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**The Effects of Ecology and Climate Change on the Conservation
of Eastern Himalayan Avifauna**

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of Eastern Himalayan Avifauna**

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Dedication

To the village it took.

'Into this wild Abyss the wary Fiend
Stood on the brink of Hell and looked a while,
Pondering his voyage; for no narrow frith,
He had to cross'

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Abstract

The Effects of Ecology and Climate Change on the Conservation of Eastern Himalayan Avifauna

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The University of Texas at Austin, 2018

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The existence of biodiversity is central to all biological sciences, and especially ecology. Without it, an entire branch of knowledge would cease to exist. Despite this centrality, there is considerable debate on the mechanisms that create and maintain diversity. This is especially true of high-diversity areas. There is also considerable debate on how we can best protect biodiversity, in order to allow the science of biology to flourish into the future. Here, I present an investigation of the processes that allow biodiversity to be maintained in the Eastern Himalayas, a critically understudied high-diversity region, as well as a systematic analysis of the conservation priorities there. I focus on birds as a charismatic, speciose and conspicuous set of taxa. I spent several months gathering fine-scale occurrence data for the breeding bird community in Arunachal Pradesh, a state in Northeast India that is at the heart of the Eastern Himalayan ecoregion. Using this data, I first show that bird species on the steep elevational gradient present in the region segregate into narrow elevational bands. I also show that this segregation can best be explained by evolutionary processes resulting from interspecies competition in the long term, and by continued interspecies competition in the short term. I then go on to demonstrate that these narrow ranges of climate tolerance will be greatly affected by climate change, with species' ranges shifting and contracting over the next 50 years. Moreover, when interspecies competition is taken to account, these extent of these predicted changes is intensified. Finally, I use these predicted distributions to create a spatially explicit map of conservation priorities. I present alternatives based on different conservation goals, as well as different projections of the extent of global climate change.

I also present an idealized map of areas most in need of protection, and compare that to the existing set of formally protected areas. Taken in their entirety, these studies present a cogent explanation for the existence of high biodiversity in one of the most special regions of the planet, as well as a roadmap toward protecting that diversity for future generations.

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Introduction

The diversity of life is central to the continued existence of life on our planet. Every species relies on myriad others to survive. In this respect, humans are like any other species, depending on gut microbes and crop plants, on domestic and game animals, on nameless and countless species that keep the ecosystems maintaining human existence intact.

Biology, the study of life on Earth, is itself predicated on the existence of a diversity of life to study. Virtually every research program in the field requires nonhuman species. The diversity of life has offered, and continuous to offer, unparalleled opportunities to understand life itself. These opportunities have been taken by generations of scientists. The amount of knowledge that has been compiled is massive, from the molecular structure of DNA to the evolutionary origins of sociality, from the inner workings of individual cells to the anatomy and physiology of blue whales. However, given the staggering extent of life's diversity, what we have learnt pales in comparison to what we yet have to learn.

The centrality of biodiversity in biology begs two questions, both of which we still do not full understand. What allows diversity to exist? And how do we make sure it continues to do so?

OVERARCHING QUESTIONS

What allows diversity to exist?

Biological communities are interacting populations of multiple species in a shared environment. Some of the earliest studies of biological communities involved the ways in which species in a community interacted with each other – phenomena such as predation, mutualisms and competition. Competition, in particular, has attracted a significant amount of attention because of its intimate relationship with diversity. Some of the earliest work on competition showed that when two species are limited by the same resource, they compete, eventually driving each other extinct (Grinnell 1904, Gause 1932, 1934). Species coexistence could be accomplished, however, if the conditions the species experienced varied (Gause 1932). Later work extended this theory, showing that two

species could coexist if they were limited by two different resources, where each species could outcompete the other for one of the two resources (Tilman 1982, Leibold 1995). This became known as the principle of competitive exclusion.

The principle of competitive exclusion is best formalized with another ecological concept, that of the niche. Two initial models of the niche were proposed. The first centered around the environmental *requirements* of an species – the type of vegetation required, a range of comfortable temperatures, etc. (Grinnell 1917). This was later reformulated as an n-dimensional hypervolume, with each axis representing some aspect of the environment critical to the survival of the species (Hutchinson 1957). The second centered around the environmental *role* that an species plays, or the impact that a species has on its environment (Elton 1927). The principle of competitive exclusion could effectively be state as the notion that two species could not coexist in the long term if they had the same ecological niche.

A problem arose quickly, called the Paradox of the Plankton. This problem consisted of the simple observation that there were apparently more species than limiting resources (Hutchinson 1958, 1961, Ghilarov 1984). This problem was especially pronounced in high-diversity landscapes. When few species were present, one could contemplate the existence of 'hidden niches' that we simply did not know about; but this was harder to contemplate when many more species were present.

The problem of the coexistence of species in diverse ecosystems has since vexed and inspired generations of ecologists. It has been the subject of intense interest and scrutiny for over half a century, and many explanations have been advanced over that time. These solutions can be divided into those invoking niche differentiation mechanisms, and those invoking neutral mechanisms. Niche differentiation mechanisms postulate that species coexistence is a result of subtle differences in niches, which can be elucidated with care. By contrast, neutral mechanisms postulate that species can have identical ecological niches, and that coexistence can nevertheless result due to other mechanisms.

