while the term ‘ecological niche’ (chapter 4) is used in the context of niche as a function of vegetation, topography, and climate variables. Following IUCN (2001) definitions of AOO and EOO, throughout the thesis, predicted suitable niche extent is considered as AOO and minimum convex hull encompassing the suitable niche extent is referred as EOO. AOO is a subset of EOO.

1.4. Focal Species

Owlets and pygmy owls (Family - Strigidae) are small-sized owls, ranging between 16 and 24 cm (Ali & Ripley 1983, Dickinson & Remsen 2013). They are mainly ambushed predators, crepuscular and nocturnal, that feed on small-sized prey such as insects, amphibians, snakes, small birds, and rodents. Because of their nocturnal nature and similarity in many morphological traits, they are difficult to identify and study (Wink et al. 2009). Six species of small-sized owls are known from India, represented by three genera – *Athene* (Boie, 1822), *Glaucidium* (Boie, 1826), and *Heteroglaux* (Hume, 1873). The genus *Athene* includes owlets, represented by four species worldwide (Figure 1) – Oriental Spotted Owlet *Athene brama* Temminck, 1821, Palearctic Little Owl *Athene noctua* Scopoli 1769, Neotropical and Nearctic Burrowing Owl *Athene cunicularia* Molina 1782, and Madagascan White-browed Owl *Athene superciliaris* Vieillot 1817. Each of the *Athene* species is further subdivided into multiple subspecies, except *A. superciliaris.* The members of *Athene* occur in all the continents, except in Australia and Antarctica. *A. cunicularia* is the single species occurring in Americas. The genus *Heteroglaux* is a monotypic genus represented by *H. blewitti* (Rasmussen & Collar 2013). The genus *Glaucidium* includes pygmy owls with 25 species spread worldwide (Dickinson & Remsen 2013). The genus *Glaucidium* is the most speciose genus among small-sized owl genera globally.

Throughout this thesis, I refer small-sized owls as ‘owlets.’

To understand the processes underlying distribution pattern of co-distributed species, I worked on three Indian owlets (Forest Owlet, Spotted Owlet, and Jungle Owlet) that are co-distributed (Figure 1), show similarity in their morphology and size, and overlap in diet and habitat-use. In the climate niche analysis, I included the Palearctic species, Little Owl, along with the three Indian owlets, to better understand broad-scale climate-driven patterns in the geographical distribution of these species. Among thus four species, the Forest Owlet is listed as Endangered in the IUCN Red List (BirdLife International 2017), and as a distinct evolutionary lineage in EDGE (Jetz et al. 2014). All other study owls are listed as Least Concern in IUCN Red-list (BirdLife International 2017).

1.4.1. Forest Owlet *Heteroglaux blewitti* (Hume, 1873)

The Forest Owlet, endemic to India (Figure 1), has been a taxonomic mystery since its discovery in 1872. After its discovery, the species was recorded from 1872 to 1883 (Hume 1873; Ball 1878), after which there were no further records for more than hundred years resulting in some researchers thinking that the species may have gone extinct. In 1997, King & Rasmussen (1998) rediscovered the species in Taloda, Maharashtra, after 113 years of its last authentic record. Since then, further extensive surveys across the central Indian landscape have resulted in numerous records of the species in Maharashtra, Madhya Pradesh, and Gujarat states. Initially, in 1988, IUCN recognized Forest Owlet as a Threatened species. As more information on the species was gathered, after its re-discovery in 1998, owing to its severely fragmented distribution and low population, it was placed in the Critically Endangered category. In 2017, additional information on the species geographical distribution and estimation of its EOO based on an Ecological Niche Model (ENM) has resulted in down-listing the species to the Endangered category (BirdLife International 2017).

The Endangered Forest Owlet is an ornithological enigma. There have been many opinions on the phylogenetic affinities of *H. blewitti* by ornithologists over the centuries. In the past, the species has alternatively been placed in either the genus *Heteroglaux* (Hume 1873, Dubois 1904, Gill & Donsker 2013, Dickinson & Remsen 2013, Rasmussen & Collar 2013) or *Athene* (Blanford 1895, Baker 1934, Ali & Ripley 1983, Monroe & Sibley 1993, del Hoyo et al. 1999, Clements et al. 2013). Additionally, some researchers have claimed *Heteroglaux* to be a subgenus of *Glaucidium* (König et al. 1999). Therefore, there remains uncertainty in the taxonomy of Forest Owlet, even after 140 years of its discovery.

The Forest Owlet is historically known to inhabit moist-deciduous forests, especially wild mango groves, characterized by the presence of streams (Hume 1873, Ali & Ripley 1983). In recent records, the species is found in tropical dry-deciduous forests, especially teak forests, teak-holding miscellaneous forests, including areas close to human habitation (Mehta et al. 2008, Rasmussen & Anderton 2012). Presently, scarce information is available on the spatial distribution of the species and causes of its restricted range. Studies (Jathar & Rahmani 2004, Mehta et al. 2008) have shown that the species occurs in old-growth teak-dominated dry deciduous forests. The breeding season is observed to be October to March in Madhya Pradesh (Mehta et al. 2008). The species is currently facing several conservation challenges such as large-scale habitat loss due to timber extraction (BirdLife International 2017) and hunting for use in witch-craft and food (Jathar & Rahmani 2004, Mehta et al. 2017).

The Forest Owlet is placed under the Schedule I of the Indian Wildlife (Protection) Act (Anon. 1972), prohibiting hunting and trade of the species. Some of the strong-holds of the species population lie in protected areas such as wildlife sanctuaries, tiger reserves, and reserve forests; however, a considerable proportion of the population has also been observed in non-protected areas. BirdLife International (2017) recommends basic research on the species ecology to understand drivers of its distribution and on-ground conservation action to conserve the species.

1.4.2. Spotted Owlet *Athene brama* (Temminck)

The Spotted Owlet listed under Least Concern in the IUCN Red List, and under Schedule IV of the Indian Wildlife (Protection) Act (Anon.1972) has a wide distribution spanning most of the Indian subcontinent except Sri Lanka (Ali & Ripley 1983, Rasmussen & Anderton 2012) (Figure 1). Dickinson & Remsen (2013) classify *A. brama* into five subspecies – *A. b. indica* Franklin 1831, *A. b. ultra* Ripley 1948, *A. b. brama* Temminck 1821, *A. b. pulchra* Hume 1873, and *A. b. mayri* Deignan 1941. Additionally, Baker (1934) and Clements et al. (2013) consider *A. b. albida* Koelz 1950, distributed in south Iran and Pakistan, as a subspecies of *A. brama*. The subspecies *A. b. indica* is distributed in the northwest region of the Indian subcontinent (Rasmussen & Anderton 2012), from southern Iran to north and central India, Nepal, Bhutan and Bangladesh (Dickinson & Remsen 2013). The species is found above the 20º N latitude (Ali & Ripley 1983).

A. b. albida is distributed in Iran and Baluchistan, and possibly some part of northwestern India (Koelz 1950). *A. b. brama* ranges throughout southern Peninsular India, below the 20º N latitude in India. *A. b. ultra* is distributed in the Lakhimpur district of northeast Assam, and north and south of the Brahmaputra and Lohit Rivers (Ali & Ripley 1983). *A. b. pulchra* is distributed in central and south Myanmar (Dickinson & Remsen 2013). *A. b. mayri* is distributed across southern continental South-East Asia, except the extreme southwest (Dickinson & Remsen 2013).

The Spotted Owlet inhabits villages and cultivation, groves of ancient trees, and ruins (Ali & Ripley 1983). It has been observed not to be associated with dense forests (Blanford 1895, Ali & Ripley 1983). The species is crepuscular and nocturnal in habit, usually seen roosting in the daytime. Studies on the diet of the species (Jadhav & Parasharya 2003, Ramanujam & Verzhutskii 2004, Pande et al. 2007, Santhanakrishnan et al. 2011, Nadeem et al. 2012) show that it feeds on beetles, cockroaches, scorpions, mollusks, other invertebrates, toads, snakes, rodents, bats, and small birds. Pande et al. (2007) suggest that Spotted Owlet pairs living around human habitation have higher breeding success as compared to those located further away due to high-value prey available in the proximity of human settlements .

1.4.3. Jungle Owlet *Glaucidium radiatum* (Temminck)

The Jungle Owlet, listed under Least Concern in the IUCN and Schedule IV of the Indian Wildlife (Protection) Act (Anon. 1972), is endemic to India and Sri Lanka (Figure 1). Two subspecies have been described for the species – *G. r. radiatum* and *G. r. malabaricum* (Ali & Ripley 1983, Dickinson & Remsen 2013). Based on morphological differences between the two subspecies, Rasmussen & Anderton (2012) claim a revision in the species status for *G. r. malabaricum*. The nominate subspecies *G. r. radiatum* is spread in Bhutan, most parts of India from lower Himalayas to extreme south and in Sri Lanka (Blanford 1895). In Sri Lanka, it is distributed in the dry zone and adjacent eastern hills (Ali & Ripley 1983; Rasmussen & Anderton 2012). *G. r. malabaricum* occurs in southwest India from 16º N latitude southwards (Ali & Ripley 1983).

The Jungle Owlet inhabits scrub to dry and moist-deciduous forests, breeding during March to May. It is mainly a crepuscular species, sometimes seen roosting and flying in the daytime (Ali & Ripley 1983). There are no recent studies on the diet of Jungle Owlet. Past studies (Ali &

Ripley 1983, Mason 1911, Whistler 1949) mention that the species feeds on insects, mollusks, small birds, lizards, small birds, and mice.

1.4.4. Little Owl *Athene noctua* (Scopoli)

The Little Owl has a much broader distribution among the focal owlets (Figure 1). Spread across most of Europe (except the United Kingdom), Asia and North Africa, the species was recently introduced to the United Kingdom and New Zealand. Dickinson & Remsen (2013) recognize thirteen subspecies of *A. noctua*. König & Weick (2008) claim that *A. noctua* is a species complex. It is listed as a Least Concern species in the IUCN Red List and Schedule IV of the Indian Wildlife (Protection) Act (Anon. 1972). The subspecies distributed in Northern India is *A. n. bactriana*.

The species is a specialist of bare ground, semi-desert habitats, often found in agricultural lands, woodland edges, and gardens (Ali & Ripley 1983, Baker 1927, Witherby 1943). Like Spotted Owlet, it is known to occupy ruins, quarries, and rocky outcrops. Subspecies *bactriana* breeds during March to June (Ali & Ripley 1983), whereas other races are known to breed during March to August (Holt et al. 2018).

1.5. Research Gaps Identified

Endemic and endangered species make good models to enhance the understanding of species distribution patterns. These species are often evolutionarily distinct and are of high conservation value. Unfortunately, most often, these are also the species on which basic research is severely lacking globally, mainly due to their rarity. Studying biogeography to uncover the role of various factors in shaping species' distributions was proposed as a part of this thesis. Species which are co-distributed with potentially overlapping niches and showing a gradient of endemicity were chosen for this research. Owlets belonging to *Heteroglaux*, *Athene,* and *Glaucidium* genera were selected as study species, and some unresolved questions surrounding their phylogeny and comparative biogeography were addressed.

As a first step, clarifying phylogenetic uncertainties are of primary importance, especially in the case of species of high conservation priority such as the Endangered Forest Owlet. Without a clear understanding of species phylogeny, it is difficult to fix conservation priorities and identify populations that need urgent attention. There have been long debates over the taxonomic position of Forest Owlet concerning *Athene* and *Glaucidium* members. The role of evolutionary biogeography in shaping geographical distributions has not been studied in the Indian owlets. Some studies point at the role of paleoclimate and climatically stable zones in structuring bird distribution (Dynesius & Jansson 2000, Jansson 2003, Ramachandran et al. 2017), which needed to be tested further, especially in case of endemic species. There is scarce information available on landscape-level factors influencing the distribution of Forest Owlet. Therefore, understanding them and identifying conservation hotspots in the light of future climate change is necessary. This is useful in devising conservation strategies that can inform land-use policies.

This first study on Indian owlets integrates genetic and ecological aspects to resolve the phylogeny of *Heteroglaux-Athene-Glaucidium* genera, highlight the importance of Quaternary climatic fluctuations on species' ranges and predict the impact of future climate change on the Forest Owlet. Further, this study determines landscape-wide factors that affect the current geographical distribution of Forest Owlet and identifies conservation hotspots in the rapidly changing landscape of central India where conservation action needs to be prioritized.

1.5.1. Research Questions

1. What are the evolutionary relationships among the members of *Heteroglaux* (monotypic genus), *Athene* (having four extant owlets), and *Glaucidium* (speciose genus of pygmy owls) genera?

2. Did the Quaternary climatic fluctuations influence ranges of Indian owlets?

3. What are the landscape-wide factors shaping the geographical distribution of Forest Owlet?

4. How may future climate change affect the geographical distribution of Forest Owlet? Which are the areas where conservation effort should be prioritized?

1.6. Objectives, Hypotheses, and Expectations

Objective 1. Resolve the taxonomic position of the Forest Owlet (*Heteroglaux blewitti*), Spotted Owlet (*Athene brama*) and Jungle Owlet (*Glaucidium radiatum*) using molecular phylogeny.

- **Competing Hypothesis 1:** *H. blewitti* and *A. brama* together form a subgenus *Heteroglaux*, nested within *Athene* (Wolters 1975).

- **Competing Hypothesis 2:** *H. blewitti* is nested within *Athene* or *Glaucidium* (König et al. 1999).
- **Competing Hypothesis 3:** *H. blewitti* belongs to a monotypic genus *Heteroglaux* (Rasmussen & Collar 2013).

Objective 2. Compare biogeographic patterns among Forest Owlet (a woodland specialist with a severely narrow range), Jungle Owlet (widespread within India but endemic to India and Sri Lanka), Spotted Owlet (a generalist, endemic to the Indian subcontinent), and Little Owl (a widespread species across Palearctic).

- **Hypothesis 1:** Endemic species are more likely to be found in climatically stable areas (*modified* Dynesius & Jansson 2000, Jansson 2003).
- ➢ **Expectation:** In a group of sympatric owlets, narrow endemics such as Forest Owlet are found in climatically stable zones as compared to widespread species such as Spotted Owlet, Jungle Owlet and Little Owl occurring in a range of climatic conditions.
- **Hypothesis 2:** The range of Little Owl was impacted by climatic changes during Last Glacial Maxima. During Last Glacial Maximum the species shifted southwards, surviving in Southern European refugia and expanded northwards post-glacially (Pellegrino et al. 2014).
- ➢ **Expectation:** Little Owl responded to colder climate during Last Glacial Maximum showing a contraction and shift in suitable climatic niche southwards, followed by northward expansion during the post-glacial period.

Objective 3. Understand the conservation requirements of Forest Owlet.

- Understanding landscape-level factors (vegetation, elevation, and climate) affecting the geographical distribution of the species.
- Examining the effect of the future climate change on the range of the species and identifying conservation hotspots.
- Examining population status using genetic data.

1.7. Overview of the Thesis

This thesis follows the theme of research questions and objectives following a deep timeline and discussing evolutionary and ecological histories of Indian owlets in four technical chapters (chapters 2 - 5). As a first step, it was essential to resolve the phylogeny of focal owlets to understand their evolutionary biogeography and probable time of divergence. The second chapter underscores the possible role of changing climate during the Plio-Pleistocene in influencing divergence and distributional ranges of the owlets. To understand these processes better, the effect of Quaternary climatic fluctuations on climatic niches of owlets was modeled, which is described in chapter three. To aid in the current conservation of the endemic Forest Owlet, its present extent of occurrence, drivers of its present geographical distribution, and possible effects of future climate change on its range were modeled which are discussed in chapter four and five. The last sections of the thesis provide a summary of the research and perspectives.

1. Chapter 1 - Introduction: This chapter provides a detailed background of the research questions and study species.

2. Chapter 2 - Phylogeny and Evolutionary Biogeography of Owlets of India: This chapter discusses objective 1, resolving long debated *Heteroglaux-Athene-Glaucidium* phylogeny. Here, I tested three hypotheses mentioned under objective 1 and concluded that *H. blewitti* is nested within the *Athene* clade, proposing *Heteroglaux* as a synonym of *Athene*. This study presents the first phylogenetic analysis of the endemic and Endangered Forest Owlet *H. blewitti* concerning *Athene* and *Glaucidium* owls, highlighting the possible role of Plio-Pleistocene climate boundary in their speciation.

4. Chapter 3 - Effect of Quaternary Climatic Fluctuations on Climatic Niches of Owlets: The discussion from chapter 2 continues in chapter 3 where I reconstructed past climatic niches of four owlets to explore if the paleoclimate was responsible for shaping the climatically suitable areas of species. Here I tested two hypotheses mentioned under objective 2. I found that historical global climate change was an important factor shaping the suitable niche extents of species; however, regional climate change cannot be overlooked, especially in the case of species requiring conservation attention such as Forest Owlet. Future efforts in research are recommended to be directed towards incorporating regional climate change scenarios, backward-time projected vegetation models, and a larger dataset in modeling species responses to better understand the likely effect of species history on their present geographical ranges.

5. Chapter 4 – Understanding the Conservation Requirements of Forest Owlet: Continuing the thread of climate change affecting species distribution, in chapter 4, I predicted suitable climatic niches for Forest Owlet for the current time period. I used additional information on vegetation cover and change in the vegetation cover to delimit areas where the species may be present. I field-validated the model and detected the presence of Forest Owlet in previously unknown locations. I then identified niche hotspots where conservation efforts should be maximized. I also performed preliminary genetic variability analysis on a population (Khandwa, Madhya Pradesh) which showed low haplotype diversity. Surveying the niche hotspots of the Forest Owlet and estimating densities, identifying habitat connectivity, and possible dispersal routes are highly recommended conservation-oriented questions for future research.

6. Chapter 5 – Effect of the Future Climate Change on the Geographical Range of Forest Owlet: In this chapter, I further explored the effect of future climate change scenarios on climatically suitable areas for Forest Owlet and predicted future conservation hotspots. I found that future climate change will affect the species niche breadth and extent and the presently recognized niche hotspots are where conservation efforts should be maximized on priority to avoid future loss. The combination of future climate change and land-use change is predicted to be detrimental to the species. Urgent conservation action in niche hotspots prone to future climate change is proposed.

CHAPTER 2: PHYLOGENY AND EVOLUTIONARY BIOGEOGRAPHY OF OWLETS OF INDIA

Introduction

Endemic and endangered species are often ecologically specialized, and there is an urgent need to better understand the ecology and phylogenetic history of endangered species to uncover features that might be crucial for conservation. Such species could be viewed as model species to understand evolutionary processes in the landscape of their occurrence (Ribeiro et al. 2011, Holmes et al. 2016. Kahindo et al. 2017). However, our knowledge of the evolutionary history of highly restricted, endemic species in the tropics is limited, due to their rarity and incomplete genetic sampling (Reddy 2014). This could have far-reaching consequences on policy level decisions regarding species conservation.

Although the phylogeny of the higher order avian taxa has undergone several changes in the past three decades (Edwards et al. 2005a, 2005b; Prum et al. 2015, Robin et al. 2017), relationships among clades remain poorly known. Owls (Order: Strigiformes) are one such group. Many rare or range-restricted species such as the Endangered Forest Owlet *Heteroglaux blewitti* (Hume, 1873), Spotted Owlet *Athene brama* (Temmink, 1821) and Jungle Owlet *Glaucidium radiatum* (Tickell, 1833) were not included in the most recently published owl phylogenies (Wink et al. 2009, Wink 2014, Wood et al. 2016).

H. blewitti, endemic to India, has been a taxonomic mystery since its discovery in 1872. Owing to its severely fragmented distribution and low population, *H. blewitti* has been categorized as an Endangered species by the International Union for Conservation of Nature and Natural Resources (IUCN) (Birdlife International 2017). There have been many opinions on the phylogenetic affinities of *H. blewitti* by ornithologists over the centuries. In the past, the species has alternatively been placed in either the genus *Heteroglaux* (Hume 1873, Dubois 1904, Dickinson & Remsen Jr 2013, Gill & Donsker 2013, Rasmussen & Collar 2013) or *Athene*

(Blanford 1895, Baker 1934, Ali & Ripley 1983, Monroe & Sibley 1993, del Hoyo et al. 1999, Clements et al. 2013). Additionally, some researchers have claimed *Heteroglaux* to be a subgenus of *Glaucidium* (König et al. 1999), owing to the tail-flicking behavior typical in the genus *Glaucidium*. Nevertheless, none of these opinions were founded on formal phylogenetic analyses.

The genus *Athene* is represented by four species - Burrowing Owl *A. cunicularia,* Spotted Owlet *A. brama*, Little Owl *A. noctua* and White-browed Owl *A. superciliaris* (Gill & Donsker 2013, Wink 2014). All the extant *Athene* members were classified in the genus *Strix* when first described. Following a revision in taxonomy (Blanford 1895), *A. brama* and *A. noctua* were placed in the genus *Athene*, a placement that remains unchanged to date. *A. cunicularia* was moved from *Strix* to *Speotyto* (Sibley & Monroe 1990) based on DNA-DNA hybridization studies and later to *Athene* (Wink et al. 2009), based on mitochondrial CYTB and nuclear RAG-1 gene data. Similarly, *A. superciliaris* was moved from *Strix* to *Ninox* (König & Weick 2008), and then to *Athene* (Wink 2014). Throughout this article, we refer *A. brama* and *A. noctua* as Eurasian *Athene* (with global distribution encompassing India) and *A. superciliaris* and *A. cunicularia* as *Athene* from Madagascar and the Americas.

Since *H. blewitti* and *A. brama* are morphologically similar in appearance (Blanford 1895) and are co-distributed (Figure 1, Supplementary Figure 1), they would be expected to form a sister group. Although Wolters (1975) hypothesized that *H. blewitti* and *A. brama* together form a subgenus *Heteroglaux*, nested within *Athene*, he did not explain this classification (Rasmussen & Collar 2013). In contrast, König et al. (1999) argue that the tail flicking behavior, a characteristic of *Glaucidium*, shown by *H. blewitti*, suggests that the species is closely related to *Glaucidium* and could be nested within *Athene* or *Glaucidium*. The current classification of *H. blewitti* in a monotypic genus *Heteroglaux* claimed by Rasmussen & Collar (2013) is based solely on an assessment of morphological (Hume 1873, Rasmussen & Collar 2013) and osteological characteristics (Rasmussen & Collar 2013), without phylogenetic data. This classification needs further scrutiny by incorporating phylogenetic information. Furthermore, a report on the hybridization between *H. blewitti* and *A. brama* (Pande et al. 2011a), was disputed (Ishtiaq 2011, Jathar & Patil 2011, Pande et al. 2011b, 2011c), and this underscores the need to examine the taxonomic status of the species. Data available on acoustic (Rasmussen & Ishtiaq 1999), morphological, osteological and behavioral characters (Rasmussen & Collar 2013) of *H. blewitti* show that the species differs from other *Athene* species in osteological features such as multiple cranial characters, especially wider, inflated anterior and posterior frontals, larger lacrimals and maxillopalatines, stouter tarsometatarsi, and behavioral features such as nonundulating flight and tail flicking. Rasmussen & Collar (2013) argue that this difference could well be at the genus level. The authors further propose that the plumage similarities in *A. brama* and *H. blewitti* could be due to convergence but given the distinct osteological and behavioral features of *H. blewitii*, another possibility is that *H. blewitti* evolved from an ancient divergence event separating the genus *Heteroglaux* from *Athene*.

I tested three proposed phylogenetic relationships as competing hypotheses - Rasmussen & Collar (2013), König et al. (1999), and Wolters (1975) using molecular data to infer phylogenetic relationships among *H. blewitti*, *A. brama*, and *G. radiatum*. This study addressed the debate about *Athene-Glaucidium-Heteroglaux* relationships using genetic data. I expect that this new phylogenetic information on an endemic and endangered species will help understand priorities in conservation strategies.

2.2. Materials and Methods

2.2.1. Taxon sampling

Based on data from extant phylogenies (Wink et al. 2009, Wink 2014, Wood et al. 2016), data were generated on the three Indian Owlets *H. blewitti*, *A. brama*, and *G. radiatum* as well as the Madagascan species *A. superciliaris*. Three out of five subspecies of *A. brama* were sampled namely *A. b. brama* (North India), *A. b. indica* (South India) and *A. b. albida* (Parts of Gujarat, Pakistan, and Iran), and two subspecies of *G. radiatum* namely *G. r. radiatum* (Peninsular India) and *G. r. malabaricum* (Southwest India). The assignment of subspecies was based on distributional limits described in Ali & Ripley (1983). For field-based sample collection from the three species of owls (*H. blewitti*, *A. brama*, and *G. radiatum*), all legalities were followed and prior permissions from State Forest Departments (Madhya Pradesh, Maharashtra, Gujarat, and Chhattisgarh) were obtained. The Madhya Pradesh Forest Department granted Dr. Prachi Mehta (a collaborator on this study) permits to capture and color tag *H. blewitii* individuals as part of an independent study on the species. The Chhattisgarh Forest Department permitted captures and blood collection, whereas our permits from Maharashtra and Gujarat were limited to visual surveying of the Forest Owlet (*H. blewitti*). Forest Owlets were captured using Bal-chatri traps, known to be the most effective trapping technique for capturing birds of prey without inflicting injury (Berger & Mueller 1959). The capture and release protocol was reviewed by the Madhya Pradesh State Forest Department's expert committee before granting the research permit. For this study, during the capture process, captured owlets were handled for a maximum of twelve minutes and were released immediately after banding and biometrics procedure. The banding procedure was carried out very close to where the owlet was captured so it could be released at the same spot. Once captured, the head of the owlet was covered with a cloth to minimize stress. Feathers that were shed were collected during the process of capture and handling from each bird. Up to two feathers per individual were collected. The feathers were stored in separate paper envelopes and the envelopes placed in airtight containers for transport. Color tagging of birds ensured that different individuals and sources for the samples could be identified. The collected feathers were used to create reference genetic data for the species. In two instances, broken eggshells fallen below known nest-sites of *H. blewitti* were collected. The genetic data collected from eggshells (Supplementary Table 1) was compared with the reference genetic data to identify species. The species identification was made using a criterion of ≥99% sequence identity with the reference data. After species assignment, further analysis on the samples was carried out. A museum feather sample of *H. blewitti* from the Bombay Natural History Society (BNHS) was collected, and the species identity was ensured using the same criteria mentioned above. In case of *A. brama* and *G. radiatum*, fallen feathers below known nest-sites outside Protected Areas or shed feathers from injured bird rescued by NGOs were collected. In addition, *G. radiatum* individuals were trapped in mist nets (in Chhattisgarh) and their blood samples were used for analysis. Spatially non-overlapping and distant nest-sites were sampled to avoid resampling the same individuals. For both the species, for ensuring species identity, the same approach as for *H. blewitti* was followed. Apart from the tree owlets, target genes were sequenced from a vouchered tissue of *A. superciliaris* obtained from the Field Museum of Natural History (details of samples and sources are provided in Supplementary Table 1 and Supplementary Figure 2).

2.2.2. Laboratory Procedure

DNA was extracted using DNeasy blood and tissue kit (Qiagen, Hilden, Germany, Product no. 69504), following the manufacturer's protocol with a few modifications. Dithiothreitol (DTT) (20 µl of 1% DTT) was added in the lysis reaction. To ensure a higher concentration of DNA and minimize loss, DNA was eluted twice in separate vials, each time in 100 µl of AE buffer, instead of the recommended one elute of 200 ul and the first elute was used for further analysis. Two mitochondrial genes (CYTB, COI), a nuclear exon (RAG-1), and three nuclear introns (TGFB2, LDH, MYO) were amplified. These genes were chosen based on previously available data on other species of *Athene* and *Glaucidium* (Wink et al. 2009, Wink 2014). All PCR amplifications were carried out after optimizations (Supplementary Table 2) of reaction conditions. The purified PCR products were sequenced in both forward and reverse directions with an ABI 3730 Genetic Analyzer and analyzed raw sequences with the ABI 3730 Genetic Analyzer software (Applied Biosystems, Foster City, USA). Two owlet specific primers were designed for amplifying COI gene from *A. brama* and *G. radiatum*. Primers for other genes available from published studies were used (Lanyon 1994, Groth & Barrowclough 1999, Bures et al. 2002, Primmer et al. 2002, Hebert et al. 2004, Hackett et al. 2008, Fregin et al. 2009, Dong et al. 2010). All the sequences from the study were submitted to GenBank (*see* Supplementary Table 3 for accession numbers).

2.2.3. Sequence Analyses and Phylogenetic Reconstruction

The sequences were viewed and manually edited in Chromas Lite 2.1.1 (Technelysium, Brisbane, Australia) and aligned using the software Geneious v7.0.6 (Biomatters, Auckland, New Zealand) (Kearse et al. 2012). Sequences of other owls were downloaded from GenBank (Supplementary Table 4). Coding sequences were translated in Geneious to check for the presence of stop codons and nuclear inserts of mitochondrial DNA (numts). Individual gene alignments were processed in MEGA v4.0 (Tamura et al. 2007) for counting the proportion of variable sites, parsimony informative sites, and singletons. Positive selection was tested, to avoid introducing possible error in phylogenetic inference as shown in (Castoe et al. 2009, Roje 2014), in CYTB, COI, and RAG-1, using HyPhy (Sergei et al. 2005) and Tajima's test of neutrality (Nei & Gojobori 1986) implemented in MEGA v4.0. The phylogenetic analyses were conducted using three different sets of data - mitochondrial (CYTB + COI), nuclear (RAG1 + TGFB2 + MYO), and concatenated (CYTB + COI + RAG1 + TGFB2 + MYO). There was a missing in-group taxon (*A. noctua*) in the LDH dataset; therefore, the LDH dataset was not included in the final concatenated analysis. The concatenated dataset contained <9% missing data. Codon-specific DNA substitution models were used (PartitionFinder v1.1.1, Supplementary Table 5) (Lanfear et al. 2012). The separate genes, as well as concatenated datasets, were tested for best-fit DNA substitution models (*details in* Supplementary Table 5). Phylogenetic analysis was conducted with maximum likelihood using RaxML v8.0 (Stamatakis 2014), Bayesian Inference using MrBayes v3.2.2 (Ronquist & Huelsenbeck 2003), and multi-species coalescent tree using BEAST (Drummond et al. 2012). Members of the Tytonidae family (*Tyto alba* and *Phodilus badius*) were used as outgroup taxa since this is the family closest to the Strigidae family with an estimated known divergence time for the Strigidae / Tytonidae split (54 Ma - 83 Ma) (Ericson et al. 2006, Brown et al. 2008, Pacheco et al. 2011, Claramunt & Cracraft 2015). PartitionFinder was used first to determine the best partitioning scheme of gene regions based on evolutionary rates. These partitions were exported in RAxML and MrBayes. In RAxML, ML+rapid bootstrap function with 10000 bootstraps was used for all analyses. In MrBayes, two runs of five chains (one cold) for 30 ± 70 million generations were conducted sampling every 1000th generation. The temperatures of the heated chains were set to 0.25. The first 25% of samples (burnin) were discarded, and the MCMC runs were continued till the standard deviation of the split frequency dropped below 0.005. Each ML and Bayesian analysis was run thrice, to ensure consistency in the results, for the concatenated dataset with the following options - partitioning of the dataset in all codon positions of coding sequences, only the third codon position of coding sequences, and all codon positions for the mitochondrial genes and only the third codon position for the nuclear exon. The concatenated dataset was used, without the LDH data, to construct species phylogeny in Beast v1.8.1. The species tree analysis does not take into consideration columns with missing data; hence, the LDH dataset for which *A. noctua* data was missing was not considered in this analysis. The analysis was carried out for 1.5 billion runs. Trees were viewed and edited in FigTree v1.4.2. Also, Densi-Tree v2.2.5 (Bouckaert 2010) was used, based on the Bayesian output of BEAST, to plot sets of trees. To test for congruency in mitochondrial and nuclear datasets, a Shimodaira-Hasegawa test (Shimodaira & Hasegawa 1999) was performed in RaxML. Also, gene jack-knifing analysis was conducted in which individual genes were serially removed from the concatenated dataset to detect which gene/s may influence the phylogenetic analysis (Hackett et al. 2008).