Niche differentiation mechanisms come in several flavors. Several researchers have argued against the view that competition is strong or important, instead positing that simple chance in dispersal and the resultant priority effects determine which species will prevail (see e.g. Goldberg and Werner 1983, Shmida and Ellner 1984, Shmida and Wilson 1985). Other researchers have postulated the existence of several 'cryptic niches' (Finlay

et al. 1997). These solutions to the Paradox effectively deny its existence, either by proposing that the number of species is in fact equal to the number of available niches, or else by proposing that the mismatch between those numbers is irrelevant. A more interesting set of solutions centers on dynamism in the system allowing for coexistence; in other words, proposing that diverse ecosystems are not at equilibrium (Connell 1978). This can be attributed to non-stasis in competitive abilities between species pairs or circular competitive networks; to periodic perturbations to the system; or to priority effects and tradeoffs between dispersal ability and competitive ability (see Wilson 1990 and Roy and Chattopadhyay 2007 for a comprehensive review of these mechanisms). The unifying factor between all of these ideas is that they all postulate some form of niche differentiation between species in a single trophic level.

A contrasting idea, the unified neutral theory of biodiversity, was specifically proposed to explain species coexistence in high-diversity regions. There are several versions of neutral theory, all of which postulate that all individuals of all species in the same trophic level in an ecosystem are ecologically equivalent, with coexistence maintained by dispersal and stochastic local extinction and colonization events (Hubbell 2001, McGill et al. 2006). Neutral theory has generated a significant amount of controversy, and some tests of its predictions have been negative (see e.g. McGill 2003, Ricklefs 2006, Dornelas et al. 2006). There is little empirical evidence to support the notion of competitive neutrality between individuals of all species in a community (Chave 2004). Nevertheless, it appears that neutral theory provides a reasonable approximation of the patterns seen in certain systems (e.g. Goldberg and Werner 1983, Fauth et al. 1990, Siepielski et al. 2010). Moreover, a weaker extension of neutral theory, which postulates that species in a community have equivalent average fitness, is well supported in stable communities (Chave 2004), and generates the same predictions as do some theories that involve niche differentiation mechanisms. It is likely that both competitive and neutral processes act together to structure biodiversity in any given system (Leibold and McPeck 2006).

One of the reasons that the Paradox of the Plankton has not reached a concrete resolution is that differentiating between neutral and niche differentiation processes in a given community is a significant challenge. The best way to 'prove' that competition is important in a given system is through experimentation (Siepielski and McPeck 2010,

Siepielski et al. 2010). In particular, if species are ecologically equivalent, their growth rates should depend on the total abundance of all species in the community and not on their relative abundances. By manipulating the relative abundances of species but not the total abundances, neutral theory predictions can therefore be tested directly. However, manipulating the abundances of species is exceedingly impractical when communities are being studied at large spatial scales, to say nothing of the ethical issues involved.

Another method of testing for neutral theory stems from another specific prediction it makes. In communities where neutral theory predominates, the relative abundances of all species in a trophic level should follow a specific mathematical distribution, a zero-sum multinomial (McGill et al. 2006, Dornelas et al. 2006, but see Etienne et al. 2007). This prediction can be tested empirically by gathering relative abundance data for species in a community. This method of testing between niche differentiation and neutral theory, like experimentation, is logistically challenging since it requires abundance data for every species in the community. This can be insurmountable when dealing with communities on large spatial scales and/or diverse communities with large numbers of species.

Faced with these challenges, ecologists have resorted to other methods. The most popular of these alternatives is the examination of patterns of co-occurrence of species. The hypothesized signature of competitive exclusion is to observe fewer species combinations and less coexistence, although care must be taken to formulate a comprehensive null model accounting for both statistical uncertainty and evolutionary processes (Diamond 1975a, Connor and Simberloff 1979, Gotelli and McCabe 2002, Warren et al. 2014).

Obtaining signatures of competition by examining patterns of co-occurrence and competitive release can be accomplished through the use of species distribution models (SDMs). SDMs are a class of correlative models in which measures of a species' presence and absence are related to environmental variables in order to form a predictive map of the species' occurrence across the landscape (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Elith and Leathwick 2009). In this sense, an SDM can be said to represent a spatial approximation of the Grinnellian/Hutchinsonian niche of a species. Disjunct spatial distributions in part represent disjunct niches, which in turn may indicate niche differentiation.

Understanding the extent to which niche versus neutral mechanisms predominate in a community has important implications for understanding the way in which diversity is maintained in that community. This in turn allows for better predictions of the future behaviour of that community. In particular, we know that climate change is expected to shift the ranges of species, causing novel species assemblages (Parmesan and Yohe 2003, Parmesan 2006, Urban et al. 2012). Understanding the degree to which newly sympatric species will compete with each other allows for a more complete understanding of the effects climate change will have on biodiversity.

How can we ensure the continued existence of diversity?

Species conservation has a long history. Some of the earliest mentions of conservation come from the *Arthashastra*, a Sanskrit text on politics composed in India around the second century BC. The *Arthashastra* recognized the importance of forests in providing goods of economic value (at that time including tiger skins and domestic elephants), and that some degree of management was required in order to ensure a reliable supply of those goods. More generally, indigenous traditions of conservation have existed across the world for as long as those communities themselves have existed, with the same general motivations (Meffe and Carroll 1997).

In Europe, the age of exploration generated an interest in natural history as strange organisms returned on ships from all around the globe. This eventually gave rise to the Linnaean system of taxonomy, in order to place these new discoveries into some context. A natural extension of this was the notion of the 'preservation of nature', which extended through the Enlightenment phase and its flowering of science in Europe and North America. Eventually, this led to the creation of protected areas, as well as early species-specific conservation efforts (Meffe and Carroll 1997).

While notions of conservation had been present for some time in academic discourse, it was not until 1985 that the principles of a new academic field, conservation biology, were given a rigorous formulation (Soulé 1985). To begin with, conservation biology was defined as a crisis discipline, wherein action may unavoidably be undertaken in the absence of full knowledge. This context is fundamental to conservation biology. This framing also led naturally to other characteristics of the field. Conservation biology is inherently multidisciplinary, with knowledge drawn from several fields (including the social

sciences) in order to maximize the efficacy of actions taken. Moreover, conservation biology was taken to be different from preexisting practices of land and resource management because of its holistic nature, concentrating on entire natural systems than on valuable target species. Conservation biology was also defined as acting on long as well as short time scales, in contrast to many management efforts where short-term sustainability was the primary focus.

In addition to this framing, Soulé laid out several basic postulates of this new field. The functional postulates included the ideas that all species live within some community or ecosystem context, that maintaining that context was essential to conservation, and that below a certain threshold ecological and evolutionary processes are disrupted. A fourth functional postulate stated that nature reserves were insufficient for the long-term persistence of large animal species, due to in part to the high extinction rates for small populations on habitat islands (MacArthur and Wilson 1967).

In addition to these functional postulates, certain normative postulates were laid out. Unlike the functional postulates, which were grounded in basic scientific knowledge, the normative postulates were intended as the philosophical and/or aesthetic underpinnings to this new field. These normative postulates can be distilled into two basic ideas. The first is that biodiversity and ecological complexity have inherent value, beyond the direct benefits they provide to human lives. The second, a corollary of the first, is that anything which reduces biodiversity, including anthropogenic species extirpations, is bad. It should also be noted that these postulates were laid out in the context of populations, not individuals; while Soulé called for every effort to be made to avoid eliminating populations, the same was not true of individual organisms comprising that population (Soulé 1985, Meffe and Carroll 1997).

Since 1985, the framing and postulates of conservation biology have been extensively debated. Recent attempts have been made to modernize and redefine the field to be more human-centric, with critiques arising from the effects of heavy-handed conservation interventions on impoverished communities (Kareiva and Marvier 2012, Marvier and Kareiva 2014). A change in the name of the field, from conservation biology to conservation science, has also been proposed in order to better reflect the holistic nature of the field. This update has been hotly disputed by other authors, on the grounds

that it pushes the balance too far towards human benefits at the cost of irreparable damage to natural ecosystems (Doak et al. 2014).

The debate between ‘old conservation biology’ and ‘new conservation science’ has important implications for the ways in which conservation decisions are made. However, it is far from the only conservation debate that has taken place. Parallel debates have taken place over every aspect of the translation of conservation philosophies into real-world action. Reserve design may serve as a single example. Whether conservation should depend on reserves in the first place has been hotly debated (Hayward and Kerley 2012, Somers and Hayward 2012). Given the existence of reserves as a conservation strategy, there has also been extensive debate about how reserves should be chosen (Diamond 1975b, Meffe and Carroll 1997). A single offshoot of this debate, regarding the benefits of single large versus several small reserves, acquired its own acronym (SLOSS) and Wikipedia page, and continues to generate scientific publications (Le Roux et al. 2015, Kendal et al. 2017). Beyond SLOSS, debates on reserve design include but are not limited to the balance between formally protected areas and reserves under other types of management; the relative importance of reserves and matrix regions; reserve complementarity; balancing total biodiversity concerns with saving rare species with small ranges; the utility of reserves created for the benefit of charismatic megafauna as conservation umbrellas; and the ethics of creating reserves in areas where local communities depend on the land for resources (Meffe and Carroll 1997). Outside the question of reserve design, similarly comprehensive debates have taken place regarding ecosystem-based versus species-specific conservation efforts, the conservation value of novel ecosystems, the utility of the invasive species paradigm in the context of conservation, and virtually every sentence from Soulé 1985 (Meffe and Carroll 1997, Kareiva and Marvier 2012, Doak et al. 2014).

In recent years, there has been increasing concern about the value that any of these academic debates have had on the effectiveness on conservation action. It is hard to deny that conservation biology is just as much of a crisis discipline as it was in 1985, if not considerably more so given the increasing threat posed by climate change (Bellard et al. 2012, Dirzo et al. 2014, Ceballos et al. 2017). There has been increasing concern about a mounting gap between the theory of conservation and its actual applications on the ground (Whitten et al. 2001, Knight et al. 2008, Caro and Sherman 2013).