2.2.4. Fossil Calibrations and Molecular Dating

Owls have an adequate fossil and sub-fossil record, largely from Europe and North America (Kurochkin & Dyke 2011); however, classification of many of the sub-fossils remains ambiguous (Mlíkovský 2002). In addition, very few phylogenetic studies of Strigiformes have used molecular dating and there is no consistency in fossil calibrations used. Only fossil calibrations with sufficient support, as discussed in (Ho & Phillips 2009, Parham et al. 2012), and those that have been used in multiple studies, were used in this study. In the present study, *A. otus* / *O. leucotis* (23.7±16.4 Ma) (Mlíkovský 1998) and the oldest *Athene* fossil (3.6±5.3 Ma) (Pavia et al. 2014) were used for calibrations. Different combinations of data (concatenated, mitochondrial, and nuclear, partitioned alignments) were used, to check for consistency in results, to obtain molecular dates after performing tests for a molecular clock (Tajima 1993) in MEGA v4.0 and using both the strict and the uncorrelated relaxed lognormal clocks. Substitution models, clock models and trees option were set to unlinked for all the partitions. Lognormal distribution was used for fossil calibrations with the means of distributions set such that 95% of the distribution probability fell within expected ranges of time intervals. BEAST was run on CIPRES portal (www.cipres.org) for 1 to 2 billion MCMC runs. The sampling frequency was set at 1000 and data was re-sampled using Log Combiner v1.8.1. The BEAST output was viewed in Tracer v1.6 and trees were combined in TreeAnnotator v1.8.1. The molecular dating results were compared with other studies to check for consistency of molecular date estimates. Results were first compared with Fuchs et al. (2008) who used Mlíkovský (1998) fossils of *A. otus* and *O. leucotis*, along with a geographical event dating which does not include our study area. Further, Strigidae / Tytonidae split dates from this study were compared with other relevant studies (Ericson et al. 2006, Brown et al. 2008, Pacheco et al. 2011, Claramunt & Cracraft 2015). Effective Sample Size (ESS) values were used as one of the- criteria to compare among analyses.

2.3. Results

2.3.1. Phylogenetic Analysis

In the concatenated tree analysis, *H. blewitti* was recovered as nested within the *Athene,* and sister to the other *Athene* from Madagascar and Americas (Figure 3 and Supplementary Figure 3). In all gene trees (Supplementary Figures 4-9), *A. brama* and *A. noctua* were sisters to each other. Similarly, *G. radiatum* and *G. cuculoides* were sisters in all the analyses. No significant

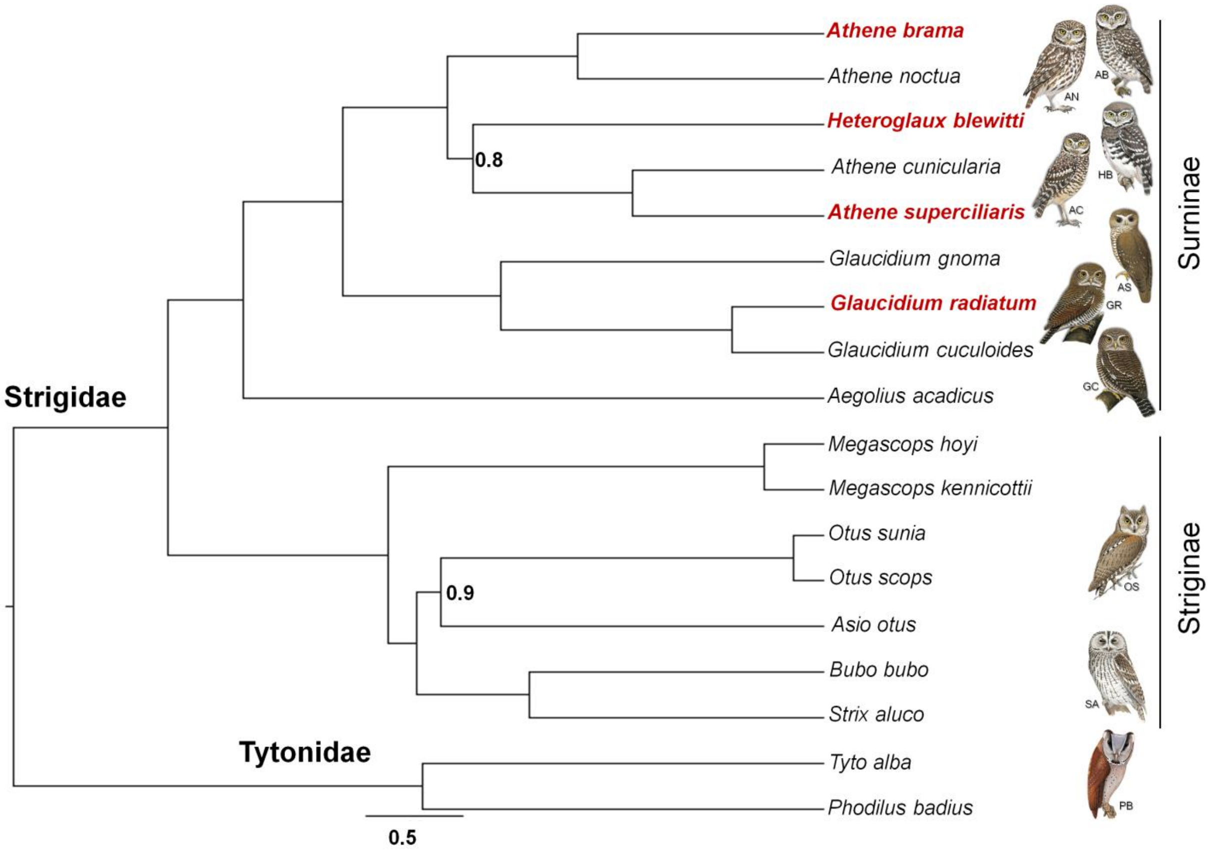

Figure 3. A species tree reconstruction using BEAST on concatenated (mitochondrial + nuclear) dataset indicate that *H. blewitti* is nested within the *Athene* clade. The brown text indicates the species sampled in the present study. The nodal values show Bayesian posterior probability (PP). All the nodes are highly supported (PP = 1) except for those where PP is mentioned as nodal value.

congruence ($P < 0.01$) was noted at the *H. blewitti* node in mitochondrial (Supplementary Figure 10) and nuclear (Supplementary Figure 11) trees when the Shimodaira-Hasegawa test (Figure 4 and Supplementary Figure 3) was performed. In the mitochondrial tree, *H. blewitti* was sister to the Eurasian *Athene* clade, whereas in the nuclear tree it was sister to *Athene* from Madagascar and the Americas (Figure 4). During gene jack-knifing, the mitochondrial tree topology was always recovered when any one of the three nuclear genes (TGFB2, MYO and RAG-1) removed from the concatenated dataset.

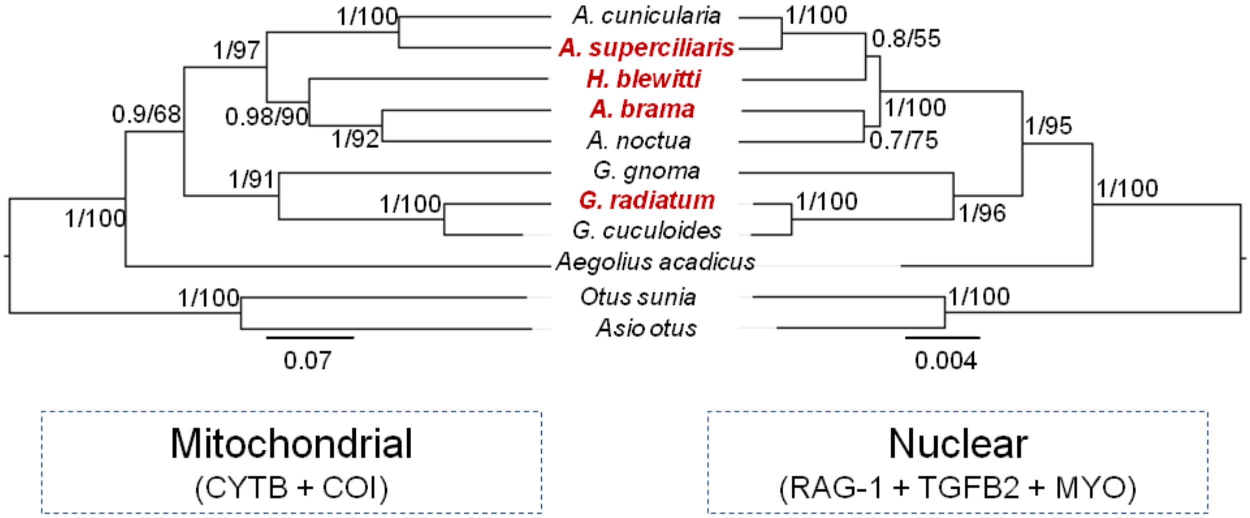

Figure 4. A Maximum Likelihood Phylogenetic tree of *Athene-Heteroglaux-Glaucidium* members. Tree constructed using mitochondrial (CYTB + COI) and nuclear (RAG-1 + TGFB2 + MYO) datasets separately to test for congruence at *H. blewitti* node. The red text indicates the species sampled in the present study. The nodal values indicate Bayesian posterior probability (0-1) separated by maximum likelihood bootstrap support (0-100).

2.3.2. Molecular Dating Analysis

The molecular dating analyses resulted in varied estimates of divergence (Table 1). Mitochondrial and concatenated datasets failed to converge in dating runs. Based on the analyses for the nuclear dataset (Table 1, analysis 2), for which ESS values were the highest and the

Tytonidae / Strigidae and *A. otus* / *O. leucotis* divergence estimates matched with the other published estimates, diversification dates were predicted for *H. blewitti* between 4.3 and 5.7 Ma, *A. brama* / *A. noctua* split between 3.9 and 5.8 Ma, *A. cunicularia* / *A. superciliaris* split between 2.2 and 3.9 Ma and *G. radiatum* / *G. cuculoides* split between 0.1 and 1.8 Ma.

Table 1. Summary of the molecular dating analysis using (uncorrelated) relaxed lognormal clock.

Attribute	**Analysis 1**	**Analysis 2**	**Analysis 3**
Dataset	Mitochondrial	Nuclear	Concatenated
Substitution model	GTR+I+G	HKY+I+G	HKY+I+G
MCMC runs (X10^7)	150	150	200
Overall ESS	<200	>>200	<200
Posterior	-13117.02	-6161.38	-16360.55
Prior	69.56	-334.72	-11.17
Likelihood	-13186.6	-5826.66	-16349.37
tmrca (AB/AN)	4.89 ± 0.63	4.82 ± 0.95	1.24 ± 0.06
tmrca (AC/AS)	4.21 ± 0.66	3.05 ± 0.86	0.97 ± 0.07
tmrca (Athene)	7.22 ± 0.6	5.28 ± 0.44	1.91 ± 0.05
tmrca (HB/AC/AS)	7.21 ± 0.61	4.94 ± 0.65	1.78 ± 0.05
tmrca (HB/AN/AB)	6.63 ± 0.65	5.26 ± 0.47	1.91 ± 0.06
tmrca (all) (Tytonidae / Strigidae)	19.33 ± 2.17	45.1 ± 2.6	4.13 ± 0.14
tmrca (Asioninae)	11.52 ± 1.01	16.36 ± 1.24	2.22 ± 0.05
tmrca (GR/GC)	2.34 ± 0.47	0.98 ± 0.85	0.46 ± 0.07

AB: *A. brama*, **AN:** *A. noctua*, **AC:** *A. cunicularia*, **AS:** *A. superciliaris*, **HB:** *H. blewitti*, **GR:** *G. radiatum*, **GC:** *G. cuculoides*, **ESS:** Effective Sample Size, **TMRCA:** Time to Most Recent Common Ancestor in the units of millions of years (Ma).

2.4. Discussion

2.4.1. *Heteroglaux* as a Synonym of *Athene*

The present analysis using mitochondrial, nuclear and concatenated datasets (Figures 3 and 4, and Supplementary Figure 4-11) showed that *H. blewitti* is nested within the *Athene* clade, rejecting the König et al. (1999) hypothesis that the species is nested within *Glaucidium*, and the Rasmussen & Collar (2013) hypothesis that *Heteroglaux* is a monotypic genus sister to *Athene*. The results also refuted the Wolters (1975) hypothesis that *H. blewitti* is sister to *A. brama*. *H. blewitti* and *A. brama* show similarity in lengths of tibiotarsus and ulna, and relatively shorter tarsometatarsi as compared to *A. noctua* to occupy an arboreal niche (Rasmussen & Collar 2013). Therefore, the results support the Rasmussen & Collar (2013) interpretation of the morphological similarities in *A. brama* and *H. blewitti* being either convergence of traits or plesiomorphies, further supported by the observation that a strong arboreal nature is absent in *A. noctua*. Two contrasting results were observed in the analysis - *H. blewitti* as a sister clade, either to *Athene* from Madagascar and the Americas (concatenated and nuclear datasets, Figures 3 and 4, Supplementary Figures 3-9 and 11) or Eurasian *Athene* (mitochondrial dataset, Figure 4 and Supplementary Figure 10), making the exact phylogenetic position of the species uncertain. Phylogenetic analyses with additional sampling of genetic markers, individuals per species, and distinct subspecies of *A. brama*, *A. noctua*, and *A. cunicularia* may help provide a better resolution. Based on the present results, *Heteroglaux* is proposed as a synonym of *Athene*, identifying *Heteroglaux blewitti* as *Athene [Heteroglaux] blewitti*.

2.4.2. Molecular Dating and Biogeography of *A. [H.] blewitti*

The overlapping dates of diversification of *A. [H.] blewitti* (4.3 Ma - 5.7 Ma), *A. brama* / *A. noctua* split (3.9 Ma - 5.8 Ma), and *A. cunicularia* / *A. superciliaris* split (2.2 Ma - 3.9 Ma), based on the nuclear dataset (Table 1, analysis 2), indicate a rapid diversification of all three owlets in India, perhaps in response to Plio-Pleistocene climatic fluctuations. This diversification is from the same period as *A. inexpectanta* (3.6 Ma - 5.3 Ma, Early Pliocene), the oldest fossil *Athene* owl from Africa. Pavia et al. (2014) argue that the genus *Athene* originated in Africa and had a much wider distribution than previously thought. Given the rich island endemic *Athene* fossil records, from Late Pliocene of Palearctic (Boev 2002), Nearctic (Ford 1966, Ford &

Murray 1967, Feduccia 1970, Bell et al. 2004), and Early Pleistocene of Palearctic (Mlíkovský 2002, Guerra et al. 2012, Bedetti & Pavia 2013), it has been speculated that *Athene* species might have undergone multiple diversifications and extinction events, possibly as a response to Plio-Pleistocene climate change, as observed in other groups such as the Western Ghats montane birds (Robin et al. 2015, 2017). Perhaps the Plio-Pleistocene climatic fluctuations and the subsequent retraction of evergreen forests (Meher-Homji 1983, Karanth 2003), during the Upper Sivalik time (1.6 Ma - 5.1 Ma) of India, facilitated *A. brama* expansion into Peninsular India, while *A. noctua* expanded northward to a cooler climate. Recent studies have shown that *H. blewitti* occupies moderately dense dry deciduous forests, with intermittent open spaces (Mehta et al. 2008, Jathar et al. 2015). This peculiar choice of habitat influenced by climate, along with prey preference and ecological interactions with other similar-sized competitors might have restricted the range of *A. [H.] blewitti*. The species' diurnal, ambushing predatory nature might be an adaptation to maximally utilize the available niche, given the presence of other co-distributed crepuscular and nocturnal owlets such as *A. brama* and *G. radiatum* in the same area. Further information on the dietary preference of *H. blewitti* and its ecological interactions with other species would help understand its adaptations. Nevertheless, the present study provides another line of evidence to the role of climatic fluctuations in the diversification of Indian birds.