A major issue that contributes to the theory-practice gap in conservation is uncertainty. Despite the framing of the field as a crisis discipline, most management plans are built on a solid foundation of basic ecological and natural history knowledge (Meffe and Carroll 1997). When such knowledge is available, it is of course invaluable. However, there is a systematic dearth of knowledge about tropical ecosystems, which have the highest species diversity and where species loss is expected to be the most severe (Brooks et al. 2002, Collen et al. 2010, Feeley and Silman 2011). In the absence of a firm base of knowledge, conservation actions lag. Despite the framing of the discipline as responding to imminent threats, decision-makers are sometimes loath to take unsupported decisions that may have counterproductive results.

Systematic conservation planning (SCP) is a formalized decision-making framework that helps translate conservation theory into action by obviating some of the need for detailed knowledge about the system (Margules and Pressey 2000). The SCP framework can certainly incorporate basic ecological knowledge if it is available. However, it can be translated into a purely spatial process. Briefly, the SCP framework consists of compiling spatial occurrence data about a set of species in a region, as well as a set of conservation goals/priorities. This information can then be used to identify regions that are the highest priority for conservation. Once such regions have been identified, implementation can then be done in a flexible matter, depending on factors such as land ownership, local community and other stakeholder engagement, availability of funds, and other sociopolitical realities. The SCP framework is therefore a powerful one for achieving conservation goals in regions where little specific knowledge is available. By gathering a spatial occurrence dataset on a large number of species present across different habitats, it is possible to create a spatial prioritization that serves the conservation goals of an entire region.

STUDY SYSTEM

As discussed in the preceding sections, high-diversity areas pose specific challenges to our understanding of how biological diversity is able to exist, and how we can best ensure that it continues to do so. The highest-diversity regions of the planet are in the tropics and subtropics, which are relatively understudied compared to temperate

regions (Collen et al. 2010, Feeley and Silman 2011). However, within these understudied areas, some are still more ignored than others.

The Eastern Himalayas are a global biodiversity hotspot (Myers et al. 2000). While the area appears to be contiguous environmentally and geographically with the Western Himalayas, it has far greater species richness (Price et al. 2006, Srinivasan et al. 2014). The Eastern Himalayas are also understudied relative to other high-diversity regions (Pawar et al. 2007). Recent explorations of the region have turned up several previously undescribed, and quite conspicuous, vertebrates (for examples see e.g. Athreya 2006a, Kamei et al. 2012, Li et al. 2015, Alström et al. 2016). More systematic and extensive work will undoubtedly find far more species currently unknown to science. The Eastern Himalayas are thus a region that demands increased attention from researchers. Apart from this need, however, there are several reasons that this region is an ideal for answering the questions I attempt to answer in this dissertation.

As mentioned, the Eastern Himalayas are extraordinarily biodiverse, with some estimates concluding that they have the second-highest density of terrestrial biodiversity on the planet (Grenyer et al. 2006). This is even more apparent in comparison to the Western Himalayas. A traditional explanation for such large-scale biogeographic patterns is historical anthropogenic effects on very long time scales. However, this does not seem to apply to this community (Mahat et al. 1986, Byers 1996). Another explanation, cycles of natural glaciation, does not completely explain this pattern either (Price et al. 1998, Srinivasan et al. 2014). Dispersal limits may be a partial explanation, with low-altitude Eastern Himalayan species being unable to colonize the West (Srinivasan et al. 2014). Another potential explanation involves seasonality, with the Eastern Himalayas having a less variable climate (Katti and Price 2003, Price et al. 2006). Unlike the tropical Andes, mountain-driven *in situ* speciation is not thought to have occurred, which could otherwise have enriched Eastern Himalayan fauna and flora (Johansson et al. 2007, Price et al. 2014). Instead, invasions from Southeast and Central Asia, followed by vicariance, are thought to have built up the biodiversity in this region, with most terminal splits dating pre-Pleistocene (Johansson et al. 2007, Päckert et al. 2012). While these factors all help explain *why* the Eastern Himalayas are more diverse than the Eastern Himalayas, they do not explain *how* the Eastern Himalayas manage to stay that way. It has been suggested

that interspecies competition is a strong force in the biological community of the Eastern Himalayas; this must somehow be reconciled with high diversity.

Mountain ecosystems present an additional challenge to current ideas regarding the problem of species co-occurrence in high-diversity communities. In particular, most dynamical resolutions to this problem, including the different variations of neutral theory, depend on the existence of landscape heterogeneity (Roy and Chattopadhyay 2007). In mountains, habitat heterogeneity has a very predictable structure, with differences between different altitudes are relatively larger than the variation in habitat at a given altitude. We may therefore hypothesize that competition in a mountain ecosystem will manifest itself as patterns of competitive exclusion between altitudes, with reduced co-occurrences between species pairs across altitudes, rather than the more complicated spatial patterns produced by dynamic niche differentiation processes or neutral mechanisms in a less predictably heterogeneous landscape (Roy and Chattopadhyay 2007). This is especially true of taxa with high dispersal capabilities that have equal access to the entirety of the landscape. The Eastern Himalayas therefore present an excellent system to study the way high diversity may be maintained in the presence of competitive species interactions.

The Eastern Himalayas are also particularly threatened by a variety of factors. Habitat loss is the largest global driver of biodiversity loss, and the problem is especially severe in this region (Brooks et al. 2002). Climate change is also expected to be a major driver of biodiversity loss (Pimm 2008, Bellard et al. 2012), and mountain regions are expected to be particularly at risk (Gibson-Reinemer et al. 2015). The Eastern Himalayas specifically are predicted to be more affected by climate change, even compared to the elevated baseline for mountains (Malcolm et al. 2006). Overhunting is also a major threat to Eastern Himalayan wildlife (Chatterjee 2008, Velho et al. 2012, Dalvi et al. 2013). It is therefore a matter of no little urgency to undertake conservation action in the region. Due to the understudied nature of the Eastern Himalayas and the paucity of basic ecological information, the SCP framework is an invaluable tool in this context. The Eastern Himalayas therefore also present an important system in which to better understand the ways in which biodiversity can be protected.

I selected birds as my study organisms. There are several reasons that birds are suitable for answering the questions I pose. To begin with, birds in the Eastern Himalayas

are extremely diverse; there are more passerine bird species per unit land area than there are anywhere in the world (Price et al. 2014). Birds also have high dispersal abilities, which has advantages when differentiating between niche and neutral mechanisms (Roy and Chattopadhyay 2007). In addition, the identification of birds to the species level in the field is well understood (Rasmussen and Anderton 2005, Grimmer et al. 2012), meaning that occurrence data can be collected through noninterventionist observational methods alone. Moreover, the taxonomy of birds is also well understood (Jetz et al. 2012). This is important, as evolutionary history can obfuscate ecological inferences and need to be explicitly accounted for (Siepielski and McPeck 2010, Warren et al. 2014).

Birds, as a group, are also known to be globally imperiled by climate change (Pimm 2008, Sekercioglu et al. 2008). In places where there are high-quality datasets for species occurrences and for past climate, shifts in species ranges have already been recorded (Tingley et al. 2012, Tingley and Beissinger 2013). Moreover, these range shifts are relatively predictable, as birds seem to maintain their environmental preferences with little evidence of rapid adaptation (Tingley et al. 2009). Birds are also found in virtually every ecotone, meaning that in conserving birds alone it may be possible to conserve most habitats and therefore most biodiversity. Finally, the region contains several species of conservation concern (IUCN 2017).

I focused my work on Arunachal Pradesh (AP), a state in Northeast India that contains a large segment of the Eastern Himalayas. The diversity of the Eastern Himalayas is largely driven by the large elevational range, and AP's elevation ranges from ~100-6000 meters. As a result, the biodiversity of AP is largely representative of the rest of the region. Moreover, AP is large enough that conservation action taken there will have a substantial effect on the entire region. Finally, many of the birds of conservation concern in the Eastern Himalayas are found in AP (Grimmett et al. 2012, IUCN 2017). This includes two little-known species that are thought to be endemic to AP (Athreya 2006, King and Donahue 2006).

CHAPTER SUMMARIES

Below, I present a summary of each of the chapters, as well as the way in which they fit into my overall dissertation.

Chapter 1 – Altitudinal limits of Eastern Himalayan birds are created by competition past and present

Introduction

Imagine a situation in which a single bird species is occupying a mountain with a large altitudinal range (and as a result, a wide range of habitats). Assume now that a closely-related species invades that mountain, as is theorized to have happened repeatedly in the Eastern Himalayas. If competitive exclusion causes modifications to the niches of both species, then there are two likely ways that coexistence might result. One possibility is that both species might retain their ecological traits but segregate spatially. The other possibility is that both species diverge ecologically in order to exploit different resources, and are therefore able to coexist spatially (Jones et al. 2011).

In order to infer competition, it is therefore necessary to examine whether the extent that a given pair of species overlap in their ranges is correlated to the differences between their ecological traits. This approach has been used at small spatial scales with species pairs or ecomorphs of particular species (see e.g. Gatz Jr 1979, Hindar and Jonsson 1982, Churchfield et al. 1999), but has seldom been applied on the scale of an entire community. I make two general assumptions. Firstly, I assume that closely related species occupy more similar ecological niches than more distantly related species, and are therefore more likely to compete (see e.g. Lovette and Hochachka 2006, Slingsby and Verboom 2006, Phillimore et al. 2008). This implies that not every species pair in the community generates useful data, as the extent to which distantly related species do or do not overlap spatially may not be a result of those species responding to each other. I also assume that specific morphological measurements correlate well with ecological traits (Willson 1969, Landmann and Winding 1993, Wainwright and Reilly 1994). Therefore, the difference in those morphological traits between any given pair of species is directly related to the ecological similarity between them.

Hypothesis:

Range overlaps between species are related to the degree of ecological similarity, with closely-related and morphologically similar species overlapping less, and closely-related and morphologically distinct species overlapping more

Methods:

I conducted surveys over three summers in AP, across a range of elevations and habitats. I used the data thus generated to model the elevational ranges occupied by each bird species encountered. I also obtained data on morphological measurements for each species, as well as their phylogenetic relatedness. I related the overlaps between pairs of species to their morphological similarities, as well as to their evolutionary relatedness

Conclusions:

I found that there is a significant relationship between morphological dissimilarity on range overlaps in closely related species, indicating that competition is an important force in setting range limits in this system. However, this relationship disappeared when examining distantly related species, meaning that those species are unlikely to have significant competitive interactions. Moreover, closely related species occupy narrow elevational bands, with less overlap than would be expected under a null model. Additionally, there is evidence that the elevations species occupy, along with their morphological traits, have evolved under some selection, and that there is a tradeoff between selection for optimal morphologies and diverging from closely related species to allow for coexistence.