The divergence estimates, based on the nuclear dataset (Table 1, analysis 2), are overlapping but more recent (15.1 Ma - 17.6 Ma) than those derived by Fuchs *et al*. (2008) for *A. otus* / *O. leucotis* split (16.7 Ma - 19.3 Ma). For the Tytonidae / Strigidae split, the divergence estimate of 42.5 Ma - 47.7 Ma (Table 1, analysis 2) overlaps with Ericsson et al. (2006) estimate of 40 Ma - 60 Ma, however, it also presents an underestimate when compared with other studies (Brown et al. 2008, Pacheco et al. 2011, Claramunt & Cracraft 2015). The molecular dating analyses runs that included mitochondrial DNA (Table 1, analysis 1 and 3) did not converge despite 1.5 to 2 billion runs, perhaps due to the saturation of signal for these deep lineages.

2.4.3. Conservation Implications

Genetic sampling of tropical birds is poor, especially in the Old World Tropics, thereby impacting, regional conservation needs (Reddy 2014, Jetz et al. 2014). Although the new information on the phylogenetic status of *A.* [*H.*] *blewitti* does not directly impact the IUCN status of the species, its ranking in international conservation listings that use phylogenetic information may change. The Evolutionary Distinct and Globally Endangered (EDGE) listing will perhaps no longer carry the same evolutionary distinctness score for the species (Jetz et al. 2014). *A. [H.] blewitti* is a species of central Indian old growth dry deciduous forests, occurring in protected as well as non-protected areas (Birdlife International 2017). Across most of its range, it is also co-distributed with *A. brama*, a phylogenetically close relative based on this study. *A.* [*H.*] *blewitti* is under severe threat of habitat loss due to large-scale logging, timber harvesting, and land-use change (Birdlife International 2017, Mehta et al. 2008, Jathar et al. 2015). *A. brama*, on the other hand, occurs in the vicinity of human habitation (Ali & Ripley 1983). Although no admixture between *A. [H.] blewitti* and *A. brama* was detected (a mitochondrial genetic distance of 16 ± 1% indicative of low sharing of alleles) in this study, hybridization cannot be wholly ruled out. In the rapidly changing human-dominated landscape of the central India, circumstances are similar to other owls such as Barred and Spotted Owls (Hammer et al. 1994) and Northern and California Spotted Owls (Barrowclough et al. 2005), where hybridization facilitated by anthropogenic activities, has led to numerous conservation challenges. With this first molecular phylogenetic study of this Endangered species, it has been demonstrated that crucial information can only be obtained through capture-based sampling that strengthens and supports ecological data collected through conventional methods. Capture-based genetic studies still do not find support from conservation managers in India (Madhusudan et al. 2006, Bawa 2009), but such studies are instrumental in providing vital information on taxonomy, evolutionary biogeography, and in identifying conservation units.

2.5. Conclusion

This study presented the first genetic analysis of *H. blewitti*, an Endangered species, and addressed the long debate on the relationships of the *Athene-Heteroglaux-Glaucidium* complex. The new information provided here will facilitate both the taxonomic revision of the *Athene* / *Heteroglaux* clade and highlight the need for studies predicting species responses to climate change. The analysis presented in this chapter needs to be followed up with further spatially explicit sampling that can be used for conservation prioritization. Further studies with more data and complete taxon sampling have been recommended to understand the biogeography of Indian *Athene* species.

CHAPTER 3: EFFECT OF QUATERNARY CLIMATIC FLUCTUATIONS ON CLIMATIC NICHES OF OWLETS

3.1. Introduction

Role of the climate change in shaping geographical distributions of species is undisputed (Walther et al. 2002, Parmesan & Yohe 2003). Species, occupying wide climatic niches, are largely tolerant to climatic changes whereas those occupying narrow climatic niches (climatically specialized), are more vulnerable to the negative impacts of climate change events; resulting in severely reduced populations and ranges (Jansson 2003, Dirnbock et al. 2011). Specialist species, most often, are endangered, endemic to a narrow geographical extent of occurrence (EOO) or requiring specific climatic and/or habitat conditions.

Birds are one of the most widely studied taxa, with information on geographical distributions, for understanding the impact of global climate change on animals. Studies on birds with respect to climate change have demonstrated far-reaching negative impacts on their distributions, ecology and evolutionary trajectories (Crick 2004; Urban 2015, Howard et al. 2018, Tomotani et al. 2018). Much information on the influence of climate change on birds comes from the spatiotemporal distribution of bird fossils, extensive and repetitive ecological surveys, and explicit past-projected Climatic Niche Models (CNMs) (Crick 2004). These studies collectively suggest that paleoclimatic changes have greatly impacted geographical ranges of several bird species (Gibbons & Wotton 1996, Hilbert et al. 2004, Robin et al. 2010, Zhao et al. 2012, Smith et al. 2013, Ramachandran et al. 2017). Regions that experience low variation in climate have been hypothesized to retain more endemic species (Dynesius & Jansson 2000). The global geographical pattern in endemic species distributions is hypothesized to be a function of responses of the species to climatic fluctuations occurring in the recent time-scale of 10-100 thousand years (Jansson 2003). According to the Jansson (2003) hypothesis, the effect of the Last Interglacial (LIG; ~120-140 Ka), Last Glacial Maximum (LGM; ~18-22 Ka), and Mid-

Holocene (MDH; ~6Ka) seem most prominent (Ramachandran et al. 2017), although not extensively tested in birds. Both the LIG and LGM time-periods represent extreme climatic conditions.

During the LIG, temperatures warmer than the pre-industrial Holocene climate prevailed globally (*reviewed in* Kukla et al. 2002; Otto-Bliesner et al. 2006). During this period, due to the warming of polar regions and melting of ice sheets, global sea levels were relatively higher than the present time (Lozhkin & Anderson 1995, Kopp et al. 2009; Dutton et al. 2015). The tropical areas exhibited strong monsoonal systems during LIG (Pedersen et al. 2017). Palynology records from tropics suggest extensive moist rainforests in Australia (Kershaw 1994), South America (van der Hammen 1974), and India (Sukumar et al. 1995, Prabhu et al. 2004) during LIG, characterized by a warm and wet climate. The LGM was most recent driest period on the earth. During this time, most of the northern parts of the earth were covered by large ice sheets with a low average temperature causing an increase in aridity and drop in sea levels (Clark & Huybers 2009). This led to a change in climate and available land area, and climate-associated changes in vegetation (Anhuf et al. 2006), possibly altering ranges of many bird species. Studies from tropical areas suggest a change in vegetation post-LIG, during LGM, mainly from moist rainforests to open dry forests or scrub-savanna vegetation (Van Der Hammen 1974, Sukumar et al. 1995, Ray and Adams 2001, Prabhu et al. 2004, Bird et al. 2005, Anhuf et al. 2006, Bose et al. 2016). Post-LGM, in the Holocene (~11.7 Ka to Present), a warmer climate than LGM prevailed in the Northern Hemisphere but the tropics were colder than in the present (Steig 1999, Mayewski et al. 2004, Wanner et al. 2008). The general trends in climate during Holocene were, cooling at polar regions, increase in aridity in the tropics, and changes in atmospheric circulation (Mayewski et al. 2004). The Holocene climate is postulated to contain cycles of warm and cold temperatures with an increase in aridity in the Indian Peninsula (Sukumar et al. 1995, Ponton et al. 2012). Several studies point towards the Indian Subcontinent experiencing multiple cycles of dry and wet periods (Randhawa 1945, Sukumar et al. 1993, Chauhan 2002, Gupta et al. 2003). During the Late Quaternary, there is evidence of an arid phase from 6 to 3.5 Ka (Sukumar et al. 1993), moist and warm climatic conditions around 1.8 to 2 Ka (Randhawa 2000, Chauhan 2002), and a short, wet phase around 0.6 Ka (Sukumar et al. 1993) in India. Such historical cycles of wet and dry phases might have reduced forested areas, with a further increase in fragmentation and isolation post-industrialization (Karanth 2003).

Studying the effect of the Quaternary climatic fluctuations on the ranges of co-distributed tropical owlets, showing a gradient of endemicity, was proposed as a part of the thesis. Six species of owlets are known from India, of which Forest Owlet, Jungle Owlet, and Spotted Owlet are co-distributed in central India (Figure 1, Supplementary Figure 1). Little Owl, sister to Spotted Owlet, mainly distributed in the Palearctic also occurs in the Indian Himalayas, partially overlapping with the Spotted Owlet in geographical distribution. Forest Owlet is an endemic woodland specialist occurring in Teak-dominated dry deciduous forests of central India (Mehta et al. 2008, 2017). Spotted Owlet and Little Owl are open habitat species occurring in a wide range of habitats such as scrubland, forest edges, savanna, dry forests, and in and around human habitation (Ali & Ripley 1983). Jungle Owlet occurs in dry to moist deciduous forests and scrublands (Ali & Ripley 1983). Results from the divergence estimation of the phylogeny of Indian owlets indicate that the Plio-Pleistocene climate change was probably a driving factor in the speciation of *Athene* and *Glaucidium* owls (Koparde et al. 2018) and possibly shaped their present geographical distribution. The change in habitat caused by the Quaternary climatic fluctuations might have created unequal opportunities for owlets to occupy suitable habitat types, given their different habitat requirements, which may explain their present geographical distribution. A recent phylogenetic study of *Athene* owls (Pellegrino et al. 2014) suggests that the distribution and populations of Little Owl might have been affected by climatic fluctuations with cycles of contraction and expansion of ranges over time. During LGM, when much of their distributional range was covered in ice, the species survived in the European Southern Refugia (Iberian, Italian, and Balkan Peninsula) and later expanded into their current range. In the present chapter, I explored if Quaternary climatic fluctuations played a role in shaping the climatic niche extents of owlets, using past-projected CNMs and tested if the endemic Forest Owlet tracked more climatically stable habitats as compared to other widespread species.

3.2. Materials and Methods

3.2.1. Data Collection

WorldClim climate dataset available at 2.5' resolution (around 5 km^2) at four time-periods, LIG (~120-140 Ka), LGM (~22 Ka), MDH (~6 Ka), and current (1960-1990) were extracted from <http://www.worldclim.org/> (Hijmans et al. 2005). Forest Owlet locations were obtained from published literature (King & Rasmussen 1998, Ishtiaq & Rahmani 2000, 2005; Kasambe et al. 2004, Jathar & Rahmani 2004, Chavan & Rithe 2009, Laad & Dagale 2014, Patel et al. 2015) and primary field observations. For other owlets, presence locations were collected from eBird (Sullivan et al. 2009, eBird 2017) and iNaturalist (iNaturalist 2017). These observations were filtered to restrict the duration to the years from 1970 to 2016 and include co-ordinate certainty below 2 km. Bioclimatic variables were clipped at two extents to be used in the analysis, at the Indian Subcontinent extent for the owlets restricted to the Indian Subcontinent (x1=55.1 E, x2=109.9 E, y1=5.0 N, y2=39.1 N) and at the Eurasia and parts of North Africa extent for Little Owl (x1=-20.08 E, x2=134.46 E, y1=0.71 N, y2=63.62 N).

3.2.2. Climatic Niche Models (CNMs)

Point locations for all the species were curated and filtered by country (excluding countries where the species is introduced or traded), date (including records from 1970 to 2016), area (including co-ordinate certainty below 2 km), and approved and reviewed status. A total of 23,243 and 202 points were retrieved for Little Owl from eBird and iNaturalist respectively. By using the country filter, points from New Zealand were avoided, where the species has been introduced recently. Finally, 2,438 and 84 points (total n = 2522) were retained from eBird and iNaturalist respectively. Similarly, 18,472 eBird and 73 iNaturalist records of Spotted Owlet were filtered to a final count of 6,042 eBird and 27 iNaturalist records (total n = 6069). For Jungle Owlet, 3,962 eBird and 20 iNaturalist records were filtered to a final count of 2743 eBird and 15 iNaturalist records (total n = 2758). For Forest Owlet, an initial dataset of 55 points was spatially filtered to 50 points avoiding overlapping points. Bias files were created for all owlets to correct for sampling bias in modeling. MaxEnt v 3.4.1 (Phillips et al. 2006) was used for CNMs. All Pre- and Post-MaxEnt data analyses were performed in Arc GIS v10.1 (ESRI 2011) and SDMToolbox (Brown 2014) in Arc GIS. Fuentes-Hurtado et al. (2016) modeling protocols were followed with slight modifications. First, a correlation analysis was performed on all 19 bioclimatic predictors for the current time-period to detect highly correlated ($r > 0.8$, $r < -0.8$) variables. In order to select the appropriate variables from pairs of highly correlated ones, all 19 variables were used in a MaxEnt run (replicate_type=bootstraps, replicate_runs=50) and variables that contributed maximally in jackknifing runs were noted. For further analysis, only those variables (from a correlated pair) were retained that had high contributions in the MaxEnt output as well as were important considering the natural history of each owlet. The final MaxEnt models were run with varying sets of predictors (*details in* Supplementary Table 6) for each owlet, with 50 bootstrap iterations. The regularization parameter was set to 1.5 to avoid overfitting of data. To determine the robustness of the model in terms of Test and Training AUC values, 25% of points used in the analysis were picked randomly and set as test points. Backward-time simulations were performed by projecting current CNM for each owlet at three time-periods, MDH, LGM, and LIG. A 10th percentile logistic training presence threshold was used to convert continuous raster maps into binary maps to better visualize the change in the extent of the niche. The 10th percentile logistic threshold is a conservative estimator of predicted suitable niches and has been applied to avoid over-fitting of models (Pearson et al. 2007, Kumar & Stohlgren 2009).

3.2.3. Post-CNM Analysis

The binary raster outputs were converted to polygons of suitable niche areas to ease measuring climatic niche extent for each owlet. Intersection and stability analyses were performed to map how climatic niches of the species shift across time-periods and to determine regions where suitable niches were always retained. For these analyses, suitable niche polygon for a time-period was superimposed on suitable niche polygons from a preceding time-period and overlapping and non-overlapping areas in both the polygons were identified. For instance, Forest Owlet LIG and LGM niche polygons were superimposed, and overlapping and non-overlapping areas were noted. Areas common to both the polygons (intersection analysis) were treated as conserved areas (niche stable) and non-overlapping areas were treated as a shift (contraction/expansion/displacement) in the suitable niche. Niche overlap analysis to compute *I* statistic (Warren et al. 2008) and niche breadth analysis to compute the B1 and B2 statistic (Levins 1968, Nakazato et al. 2010) were performed using ENMTools v1.4.4 (Warren et al. 2010) to explore niche overlap across time-periods and species. The B1 index (Levin's index) is referred as inverse concentration and B2 index as uncertainty index. The higher values in case of both the indices represent broader niche. A recent post (<http://enmtools.blogspot.in/2018/01/best-to-avoid-using-b1-breadth-metric.html#comment-form>) by Warren (2018) suggests avoiding usage of B1 statistics as it is sensitive to sample size. The niche overlap index (*I* statistics) is computed based on the difference between suitability scores at each grid cell compared between two or more CNM outputs (Warren et al. 2008). Niche overlap indices vary between 0 and 1. Finally a climatic heterogeneity layer was created for each time-period using SDMToolbox in Arc GIS. The climatic heterogeneity is cumulative weighted heterogeneity of the first three PCs of climate data. Depending upon the Eigen values, heterogeneity of first three PCs is summed up and standardized in a percentage (0-100) scale (<http://sdmtoolbox.org/technical-info#Uni3>). Climatic heterogeneity information was extracted from suitable niche polygons to test if the owlets are tracking areas with lower heterogeneous (more stable) climatic conditions, expecting that the endemic Forest Owlet will be nested in the climatically less heterogenous zone as compared to the widespread owlets.

3.3. Results

3.3.1. Climatic Niche Extent and Niche Breadth of Owlets

The models had a low false positive rate (model summaries in Supplementary Table 6). The Forest Owlet underwent a cyclic reduction and expansion in its suitable niche extent throughout the four time periods (Figure 5, Table 2) with the maximum niche breadth and extent of the suitable niche attained during the LIG and minimal during the current time period. The suitable niche areas for the Forest Owlet in central India and the northern Western Ghats appeared to be conserved across time (Supplementary Figure 12F). Results for the Spotted Owlet indicate that climatically suitable areas for the species underwent an expansion during the LGM and progressive reduction in MDH and current time periods (Figure 5, Table 2). Climatically suitable areas for the Jungle Owlet showed a progressive expansion post-LIG up to the current time period (Figure 5, Table 2). Post-LIG, during the LGM period climatically suitable areas for the Little Owl reduced, but progressively expanded post-LGM up to the current time period (Figure 5, Table 2). I detected a southward shift during the LGM and northward expansion post-LGM in the suitable niche areas of the Little Owl (Supplementary Figures 15 and 16).

Table 2. The niche extent and breadth of owlets across study time-periods.

Species	Time period	Suitable Niche Area (km^2)	Niche Breadth – B2 (*100)
Forest Owlet	Current	21197	82.69
	MDH	486051	93.4
	LGM	140794	93.62
	LIG	1261067	94.76
Spotted Owlet	Current	941649	93.55
	MDH	1474825	94
	LGM	1714729	94.58
	LIG	812163	93.14
Jungle Owlet	Current	260700	90.50
	MDH	6297	85.37
	LGM	2425	85.67
	LIG	478	85.51
Little Owl	Current	1781868	92.72
	MDH	289030	82.1
	LGM	301570	79.12
	LIG	360646	78.54

B2: Niche breadth in the range of 0 to 1 (low to high).

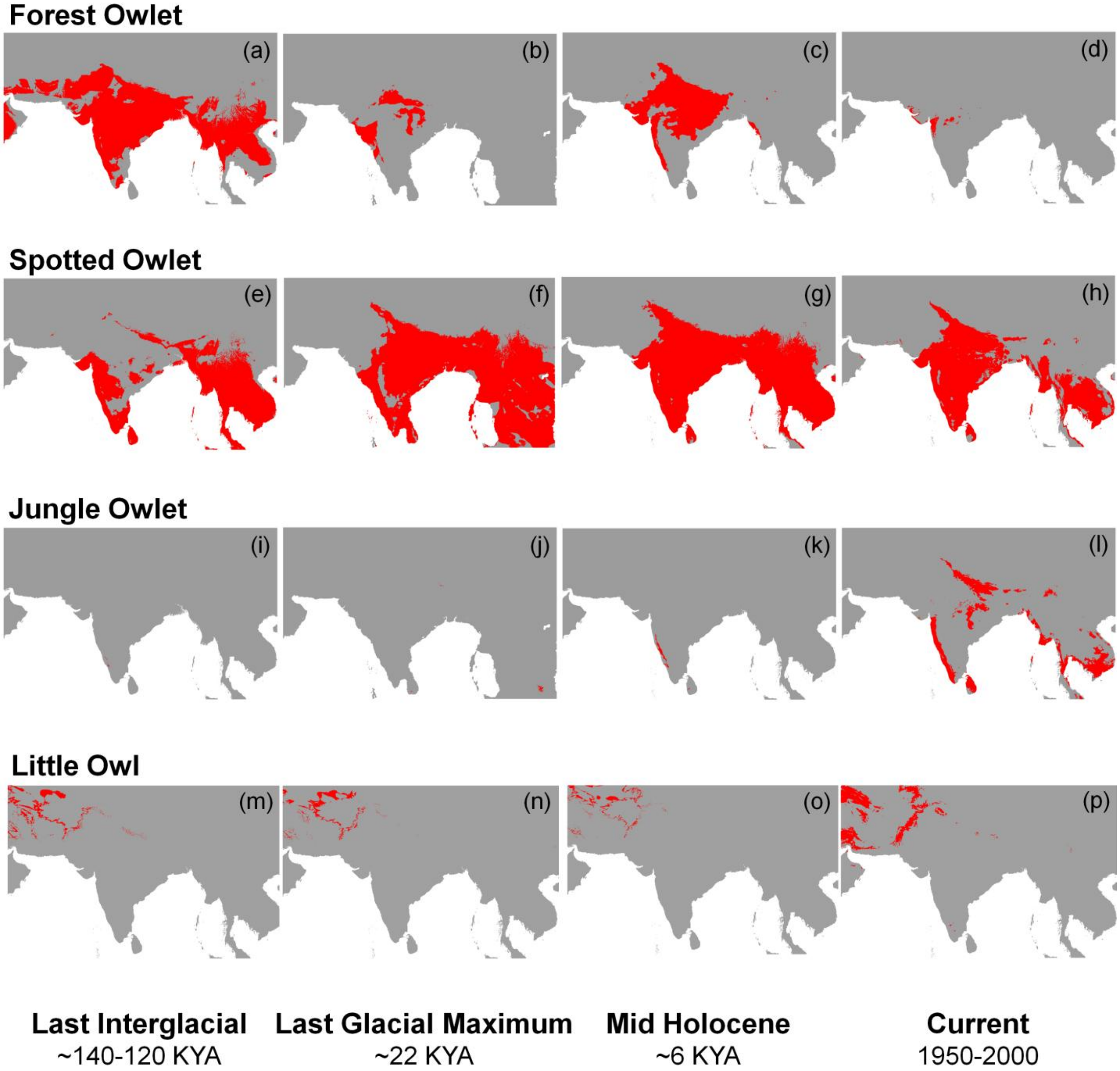

Figure 5. Binary maps of suitable climatic niche extents suggest that Quaternary climatic fluctuations affected all owlets differently. The red and grey colors indicate suitable and unsuitable niche areas respectively. **2a-2d:** The Forest Owlet maps; **2e-2h:** The Spotted Owlet maps; **2i-2l:** The Jungle Owlet maps; and **2m-2p:** The Little Owl maps. The suitable niche area map of the Little Owl is clipped to match the modeling extent used for other owlets for a comparative purpose.

3.3.2. Climatic Heterogeneity and Niche Overlap

I detected overlap (I = 0.62 – 0.98) in the climatic niche of the Forest Owlet across the four time periods (Supplementary Table 7). A similar pattern was seen for the Jungle Owlet (I = 0.59 – 0.86) and Spotted Owlet (I = 0.94 – 0.98). For the Little Owl, niche overlap was the least (I = 0.29 – 0.59) across the four time periods. When comparing overlap between pairs of species for each time period, high niche overlap was observed between the Forest Owlet and Spotted Owlet (I > 0.9), except for the current time period (I = 0.66). The Spotted Owlet, Jungle Owlet, and Little Owl showed high niche overlap only in the current time period (I > 0.8). The modeled niches of all the owlets were nested in climatically stable areas throughout the four time periods (Figures 6 and 7, Supplementary Figure 17, Supplementary Table 18). In the current time period, all owlets occupied areas with higher climatic stability than in the past.

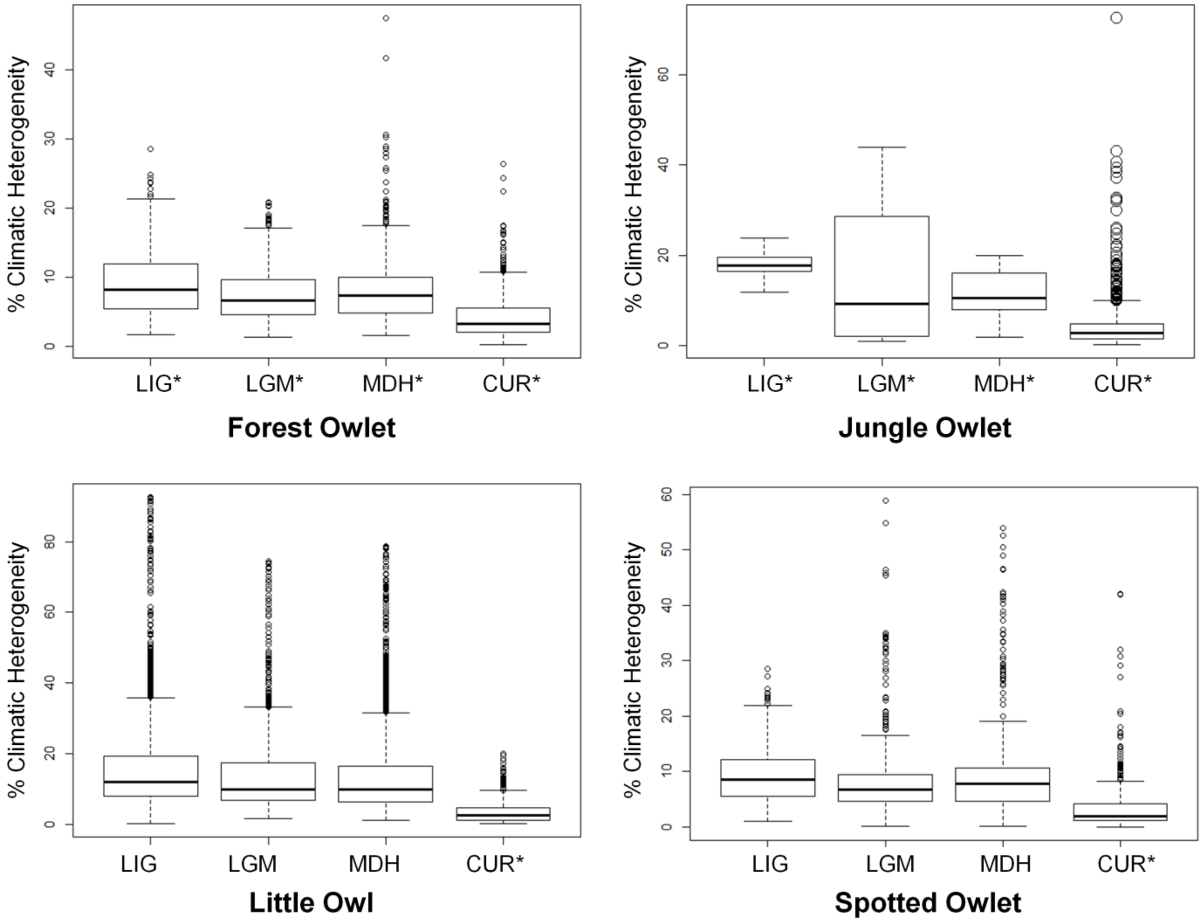

Figure 6. The species-wise arrangement of the climatic heterogeneity values (ranges from 0 - highly homogeneous and 100 – highly heterogeneous) extracted from 1000 random points selected from the suitable niche areas of the study owlets. LIG: Last Interglacial, **LGM:** Last Glacial Maximum, **MDH:** Mid-Holocene, **CUR:** Current. *****indicates that the values differ significantly (*p* < 0.001, One-way ANOVA test) from any other category.

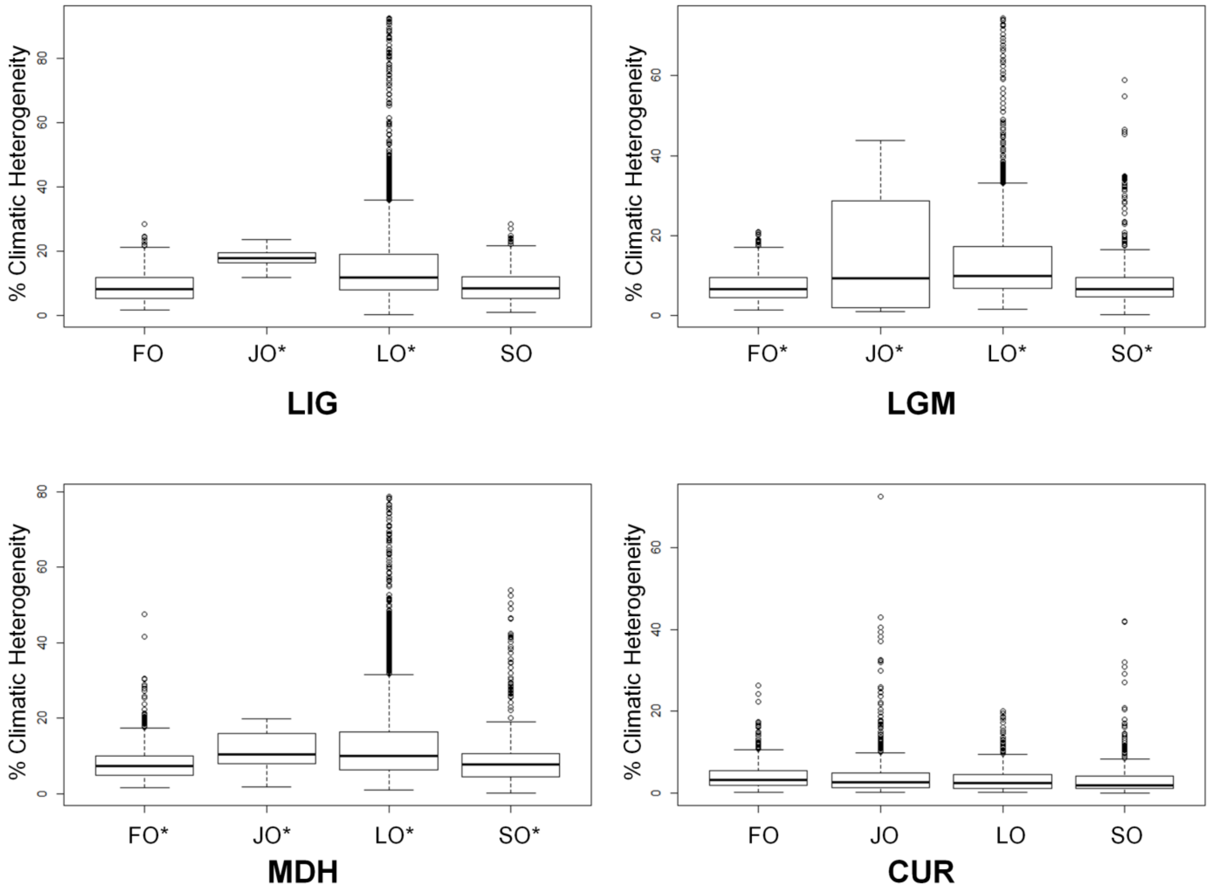

Figure 7. The time-period-wise arrangement of the climatic heterogeneity values (ranges from 0 - highly homogeneous and 100 – highly heterogeneous) extracted from 1000 random points selected from the suitable niche areas of the study owlets. LIG: Last Interglacial, **LGM:** Last Glacial Maximum, **MDH:** Mid-Holocene, **CUR:** Current, **FO:** Forest Owlet, **SO:** Spotted Owlet, **LO:** Little Owl, **JO:** Jungle Owlet. *****indicates that the values differ significantly ($p < 0.001$, One-way ANOVA test) from any other category.

3.4. Discussion

3.4.1. Quaternary Climatic Fluctuations and the Geographical Ranges of Owlets

Assuming that the owlets have tracked the climatically suitable areas predicted by our models, we detected variable responses of the four owlets to the Quaternary climatic fluctuations. The, currently severely range restricted Endangered Forest Owlet showed distinct cycles of reduction and expansion in the suitable niche extent; whereas other currently widespread owlets showed either an overall progressive expansion or reduction in the suitable niche extent (Figure 5, Table 2). The changes in the suitable niche extents among the Indian owlets might be a function of climate and climate-mediated changes in habitat, prey, and interactions among these species. Currently, the Forest Owlet is sympatric with Jungle Owlet and Spotted Owlet whereas the Jungle Owlet and Spotted Owlet overlap in occurrence in parts of their overall distributional ranges.

The niche extent and breadth of Forest Owlet was at its maximum during the LIG (Table 2), which was wetter and warmer than the climate during the pre-industrial Holocene. During this time-period, other co-distributed owlets had relatively constricted climatically suitable areas in the Indian Subcontinent. During LIG, Jungle Owlet, which has a relatively younger divergence (1.8 - 0.1 Ma, Koparde et al. 2018), might have survived in pockets of the south Western Ghats, especially in the eastern parts of the Western Ghats (Figure 5). Considering the LIG scenario (Figure 5), it appears that Jungle Owlet had an insignificant presence in Peninsular India and hence would have played a negligible role as a possible competitor to other Indian owlets at this time. Little Owl was widespread across the Palearctic in LIG and occupied relatively northward areas as compared to its suitable niche extent during the LGM.

During the LGM, possibly as a response to the prevailing drier climate, the climatically suitable areas for the Forest Owlet reduced drastically. This is in tune with their known associations with forests and open habitats respectively. In the LGM, observations of drastic vegetation change in Indian Peninsula from moist rainforests (Sukumar et al. 1995, Prabhu et al. 2004) to tropical grasslands (Ray & Adams 2001) indicate that the LGM climate possibly generated habitat suitable for Spotted Owlet. The niche extent of Jungle Owlet, however, showed a slight increase during LGM when compared to LIG, possibly occupying a diversity of habitats (moist to dry forests to scrublands).