Chapter 2 – The effects of climate change and species interactions on ranges of Eastern Himalayan birds**Introduction**

From chapter 1, we know that species have relatively narrow altitudinal bands that they occupy, and that competition is important in setting limits on species ranges. We know that climate change is likely to cause shifts in species ranges globally, and that this has been observed in birds (Parmesan and Yohe 2003, Tingley et al. 2009). This can potentially imperil bird species, and change our understanding of the conservation actions required to preserve them (Sekercioglu et al. 2008, Langham et al. 2015). It is therefore natural to ask, in the Eastern Himalayan system, what precise effects climate change will have on species' ranges. However, the exact degree of climate change expected over the

next 50 years is not yet perfectly known, and differences in projected climate may result in different predictions of the effect on species (IPCC 2014).

Hypothesis:

Species ranges will shrink due to climate change by the year 2070, but the extent of the changes to species ranges will depend on the degree of projected climate change. Additionally, accounting for competition will affect the degree of projected changes to species' ranges.

Methods:

I used the surveys described in chapter 1 to construct spatially explicit models for each species, using climate data. I then projected these maps forward to the year 2070 under four different climate scenarios. I analyzed the changes to the ranges of individual species under each scenario. I also used the survey data to calculate an index of the strength of pairwise competition between closely-related species, and applied those to the spatial models of species' distributions. I then analyzed the difference that incorporating competition made in analyzing species' ranges.

Conclusions:

I found that species' ranges are expected to contract overall, although there is significant variation. The climate change scenario chosen significantly impacts the projections of changes in range size for each species. Moreover, the centroids corresponding to individual ranges are also expected to shift, with larger shifts expected for more extreme climate change. Species are expected to vary widely in their altitudinal movements, but some of that variation can be accounted for by species' sensitivity to precipitation relative to temperature. Finally, accounting for competition can dramatically affect the outcomes for certain species, with the most extreme climate change projections also having the largest effects of competition.

Chapter 3 – Systematic conservation planning for Eastern Himalayan birds

Introduction

From chapter 2, we know that climate change is expected to shrink the ranges of a majority of Eastern Himalayan bird species, potentially threatening their future existence. The current set of protected areas in AP were largely designed for the benefit of a few charismatic megafauna; they were not designed with climate change resiliency in mind. To counter this, an SCP framework can be utilized to identify areas that are a priority for conservation action based on both present and potential future distributions (Margules and Pressey 2000).

Hypothesis:

Current protected areas do not adequately protect overall biodiversity. An increase in the total land area under protection is also required to meet conservation goals.

Methods:

I used the SDMs generated in chapter 2 to conduct a spatial prioritization using Zonation software. I created maps that explicitly included and excluded protected areas based on current and future distributions, as well as maps that prioritized overall range-weighted biodiversity over maps that prioritized rare species in less diverse locations. I weighted species according to their IUCN status, with additional considerations for endemism (Grimmett et al. 2012, Birdlife International 2017, IUCN 2017)

Conclusions:

I found that high-value areas identified by Zonation overlapped little with the current system of protected areas. However, as a larger percentile of the Zonation output was selected, the overlap with current protected areas increased non-linearly, indicated that those protected areas are nevertheless located in relatively high-value regions. Not all protected areas are created equally, with some providing far more conservation value than others. There is a general concordance between maps that prioritize overall diversity and maps that prioritize individual species. There are differences in the areas identified as being important for conservation under current versus potential future distributions;

however, several protected areas provide value under both current and future distributions, and therefore should be a priority for future funding and resources.

Chapter 1 – Altitudinal limits of Eastern Himalayan birds are created by competition past and present

ABSTRACT

The degree to which interspecific competition structures high-diversity communities is a long-debated topic. An alternative to niche-differentiation mechanisms, neutral theory, has been proposed as an alternative to explain the stable coexistence of species in such communities. Elucidating the importance of these mechanisms in structuring a community can be accomplished by looking at the effects of species interactions on range limits. However, this has to be done carefully, as underlying phylogenetic patterns can confound the results. I hypothesize that in a high-diversity community where competitive interactions predominate, there will be a relationship between pairwise range overlaps and morphological differences between species, and that this relationship will vary based on phylogenetic relatedness. Moreover, I hypothesize that both morphological traits and altitudinal traits depart from a Brownian motion evolution model, resulting in species trait covariances having a phylogenetic component. The degree to which niche versus neutral mechanisms predominate in a particular community can have important effects on our ability predict the response of that community to perturbations, most notably climate change, when shifting species' ranges may result in novel species assemblages. I present a study on the avifauna of the Eastern Himalayas, among the most biodiverse places on the planet. I find a significant relationship between morphological dissimilarity and range overlaps of species pairs. However, as more distantly related species pairs are included in the analysis, this pattern disappears, indicating that competitive interactions predominate in closely related species. I also find that closely related species are significantly more altitudinally stratified than a null model would predict, indicating that interspecies competition may have played a role in determining the thermal tolerances of species on evolutionary timescales. This is further suggested by the fact that altitudinal ranges themselves are phylogenetically overdispersed at the genus level, as are morphological traits. This effect disappears when the entire phylogeny is examined, with morphology and altitude being phylogenetically underdispersed. Model-fitting suggests that individual clades have evolved towards local