Climatically suitable areas for the Little Owl showed a southward shift during the LGM and a post-glacial northward expansion (Supplementary Figures 15 and 16). The suitable niche areas for Little Owl during the LGM were not restricted to the European Southern Refugia, but widespread occupying a larger area than previously thought. Our results lend support to the Pellegrino et al. (2014) hypothesis of southward range shift of the Little Owl during the LGM.

The expansion in the suitable niche extent of Forest Owlet, during the MDH, could be due to prevailing climatic conditions that were comparable to LIG and when woodlands were widespread. In case of the Jungle Owlet, climatically suitable areas increased during the MDH and spread into the Western Ghats, overlapping with suitable areas for the other owlets. There is increasing evidence supporting multiple warm and cold climate cycles (Randhawa 1945, Sukumar et al. 1993, Chauhan 2002, Gupta et al. 2003) and aridification (Ponton et al. 2012) in the tropics during the Holocene. In Early Holocene, there is evidence of changing vegetation in the Western Ghats (Kumaran et al. 2014, Srivastava et al. 2015). Post-MDH until the current time period such short-term climatic fluctuations might have further impacted the suitable niche extents of the Indian owlets. The possible climate-mediated vegetation changes post-MDH and human-mediated land-use change post-industrialization might have impacted forest-associated species such as Forest Owlet and Jungle Owlet, and open habitat associated species such as Spotted Owlet and Little Owl differently.

Although the owlets overlap in geographic distributions, there are few studies examining resource sharing among the species (Rasmussen & Ishtiaq 1999, Ishtiaq 2000, Jathar & Rahmani 2004, Yosef et al. 2010, Mehta et al. 2018). Interspecific interactions and resource use when factored into ENMs could improve predictions (Araújo & Luoto 2007, Wisz et al. 2013). Incorporating data on recent as well as paleoclimatic fluctuations generated for time periods not covered in this study is recommended, to obtain a more comprehensive picture of species responses to climate change.

3.4.2. Suitable Niche Extents of Owlets and Climatic Heterogeneity

Following the hypothesis of endemic species occupying climatically stable areas (Dynessius & Jansson 2000, Jansson 2003), over a gradient of range extents, we expected the following pattern: the Forest Owlet (forest-associated species with the lowest EOO) would occupy climatically stable areas to a greater extent across all time periods, followed by the Jungle Owlet (associated with forest and scrubland), Spotted Owlet (associated with open habitat and human settlements), and Little Owl (associated with open habitat and human settlements but with the largest EOO). Our results showed that the predicted suitable niche areas of all owlets were nested in climatically stable areas but to differing degrees in various time periods. For the Forest Owlet suitable niche areas were located within climatically stable areas during all four time periods but for the Jungle Owlet and Spotted Owlet this was not consistent across all time periods (Figures 6 and 7, Supplementary Table 8). During the current time period, modeled niches of all the owlets are within climatically stable areas (Figures 6 and 7) unlike during the MDH. The current nested geographical distributions of the owlets (Figure 1) could perhaps be explained by habitat tracking, presuming that the modeled niches are good proxies for actual geographical distributions, The climate refugia for each owlet is different and needs to be mapped and projected considering future climate change for focused and effective conservation planning (Hannah et al. 2007).

3.4.3. Caveats

There is no definitive way to empirically validate the past distribution models constructed for the study species and hence interpretations are presumptive. Non-availability of fossil data for focal species makes it difficult to examine the accuracy of the past distribution models. The two central assumptions of the study are, a) suitable niche extent is a proxy for the geographical range occupied by a species and b) the current species-environment relationships have been maintained in the past. We recommend validating the past distribution models with the help of fossil occurrence data whenever available. Apart from these major issues, the quality and accuracy of the predictor dataset and its projections is of concern (*reviewed in* Nogués-Bravo, 2009).

3.5. Conclusion

The information presented here can be helpful in deciphering the biogeography of highly range-restricted and endangered species such as Forest Owlet with respect to other co-distributed species. Future research in this area should focus on larger datasets incorporating information on regional climate to better understand the effect of Holocene climatic fluctuations on species. Understanding the impacts of past climate on species is vital for long-term conservation planning for range-restricted and endangered species, especially given the current and future climate change scenarios.

CHAPTER 4: UNDERSTANDING CONSERVATION REQUIREMENTS OF FOREST OWLET

4.1. Introduction

Understanding species-specific conservation requirements necessitate fundamental studies on the species ecology and threats to its persistence. The endemic and Endangered Forest Owlet has a severely reduced and fragmented population, distributed across central India (BirdLife International 2017). Presently the species appears to be distributed across 3-4 spatially distant populations (Mehta et al. 2015) across three central Indian states – Gujarat, Maharashtra, and Madhya Pradesh. Since its re-discovery in 1997 (King & Rasmussen 1998), several studies have been conducted on its status and distribution (*listed in* Supplementary Table 9) including the use of predictive tools such as Ecological Niche Models (ENMs) (Jathar et al. 2015). Jathar et al. (2015) used ENMs with Normalized Difference Vegetation Index (NDVI) data, based on the association of Forest Owlet with dry deciduous Teak-dominated forests, to estimate the Area of Occupancy (AOO) and Extent of Occurrence (EOO) of the species. However, their reliance on solely vegetation-based predictors and use of short-term (two years, 2012-2013) data for constructing ENMs were limitations that could lead to unreliable predictions. That information along with additional data available on the population size of the species has resulted in the down-listing of Forest Owlet from the Critically Endangered category to Endangered (BirdLife International 2017).

Despite the currently available information, the limits of the geographical range of Forest Owlet remain uncertain. Except for the ENMs, there is no information available on connectivity between the fragmented populations. As discussed in chapters 2 and 3, the climate is among the broad-scale factors impacting the geographical distribution of Forest Owlet. It emphasizes the need to include climate data as a predictor along with topography and vegetation-based predictors. To understand connectivity between populations and measure conservation status of population/s estimating genetic variability is necessary. High genetic variability across populations and within a population could suggest a more significant overall population and connectedness among the subpopulations. Such studies can provide valuable information such as how the species is faring *vis a vis* fragmented populations and connectivity as well as the long-term prospects for the species to adapt to a changing environment (Amos & Balmford 2001).

With meager conservation planning and effort, Forest Owlet is currently facing a population decline (BirdLife International 2017). The decline is attributed to human-mediated habitat destruction, land-use change, and possible poaching (Jathar & Rahmani 2004, Mehta et al. 2008, Mehta et al. 2017). Given this background, it is vital to understand the limits of the geographical distribution of the species, the factors affecting it, and conservation status of Forest Owlet populations.

In this chapter, I used ENMs to predict Forest Owlet's geographical distribution, using two approaches – multi-data model (climate, elevation, vegetation-based predictors) and Jathar et al. (2015) approach using long-term vegetation data (six years, 2011-2016), to calculate AOO, EOO and niche hotspots where conservation efforts can be prioritized. I performed a genetic analysis of mitochondrial DNA using feathers sampled from individuals of the Khandwa (Madhya Pradesh) population, to estimate intra-population genetic diversity. Based on this work, I provide recommendations for conservation action.

4.2. Materials and Methods

4.2.1. Ecological Niche Models (ENMs)

During this study, Ecological Niche Models (ENMs) were constructed and tested in two phases.

Phase I

The size of the home-range of Forest Owlet is unknown. Little Owl *Athene noctua,* a similar sized and phylogenetically close relative of Forest Owlet, has a territory size of 250 m^2 (Finck 1990, Exo 1992) and home-range of 1.8-95 ha (~0.02-1 km^2) (Grzywaczewski 2009). Hence, for Forest Owlet, raster cell sizes of 1 km^2 (30 arc second) were used to construct ENMs. Forest Owlet GPS location data available from scientific publications and direct observations, since its re-discovery in 1997 till 2015 were collected (n=48). Duplicates or overlapping Forest Owlet presence points at the scale of the raster cell size (30 arc second) were removed. The final trial dataset contained 40 non-overlapping presence points of Forest Owlet (Supplementary Table 10).

The choice of predictors was based on the natural history and ecology of Forest Owlet (Ishtiaq & Rahmani 2000, Jathar & Rahmani 2004, Ishtiaq & Rahmani 2005, Mehta et al. 2008). Surface-interpolated climate data from WorldClim (<http://www.worldclim.org/>, Hijmans et al. 2005), remotely-sensed vegetation data from Bhuvan (<http://bhuvan.nrsc.gov.in/>) and Digital Elevation Model (DEM) data, available from ArcGIS data basin (<https://databasin.org/datasets/366a1bef53344c02bcd7d7611d5f61f7>) were used for the Phase I of ENMs. The Bhuvan portal hosts vegetation data, mainly Vegetation Fraction (VF) and NDVI data, collected using Oceansat-2 Ocean Color Monitor (OCM2) sensor. VF is the percentage of canopied vegetation occupying a grid cell and necessarily is an estimate of vegetation cover. NDVI provides an estimate of green vegetation occupying a grid cell. For calculating VF, estimating NDVI is an intermediate step. Since Forest Owlet is known to be associated with Teak-dominated dry deciduous forest (Jathar & Rahmani 2004, Mehta et al. 2008), VF and NDVI were used in ENMs. Fifteen-day composites of VF were downloaded for 2011-2015 (five years) and NDVI for 2012-2015 (four years), according to the availability of data. The WorldClim portal provides high resolution (30 arc seconds, ~1 km^2) surface-interpolated climate data, summarized for the period from 1960 to 1990. The WorldClim data is not very accurate for tropical countries such as India (New et al. 2002), but this was the only dataset available with a more extensive temporal coverage of climate, during the first phase of building the ENM. This was resolved in Phase II, by replacing the WorldClim data with the Chelsea dataset (Karger et al. 2017) which is remotely-sensed climate data. The geographical extent of ENMs was limited to the major part of central India (*following suggestions by* Thuiller 2004, VanDerWal et al. 2009, Fourcade et al. 2014) to minimize errors related to the geographical extent of the model. Annual mean NDVI (AVG_NDVI), annual mean VF (AVG_VF), the standard deviation in VF (STDEV), and the average change in VF per year calculated for five years (VFDELTA) were derived from NDVI and VF data. Arc GIS v10.1 software (ESRI 2011) was used for layer processing and analysis. After data processing, 1000 random points were extracted from eleven predictor layers and only one variable from each pair of highly correlated variables ($r > 0.8$ or $r < -0.8$) was retained (R software; R Core Team 2013). The final dataset included ten predictors. ENMs were constructed using MaxEnt v 3.4.1. (Phillips et al. 2006) and model outputs were processed in ENMTools v1.4.4 (Warren et al. 2010). MaxEnt settings used were - auto features, 50 bootstraps, and regularization parameter=1.

The average raw outputs were processed in ENMTools to obtain model Akaike Information Criteria (AIC), AIC corrected for small sample size (AICc), and Bayesian Information Criteria (BIC) value. Model selection was based on AICc values, as these values are more informative than BIC and AIC values (Warren & Seifert 2011). A hierarchical model selection approach based on AICc values along with jackknifing analysis in MaxEnt was used to reduce the number of variables. The niche suitability map was converted to a binary map using two thresholds - 10th percentile logistic threshold (low suitability) and average logistic value for training points (high suitability).

The output of the Phase I ENM was field-validated, by conducting a series of surveys to detect the presence of Forest Owlet in areas predicted with high probability by the model. For the field survey, four areas in Gujarat (survey samples=39) were selected. The field surveys were rapid, spanning fifteen days. During the field surveys, a visual scanning transect method was used to detect Forest Owlets, as the Forest Department did not permit call playback based surveys. Call playback surveys are considered to be more efficient in detecting owls (Zuberogoitia & Campos 1998) and have been used in several studies to detect Forest Owlet (Ishtiaq & Rahmani 2000, Jathar & Rahmani 2004, Mehta et al. 2008).

Phase II

In addition to the presence points used in Phase I, additional presence points from personal observations and published records post-2015 (n=36) (after individually verifying the location accuracy from each concerned data owner) were included in Phase II. Spatial filtering was repeated to avoid overlapping points, as performed in Phase I (Supplementary Table 11). The final presence point file contained 73 non-overlapping points collected between 1997 and 2017. Two analyses were performed using the following predictors – elevation and remotely-sensed vegetation and climate data (analysis I, multi-data model) and Principal Components (PCs) of NDVI data following Jathar et al. (2015) (analysis II, NDVI model). In the analysis I, remotely-sensed vegetation and climate data were retrieved from Bhuvan and Chelsea portals respectively. Chelsea portal provides high resolution (30 arc seconds, ~1 km^2) remotely-sensed climate data, summarized for 1979-2013, which also incorporates topo-climate such as orographic rainfall and wind fields (Karger et al. 2017). Such climate data is more robust for ecological niche modeling as compared to surface-interpolated data (Deblauwe et al. 2016, Maria & Udo 2017). Additional data for the year 2016 was collected for predictors from Bhuvan. For analysis II, following Jathar et al. (2015), PCs of NDVI were used to construct ENMs. For this, a Principal Component Analysis (PCA) was performed on 93 files (from 120 files) of the 15-day composites of NDVI for the years 2012-2016. The first five, twelve and twenty PCs that captured 97%, 98% and 99% of the total variation in NDVI data respectively were retained. Accordingly, ENMs were constructed to match the Jathar et al. (2015) methodology. Phase II model outputs were tested *in silico* through partitioning of the total dataset, by randomly picking 25% of points used in the analysis and setting as test points. A hierarchical model selection was performed, and binary maps were created, following the Phase I procedure, for two sets of analyses separately. Since analysis I and II produced different map outputs, an intersection map was prepared for guiding future survey efforts in critical areas. The niche space occupied by Forest Owlet was derived by extracting predictor values from owlet presence location, as additional information.

4.2.2. Genetic Analysis

During collaborative fieldwork with Dr. Prachi Mehta (Wildlife Research and Conservation Society, Pune, India) Forest Owlet individuals from Khandwa, Madhya Pradesh population were captured, tagged, and shed feathers were collected for genetic analysis. The capture, sample collection, gene amplification, and sequence alignment protocols are described in the methods section of Chapter Two. Cytochrome B-oxidase (CYTB) and Cytochrome Oxidase I (COI) data for 25 and 29 individuals were generated respectively. CYTB and COI alignments were subjected to pair wise genetic distance analysis performed in MEGA v5.0 (Tamura et al. 2013). The alignments were exported as Phylip files, and median-joining network analysis (Bandelt et al. 1999) was performed in Network v5.0.0.3 (<fluxus-engineering.com>). Intra-population indices were calculated in DNA SP v6.11.01 (Rozas et al. 2017). Neutrality tests (Tajima's D and Fu's F) were performed to test if the population is under selection. Tajima's D (Tajima 1989) is a measure of the difference between two statistics – the number of segregating sites and the mean number of pair wise differences. Fu's F statistic, apart from indicating population neutrality, provides information on population expansion and reduction (Fu 1997).

4.3. Results

4.3.1. Forest Owlet Distribution and Niche Hotspots

Results from the two phases of modeling are summarized in Supplementary Table 12. Field surveys for Phase I model validation, resulted in the detection of two positive sites of the 39 potential sites surveyed in Gujarat, with a low success rate (5.1%) (Supplementary Table 13, Supplementary Figure 18). From the second phase of modeling, model M1 (analysis I, multi-data model) (Supplementary Figure 19) and MN1 (NDVI first five PCs, analysis II) (Supplementary Figure 20) were selected as the models of choice, given their lower AICc values as compared to the other models (Supplementary Table 12). Temperature (mean temperature of wettest quarter), precipitation (precipitation seasonality), elevation and vegetation factors (annual mean VF and average change in VF per year) were top predictors in explaining the niche of Forest Owlet when ENMs were constructed using climate, topography, and vegetation data (M1 model, Table 3, Supplementary Figure 19). Both M1 and MN1 models differed in the predicted suitable niche extent and breadth (Table 3). Seven niche hotspot clusters were identified (Figure 8) as a result of the intersection analysis on M1 and MN1 outputs. Most of the clusters were in the Satpuda Mountains (South Madhya Pradesh) and eastern parts of northern Western Ghats (west Maharashtra and southeast Gujarat). Forest Owlet is predicted to occupy low to mid-elevation (67 - 758 masl) forest areas with moderate temperatures (11 ºC – 42 ºC), precipitation (0 mm – 1392 mm) and annual mean VF (41% – 60%), which do not experience rapid turnover in annual mean VF (change in annual mean VF = -3 to 2) (Table 4).

Table 3. Summary of top models short-listed based on AICc values during Phase II of modeling.

Model	Top five predictors	Area of occupancy in km^2		B2*100
		Low probability of occurrence (above 10th percentile logistic threshold value)	**High probability of occurrence** (above median presence point suitability value)	
M1 (Multi-data Model)	DEM, BIO11, BIO15, VFDELTA, AVG_VF	58588 (PA = 2575)	5972 (PA = 530)	86.6
MN1 (NDVI Model)	First five PCs of NDVI data	82350 (PA = 7301)	27825 (PA = 3430)	87.57
Intersection Output	Intersection of mixed (M1) and NDVI-based (MN1) models	23284 (PA = 1871)	4041 (PA = 520)	NA

DEM: Elevation; **BIO11:** Mean temperature of wettest quarter; **BIO15:** precipitation seasonality; **VFDELTA:** change in vegetation fraction per year calculated for six years (2011-2016); **AVG_VF:** mean annual vegetation fraction calculated for six years (2011-2016); **NDVI:** Normalized Difference Vegetation Index; **PA:** Area that falls within Protected Areas (Wildlife Sanctuaries and National Park); **NA:** Not applicable.

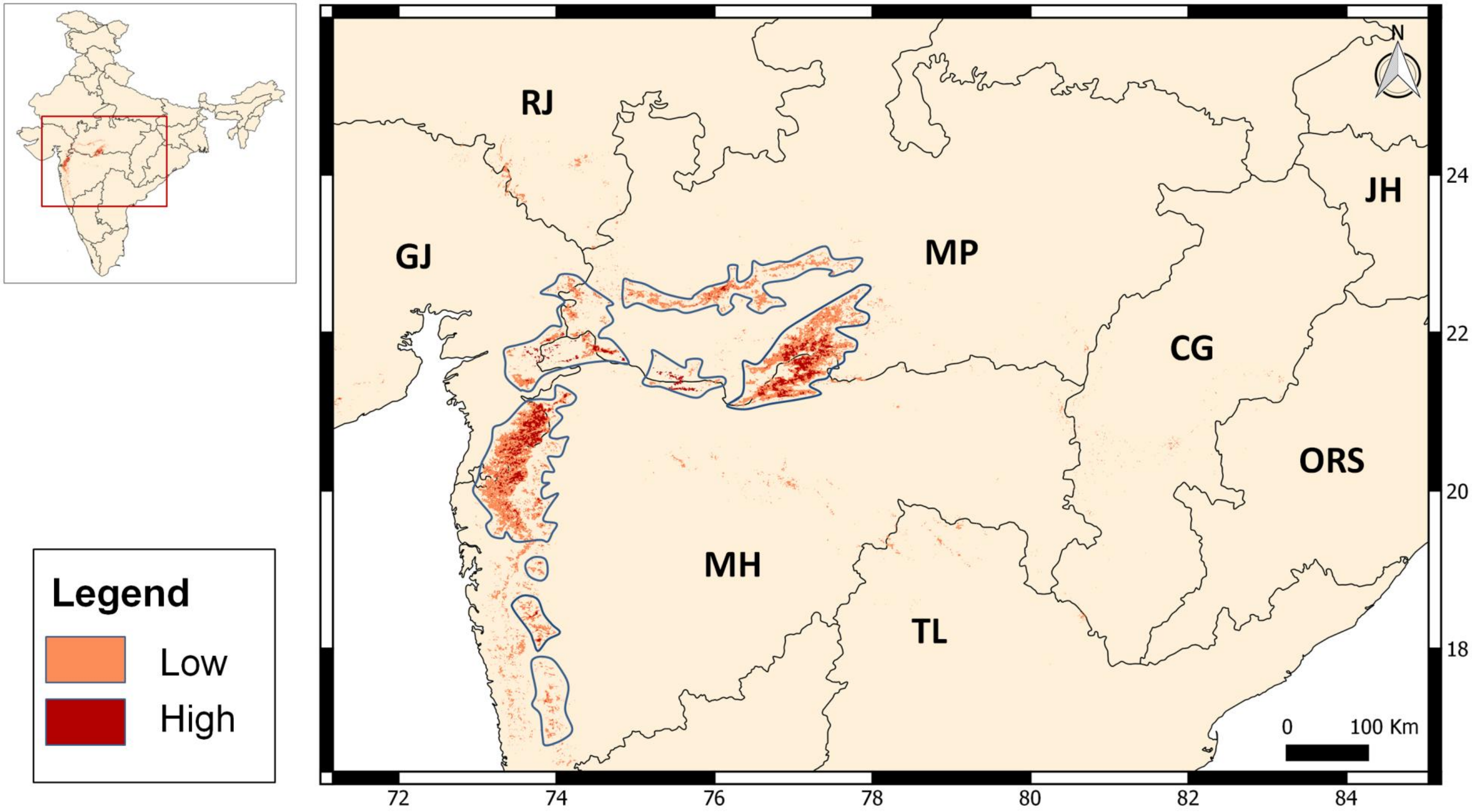

Figure 8. The niche hotspot cluster map produced by intersecting map outputs of models M1 (multi-data model) and MN1 (NDVI model) from Phase II of ENMs. The clusters are delineated in blue polygons. **GJ:** Gujarat, **RJ:** Rajasthan, **MH:** Maharashtra, **TL:** Telangana, **MP:** Madhya Pradesh, **CG:** Chhattisgarh, **ORS:** Odisha.

Table 4. The niche space of the Forest Owlet derived from presence locations (n=76).

Predictor	**Range**	**Average**	**Standard deviation**
Annual mean temperature (ºC)*	23 to 27	25.78	0.92
Mean maximum temperature of the warmest month (ºC)*	34 to 42	38.53	2.25
Mean minimum temperature of the coldest month (ºC)*	11 to 17	12.58	1.72
Mean temperature of the warmest quarter (ºC)*	27 to 34	31.03	1.64
Mean temperature of the coldest quarter (ºC)*	18 to 24	20.90	1.55
Mean temperature seasonality (standard deviation *100)*	1903 to 4149	3213.79	769.36
Annual mean precipitation (mm)*	626 to 3419	1504.01	872.47
Mean precipitation of wettest month (mm)*	233 to 1392	552.97	377.91
Mean precipitation of driest month (mm)*	0 to 6	0.82	1.38
Mean precipitation seasonality (Coefficient of Variation)*	121 to 157	140.34	9.68
Elevation (masl)	67 to 758	379.01	149.22
Annual mean vegetation fraction (%)	41 to 62	53.79	4.11
Standard deviation in annual mean vegetation fraction	5.5 to 19	12.70	3.26
Change in annual mean vegetation fraction per year**	-3 to 2	-0.49	1.06

*this data is summarized climate data for 1979-2013; **the negative sign indicates an increase in VF.

4.3.2. Genetic Analysis of the Khandwa Population

The summary of intra-population indices is presented in Table 5 and haplotype networks in Supplementary Figures 21A and 21B. The results showed low haplotype diversity and low overall mean genetic distance among individuals in the Khandwa population for both genes (CYTB and COI). Neutrality tests (Tajima's D and Fu's F statistic) showed non-significant results for both the loci.

Table 5. Summary of intra-population indices based on genetic comparisons of two mitochondrial loci collected from Forest Owlet individuals from Khandwa population.

	CYTB	**COI**
Number of Taxa	25	29
Base Pairs	961	651
Haplotypes	6	3
Overall Mean Genetic Distance	0.002 ± 0.001	0.001 ± 0.001
Haplotype Diversity ± S.D.	0.767 ± 0.042	0.443 ± 0.069
θ π ± S.D.	0.00163 ± 0.0008	0.00136 ± 0.0006
θ s ± S.D.	0.00163 ± 0.0006	0.00078 ± 0.0005
Tajima's D (*p value*)	-0.04204 (0.5)	1.5338 (0.7)
Fu's F Statistic (*p value*)	-0.594 (0.2)	2.978 (0.17)

S.D.: Standard deviation.

4.4. Discussion

4.4.1. Broad-scale Factors Affecting the Niche of Forest Owlet

This study incorporates a sizeable spatial scale to understand broad-scale factors affecting Forest Owlet's distribution. The Phase I model and subsequent field-validation, suggest that at the scale of the owlet's range, vegetation along with climate and topography are reliable predictors of the owlet's suitable niche. Field sampling for the validation of the Phase I model was relatively rapid and done without using the call playback method. Although a relatively high number of predicted sites were sampled during field-validation, the success was low. Yet, the validation records are from new locations where the species was not recorded earlier.

Phase II models which used a more robust predictor dataset, reveal that apart from the present structure of the vegetation, the history of change in vegetation and rate of this change may affect the owlet's distribution. Areas experiencing a rapid change in vegetation or drastic fluctuations in vegetation fraction are the areas where the owlet is less likely to occur. Forested areas which are prone to large-scale timber harvesting are predicted to affect the owlet's occurrence severely, possibly resulting in the local extinction of the species from such sites. The Forest Owlet is mainly known from Teak-dominated dry deciduous forests (Jathar & Rahmani 2004, Mehta et al. 2008). These forests have been considered as timber harvesting forests historically by conservation managers and currently by native people. They are among the most severely impacted forests in India reeling under anthropogenic pressure including timber harvesting, livestock grazing, forest fires, and land-use conversion (Sagar & Singh 2004, Miles et al. 2006, Anitha et al. 2009, Agrawal et al. 2016). Results presented here suggest that conserving a land-use change sensitive species in a rapidly transforming landscape of central India will be a conservation challenge.

4.4.2. Niche Hotspots of the Forest Owlet

The NDVI-based model (MN1) predicted a much more extensive area suitable for the species as compared to the multi-data model (M1). NDVI-based maps produced during this study were similar to results from Jathar et al. (2015). In this study, results from multiple approaches were used to produce an intersection map and seven priority clusters for Forest Owlet were delineated. As suggested by Mehta et al. (2015), the niche hotspot clusters can be assumed to represent subpopulations. The connectivity between subpopulations is not known. Surveys in areas predicted by the intersection model, outside the known localities of presence, are required to validate the model and refine it further.

Apart from the recognized niche hotspots, secondary suitable niche areas were observed in intervening areas of niche hotspots and to the extremities, especially in central Maharashtra, north Telangana, Maharashtra-Madhya Pradesh-Chhattisgarh border, and south Rajasthan. Most of the secondary suitable niche areas are isolated but need to be surveyed to get an estimate of Forest Owlet's range. The predictive power of MaxEnt is limited at locations away from trial points, and hence the secondary suitable niche areas can be treated as low priority areas for future surveys, however, should not be ignored completely, given the rarity of the species.

4.4.3. Genetic Variability

The genetic variability results presented here are preliminary. The only comparable study from other *Athene* owlets is Pellegrino et al. (2014). Pellegrino et al. (2014) sampled COI sequence from 26 populations of Little Owl (taxa = 276) across Europe and found high overall haplotype diversity (haplotypes = 34, haplotype diversity = 0.819 ± 0.018). Combined ND2 and CYTB data from Madagascar Scops-owl *Otus rutilus*, endemic to Madagascar, also shows relatively high haplotype diversity (taxa = 34, haplotypes = 19, haplotype diversity = 0.902) (Fuchs et al. 2007). Comparing present results with Pellegrino et al. (2014) and Fuchs et al. (2007), low haplotype diversity and overall mean genetic distance indicate high sharing of alleles among Forest Owlet individuals of Khandwa population. The non-significant results generated after performing neutrality tests (Tajima's D and Fu's F) indicate that the sampled population is not under genetic drift or selection for sampled loci. The data presented here is still inadequate in size and populations sampled. The population history and inbreeding status of the population cannot be inferred solely from mitochondrial data. Studies analyzing Single Nucleotide Polymorphisms (SNPs) across populations are recommended to understand population histories, genetic connectivity, and to identify conservation management units.

4.5. Conclusion

In this chapter, I identified broad-scale correlates of the geographical distribution of Forest Owlet and underscored that rapid land-use change might be a primary factor affecting Forest Owlet's geographical distribution. I suggest that urgently required conservation intervention for the species is to concentrate conservation efforts in the niche hotspot clusters identified and delineate the owlet's area of occupancy to conserve it in both the changing landscape and climate. I recommend future researchers to use ENMs constructed in this study to maximize their survey efforts, identify possible dispersal corridors, and conduct studies on dispersal, and genetic and habitat connectivity.

CHAPTER 5: EFFECT OF FUTURE CLIMATE CHANGE ON THE GEOGRAPHICAL RANGE OF FOREST OWLET

5.1. Introduction

The present era of Anthropocene marks accelerated species extinction caused mainly due to human activities (Barnosky et al. 2011, Pievani 2014, Ceballos et al. 2017). An increased extinction risk from climate change, influenced by industrialization and other anthropogenic activities, as is expected for multiple taxa and habitats (Thomas et al. 2004, Moritz et al. 2008, Sekercioglu et al. 2008, Tingley et al. 2012). In the changing climate and land-use scenario, rare and endangered species are more prone to an increased extinction risk (Jetz et al. 2007, Pimm & Jenkins 2011), given their small geographic range sizes and low densities (Pimm et al. 2014). Assessing the effects of climate change on rare and endangered species would hence strengthen conservation planning and action to minimize their extinction risk, by factoring in possible future changes to impacts on species.

Forward-time Climatic Niche Models (CNMs) developed under future climate change scenarios are often used to predict possible impacts of future climate change on individual species ranges and areas undergoing species turnovers (Pounds et al. 1999, Thomas et al. 2004, Bálint et al. 2011, *summarized in* Moritz & Agudo 2013). Such predictive modeling can be instrumental in identifying climatic niche refugia (Ashcroft 2010) and planning conservation, to better manage species under changing climate and land-use settings.

The present status of the rare and Endangered Forest Owlet is critical. Results from modeling suggest that the species is impacted by Quaternary climatic fluctuations (Chapter 3) and is also sensitive to changes in land-use (Chapter 4). Given this background and the threat status of the species, knowledge on its range dynamics under future climate change is urgently required to plan its conservation. In this chapter, I modeled the owlet's climatic niche based on surface-interpolated climate data and projected it for 2050 under two greenhouse gas concentration scenarios, to predict the change in the niche. Here, I assume that the climatically suitable area is a proxy for geographical range of the species. This chapter provides insights into Forest Owlet's range dynamics under a changing climate and identifies areas of conservation priority.

5.2. Material and Methods

5.2.1. Data Collection and Processing

For the forward-time CNMs surface-interpolated WorldClim climate data was used (Hijmans et al. 2005) for which projections are available for current (1960-1990) and future (2050) climate. Two Representative Concentration Pathways (RCPs), RCP2.6 and RCP8.5, that project the present climate data based on the trajectories of the anthropogenic contribution to the greenhouse gas emission (Moss et al. 2010) were selected. RCP2.6 (0.3 °C to 1.7 °C rise) assumes that global greenhouse gas emission will peak between 2010-2020, and then decline. This scenario assumes the global mean temperature will not rise beyond 2 ºC (Vuuren et al. 2011). RCP8.5 (2.6 °C to 4.8 °C rise) assumes continued increase in greenhouse gas emissions throughout the 21st century (Riahi et al. 2011) in the absence of climate change policies. Both the scenarios are extreme scenarios. One dataset (RCP2.6) is under circumstances of extraordinary efforts to control greenhouse gas emission, while the other (RCP8.5) assumes no control. For both the scenarios, data for three Global Circulation Models (GCMs), namely, CCSM4, HadGEM2-AO, and MIROC-ESM were retrieved to check for consistency in predictions. The same Forest Owlet presence points used in phase II of the analysis in Chapter 4 (n=77), were used for the CNMs in this chapter.