clade-specific fitness peaks, while within-clade results show evidence of niche partitioning. I interpret these results as a tension between competition on shorter time scales and selection on longer time scales, where competition forces closely-related species away from fitness peaks in order to allow for niche separation and hence coexistence, suggesting that this effect is partially responsible for the more recent diversification of Eastern Himalayan avifauna. There appears to be a positive correlation between diversification along functional traits and altitudinal/thermal tolerance, suggesting that divergence along a single axis is insufficient to ensure stable coexistence.

INTRODUCTION

The strength of interspecific competition is an oft-debated topic in community ecology, particularly as it pertains to high-diversity ecosystems. Interspecific competition has long been thought to reduce diversity through competitive exclusion (Gause 1932, 1934, Wilson 1990, Leibold 1995). The principle of competitive exclusion generally states that stable coexistence between two species cannot occur if those species share the same niche, in the absence of other mechanisms such as dispersal limitations (Roy and Chattopadhyay 2007). High-diversity areas pose a challenge to this idea, as there are seemingly far fewer niches than there are species in such ecosystems, a contradiction referred to as the Paradox of the Plankton (Hutchinson 1958, 1961, Ghilarov 1984).

Niche differentiation is a process in which new niches can be created for species in a community by partitioning existing niches. This process may be mediated by competition on ecological and/or evolutionary timescales, creating new niches for species in a community and hence reducing the mismatch between the total number of species and the number of available niches. As a result, high diversity can exist stably in the presence of strong competitive interactions. In addition to niche differentiation, several other ideas have been proposed to explain species coexistence despite strong competitive interactions, among which are non-stasis in competitive abilities between species pairs or circular competitive networks, periodic disturbances, and/or priority effects and tradeoffs between dispersal ability and competitive ability (see Wilson 1990 and Roy and Chattopadhyay 2007 for a comprehensive review of these mechanisms). All of these mechanisms allow for strong interspecies interactions that nevertheless result in stable coexistence.

An alternative paradigm, the unified neutral theory of biodiversity, has also been proposed as an explanation for species coexistence in high-diversity ecosystems. This alternative postulates that all individuals of all species in the same trophic level in an ecosystem are ecologically equivalent and therefore competitively neutral, with coexistence maintained by dispersal and stochastic local extinction and colonization events (Hubbell 2001, McGill et al. 2006).

Neutral theory has generated a significant amount of controversy, and some tests of its predictions have been negative (see e.g. McGill 2003, Ricklefs 2006, Dornelas et al. 2006). There is little empirical evidence to support the notion of competitive neutrality between individuals of all species in a community (Chave 2004). Nevertheless, it appears that neutral theory provides a reasonable approximation of the patterns seen in certain systems (e.g. Goldberg and Werner 1983, Fauth et al. 1990, Siepielski et al. 2010). Moreover, a weaker extension of neutral theory, which postulates that species in a community have equivalent average fitness, is well supported in stable communities (Chave 2004).

Testing whether strong interspecies interactions or neutral theory predominate in a given community is a complicated task. Several potential methods have been proposed in the literature as the debate between these paradigms has been conducted. Experimental manipulations are the gold standard of evidence, and provide the strongest claims for neutral theory (Siepielski and McPeck 2010, Siepielski et al. 2010). Neutral theory predicts that species' growth rates are governed primarily by absolute abundances of organisms in a community, rather than the relative abundances of individual species in that community. Experimental manipulations of abundance can therefore provide persuasive evidence. However, such manipulations verge on impossible when communities are investigated at the landscape scale. Another prediction of neutral theory is that the relative abundances of species in a community should form a zero-sum multinomial distribution (Etienne et al. 2007). This can be empirically tested if the relative abundances of all species in a community are available (McGill et al. 2006, Ricklefs 2006). Again, however, this can pose formidable logistical challenges when examining highly diverse communities at a landscape scale.

Patterns of species coexistence have been used as a proxy for testing competition for many years since the classic studies by Diamond (Diamond 1973, 1975). With the

increasing availability of phylogenetic data, a spiritually similar equivalent is the age-range correlation, where the range overlaps of species are correlated with their phylogenetic relatedness – a negative relationship is assumed to indicate the presence of competitive interactions between them that have mediated secondary contact post-speciation (Fitzpatrick and Turelli 2006). However, neither of these approaches can be applied naïvely. Null models are required to properly interpret co-occurrence data (Connor and Simberloff 1979, Gotelli and McCabe 2002), with pairwise analyses being suggested as a preferable alternative (Veech 2014). On the other hand, age-range correlation analyses can be affected by signals from allopatric speciation alone, in the absence of any secondary contact (Warren et al. 2014). A careful approach accounting for both evolutionary dynamics and phylogenetic confounders is required to correctly understand the implications of community-wide co-occurrence data.