5.2.2. Data Analysis

MaxEnt v 3.4.1 (Phillips et al. 2006) was used for ecological niche modeling with auto features on, random test percentage set to 25%, 50 bootstraps, and regularization parameter set to 1. The CNM outputs were processed in ENMTools v1.4.4 (Warren et al. 2010) to compare AICc values in a hierarchical model selection approach. This protocol is mentioned in the methods section of Chapter 4. Additionally, a Principal Components Analysis (PCA) was performed on the current climate data. The first three (PC1 to PC3) and six (PC1 to PC6) PCs that captured 95% and 99% of the total variation in the climate data respectively were retained for CNMs. The best current

CNM was used as a background CNM for future predictions. Future CNMs were constructed for each GCM (CCSM4, HadGEM2-AO, and MIROC-ESM) for each scenario (RCP2.6 and RCP8.4). The resulting three CNMs for every scenario were averaged to produce an average CNM for each scenario. CNM per scenario was compared with the current CNM to understand the effect of climate change on Forest Owlet's niche. The 10th percentile logistic threshold value was used to convert the probability map into a binary map to ease the measurement of the suitable niche extent. Finally, RCP maps were overlaid on the current CNM to identify areas that need urgent conservation attention and long-term monitoring and protection.

5.3. Results

5.3.1. Forward-time Niche of Forest Owlet

The hierarchical model selection resulted in identifying the best current CNM which included six climate variables (MWCM1, Supplementary Table 14). An expansion in suitable niche extent was detected under RCP2.6 and reduction under RCP8.4 (Table 6). The trend in niche breadth was an overall reduction under both the RCP scenarios. Under both the RCP scenarios, an eastward shift in suitable niche areas as compared to the current niche was detected (Figures 9 and 10). The majority of suitable niche areas shared between the current and two RCP CNMs were found to be located at presently identified niche hotspot clusters (Chapter 4 - Figure 8).

Table 6. The summary of the current and future-projected CNMs.

Model	**Suitable niche extent in Km^2**	**B2*100**
current	55714	89.81
RCP2.6	66827	86.37
RCP8.5	44210	85.21

B2: Niche breadth statistic (*refer section 3.2.3.*).

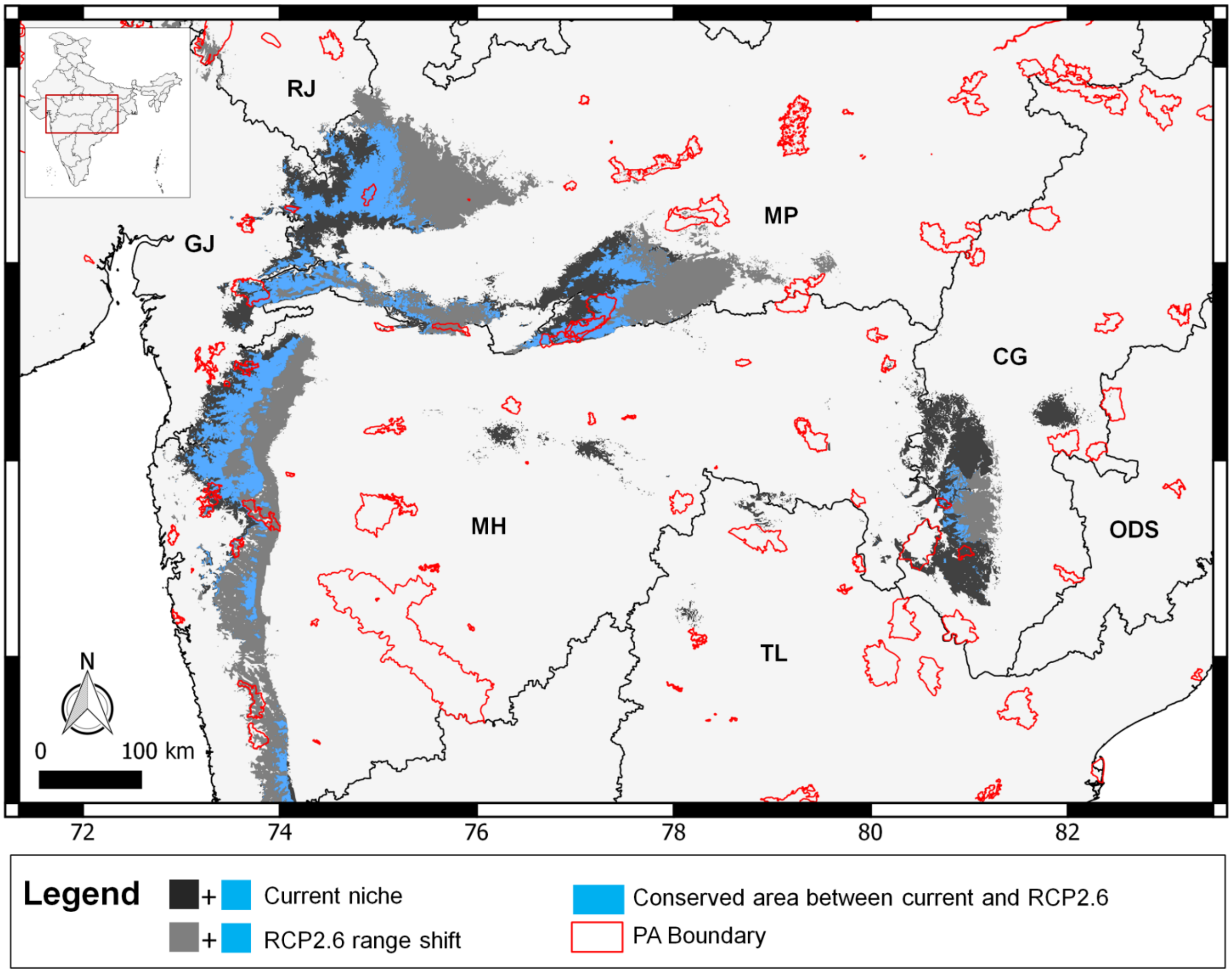

Figure 9. Future-projected CNM under RCP2.6 shows slight expansion in the suitable niche extent, however, shifting the suitable niche areas eastwards as compared to the current model.

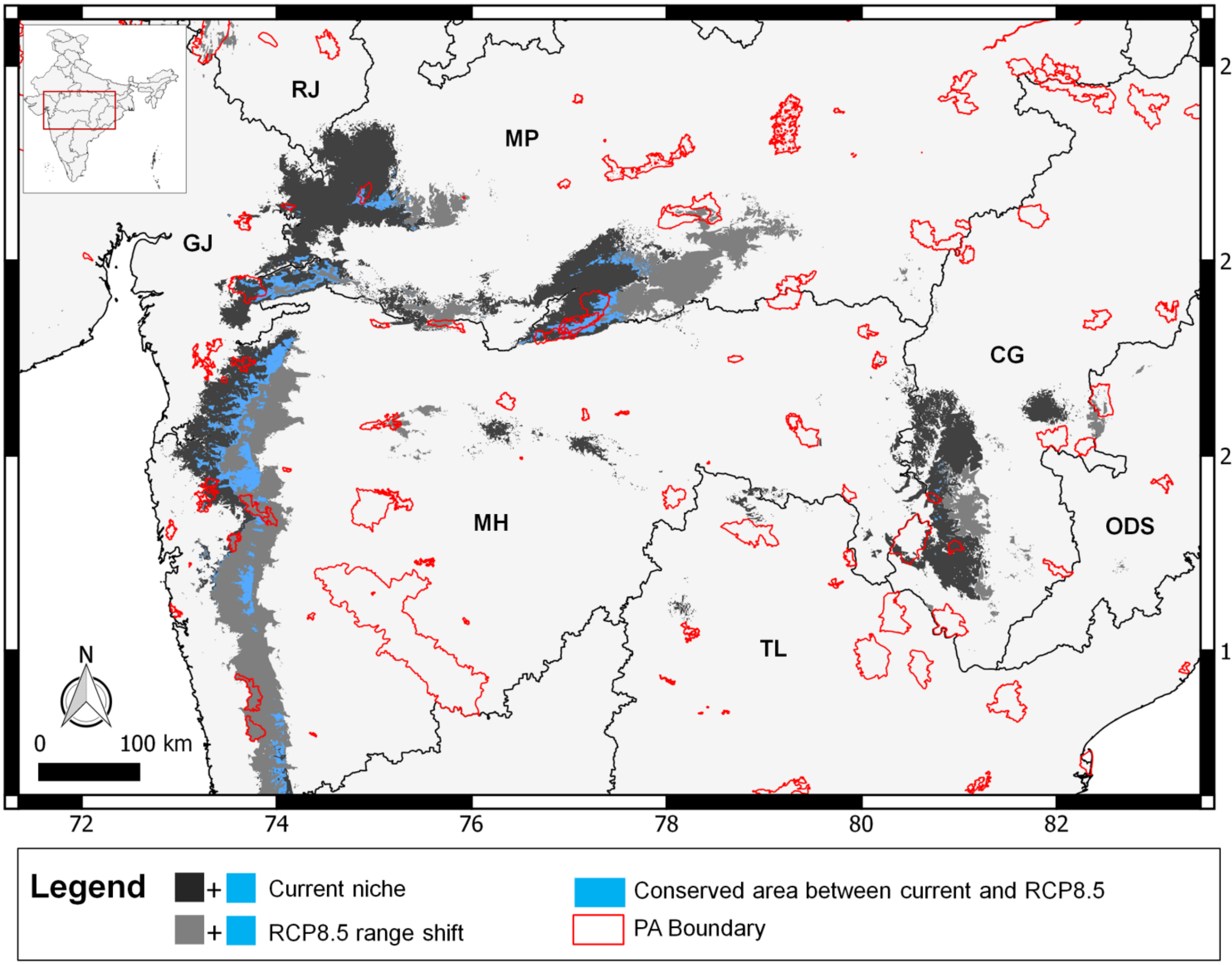

Figure 10. Future-projected CNM under RCP8.5 shows a drastic decline in suitable niche extent, shifting the suitable niche areas eastwards as compared to the current model.

5.4. Discussion

5.4.1. Future Climate Change Might Decrease Climatically Suitable Areas of Forest Owlet

Results presented here indicate an increased risk of local extinction (reduced niche breadth and extent) due to the impact of climate change on Forest Owlet if greenhouse gas emission is not controlled (RCP8.5 scenario). I report 20.5% reduction in the suitable niche extent under RCP8.5 as compared to the current. Even under the most conservative RCP scenario (RCP2.6), a declining trend in the niche breadth of the owlet is reported. Apart from the fluctuations in the suitable niche extent (Table 6, Figures 9 and 10), an eastward shift in the suitable niche areas was detected, which indicates future tracking of a suitable temperature-precipitation regime by the owlet. However, climatic niche models are limited in predicting habitat suitability as suitable niche is also predicted in highly urbanized areas where the owlet does not occur. The eastward shift in suitable niche areas is perhaps as much a concern as the decrease in overall suitable niche extent and breadth. The area of occupancy of the owlet is a subset of its predicted extent of occurrence; hence, reduction in the extent of occurrence is of primary concern.

Forest Owlet is known to be impacted by Quaternary climatic fluctuations (Chapter 3), and forward-time predictions of its niche indicate that future climate change is likely to affect the species severely. The Forest Owlet has a narrower niche as compared to co-distributed small owls (Chapter 3, Table 2) and is also affected by the land-use change (Chapter 4) and other anthropogenic disturbances (Mehta et al. 2017). The habitat of Forest Owlet, chiefly dry deciduous forests in central India, is predicted to be highly vulnerable to future climate change (Sharma et al. 2017), prone to future forest fragmentation and loss. This calls for added conservation efforts in the identified niche hotspot clusters of Forest Owlet (Chapter 4 - Figure 8) as these are the same areas which are going to experience a reduction in extent (as well as are the focal points of future distribution of the species) (Figures 9 and 10), even if only the climatic niche is considered.

5.4.2. Caveats

Like other CNMs, the future change in climatically suitable areas based on present CNMs need to be interpreted with caution. The climate data used in this chapter is surface-interpolated which is highly error-prone, especially for tropical countries which show a wide variation in local climate and also lack a good network of weather stations to capture data (Deblauwe et al. 2016, Maria & Udo 2017). Therefore, the future-projection of the surface-interpolated climate data for India is less accurate. I recommend using highly accurate climate data and a higher number of presence locations spread across the range of the species to capture the variation in climate space. CNMs which include presence and pseudo-absence data might predict with a higher accuracy.

5.5. Conclusion

This chapter provides a possible view of the range dynamics of Forest Owlet in a future scenario and recommends urgent conservation action to save the habitat and species in the identified niche hotspots. Forest Owlet is a flagship species of Teak-dominated dry deciduous forests of central India, which are under severe anthropogenic and climate change threat. To conserve the species, its highly vulnerable habitat to anthropogenic activities needs to be protected in the light of the impact of future climate change on the species range and its habitat.

CONCLUSION

The present study attempts to resolve the phylogeny of four owlets from India that have varied extents of distribution ranges and explores climatic conditions impacting their niches in the past, present and future scenarios. The new phylogenetic information suggests treating *Heteroglaux* as a synonym of *Athene*. The phylogenetic information provides divergence estimates and underscores the possible role of Plio-Pleistocene climatic fluctuations in speciation of Indian owlets.

Based on the past-projected climatic niche models, it is suggested that Quaternary climatic fluctuations played a major role in shaping the suitable climatic niche extents of the study owlets. Suitable climatic niche areas of all owlets examined underwent cycles of expansion and reduction or a gradual expansion or reduction since the Last Interglacial. For each owlet, the modeled niches were nested in climatically stable areas. In the current time, the suitable niche areas of all owlets occupied regions with higher climatic stability than in the past.

The ecological niche models constructed for the Forest Owlet based on the present climate, vegetation and topography data resulted in identifying broad-scale correlates of the geographical distribution of species and conservation priority areas. The spatial analysis revealed that rapid land-use change may be a major factor that impacts the niche of Forest Owlet. The population status analysis of the Khandwa population of Forest Owlet suggests high sharing of alleles, necessitating sampling more populations to understand connectivity and possible dispersal corridors.

Reduction and shift in current climatically suitable niche areas were detected when the climatic niche of Forest Owlet was projected in 2050, suggesting the need of urgent conservation action focused on the identified niche hotspots.

The present study tries to uncover ecological and evolutionary processes underlying the present geographical distribution of four owlets by combining results from molecular phylogeny and climatic niche models. The study suggests speciation of *Athene* members during the Plio-Pleistocene boundary, explores how Quaternary climatic fluctuations impacted their climatic niches, and points to a nested pattern of suitable climatic niche areas of owlets in regions with higher climatic stability in the current time as compared to the past. With respect to the Endangered Forest Owlet, I delineate the suitable climatic niche areas, investigate genetic status of a population of the species, and predict the impact of future climate change on the extent of its suitable climatic niche areas. I recommend obtaining reliable estimates of population densities and habitat and genetic connectivity of study owlets in order to plan the conservation of the owlets. The information presented here underscores the need of basic research on tropical species and its application in their conservation.

SUMMARY

The present study tries to explore ecological and evolutionary processes underlying the geographical distribution of co-distributed owlets of similar morphology and ecology. The new phylogenetic information suggests treating *Heteroglaux* as a synonym of *Athene*. The phylogenetic information provides divergence estimates and underscores the possible role of Plio-Pleistocene climatic fluctuations in speciation. Based on the past-projected climatic niche models, it is suggested that Quaternary climatic fluctuations played a major role in shaping the extent of the suitable niche areas of the owlets. Spatial analysis on suitable niche areas and climatically stable regions revealed that the suitable niche areas of all owlets are nested in climatically stable regions. The ecological niche models constructed for the Forest Owlet, which were field-validated resulted in identifying correlates of the species distribution and conservation priority areas. In the backdrop of future climate change, range reduction and shift scenarios were detected when niche modeling was performed under two future climate change scenarios. The population genetic analysis on the Khandwa population of Forest Owlet suggests high sharing of alleles. However, further sampling including additional populations are required to understand connectivity and possible dispersal corridors. The results of this study suggest that the present geographical distribution of the co-distributed owlets is a function of the evolutionary and ecological history of the species and the history of the landscape of their occurrence, which affects each species differently. The present study is the first of its kind study on Indian owlets, providing information on their evolutionary biogeography and underscores the need of basic research on tropical species. The present study can be improvised with additional sampling of genetic information for phylogeny and population genetics, inclusion of accurate climate and vegetation data matrices and increasing spatial coverage of field-testing of niche models.

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