A better understanding of the preponderance of niche versus neutral dynamics in a community can lead to a better understanding of species' range limits. The mechanistic limitations of a species' range arise from a complex set of evolutionary and ecological factors (Sexton et al. 2009). Species are subject to physiological limitations that in turn may have arisen from purifying selection due to competition (Kearney and Porter 2009). In the short term, by contrast, interspecies competition can help set the range limits of species even in the absence of physiological limitations (Cahill et al. 2014, Elsen et al. 2017, Srinivasan et al. 2018). On the other hand, dispersal may affect local adaptation at the edges of a species' range in the absence of any ecological factors (Bridle and Vines 2007). Similarly, parasites and pathogens can also impose selective pressures that help set range limits (Mendes et al. 2005).

Understanding the mechanisms behind the maintenance of range limits is critical in understanding how spatial ranges may change in response to changing environments. Species whose ranges limits are partially determined by competitive interactions may suffer increased losses if climate changes forces the Grinnellian niches of the species involved into greater sympatry. Alternatively, species may benefit from the displacement of a competitor. Moreover, species whose range limits are determined by ecological rather than physiological barriers may be better able to adapt rapidly to climate change. Alternatively, species who are subjected to hard physiological limits due to selection for a

narrow range of climate tolerances may be unable to adjust to changes in climate, and therefore experience range shifts.

The Eastern Himalayas are a global biodiversity hotspot (Myers et al. 2000, Price et al. 2014). In particular, they have the highest passerine bird density on the planet (Price et al. 2014). Invasions from Southeast and Central Asia, followed by vicariance, are thought to have built up the biodiversity in this region, with most terminal splits dating pre-Pleistocene (Johansson et al. 2007, Päckert et al. 2012). This implies that the avian community in the Eastern Himalayas has likely been static in composition for a long period of time. Birds are a tractable study system as they are numerous and conspicuous, they can be readily identified to the species level in the field, and their taxonomy has been well established (Jetz et al. 2012). Therefore, the Eastern Himalayan avifauna offers an excellent system to test the degree to which competitive dynamics might affect species ranges on both short-term and evolutionary timescales; studies on individual clades have indicated that competition is important (Richman and Price 1992, Landmann and Winding 1993, Price 2010). Of particular interest, recent studies centered around a subset of breeding mid-elevation species have indicated that abiotic factors are more important than biotic factors in setting range limits of Himalayan birds (Elsen et al. 2017, Srinivasan et al. 2018); however, narrow ranges of thermal tolerance may themselves have evolved as a consequence of niche differentiation over evolutionary timescales.

I developed a number of hypotheses regarding the effects of competition, both short-term and on evolutionary time scales, on species ranges and traits. I based my hypotheses on the idea that following post-speciation secondary contact, coexistence could be maintained by divergence in thermal tolerance, resulting in altitudinal stratification. Alternatively, species pairs could diverge along functional trait axes, resulting in a change in Eltonian niche and again allowing for coexistence. I therefore hypothesized that competition would result in a positive correlation between pairwise range overlaps and morphological differences. Moreover, I hypothesized that this correlation would only apply to closely related species. I also anticipated that measures of phylogenetic dispersal for both traits and occupied altitudes would show positive phylogenetic autocorrelation (i.e. underdispersal of traits) when examining the entire phylogeny, as closely related species converge on fitness peaks suitable for a given life history. On the other hand, examining the same measures of phylogenetic autocorrelation on small clades would

show the opposite pattern, due to competition forcing species away from optimized traits to allow coexistence.

The importance of determining whether niche differentiation or neutral theory are more important in determining community dynamics arises from the differences in projections made under both assumptions, particularly for novel species assemblages. This is especially pressing in the context of climate change, a potential major driver of such novel assemblages (Parmesan and Yohe 2003). Climate change has already caused shifts in species' ranges, and this is expected to accelerate over the next century (Parmesan and Yohe 2003, Parmesan 2006, Bellard et al. 2012). As species move around on a continental scale, species currently found in allopatry/parapatry are likely to come into contact. It is therefore critical to understand whether these species may then exclude each other due to competition, or whether they will be able to stably coexist.

METHODS

Surveys:

Surveys were conducted in the state of Arunachal Pradesh, NE India (Fig. 1.1a) from 2013-2015. Surveys were carried out during the monsoon (May-July), which is the breeding season for the majority of the regional avifauna. 201 survey points were selected at elevations ranging from 118-4354 meters in altitude; areas both along and away from roads were included, as were points from both protected and non-protected areas. Efforts were made to randomize across vegetation types at particular altitudes. At each survey point, two observers compiled comprehensive lists of all species seen/heard at ten minute intervals. Most sites were visited multiple times in order to assess detectability; sites were visited for an average of 9 intervals (range 1-30). In all, surveys totaled 328 hours of effort. Point localities for some species, generally those of conservation concern, were also collected opportunistically. We were able to record 375 species, 215 of which were recorded at a minimum of five survey points (Appendix A).

Modelling elevational ranges and range overlaps:

For each species at each point, the data consisted of a series of successes (1) or failures (0) to detect the species at each interval. I modelled the elevational range using a

generalized additive model (GAM) with a logit link function on this binomial data; I constrained the fit to a cubic smoothing spline with three knots, as elevational ranges are generally unimodal. The GAM output was then normalized to have a maximum value of 1. Pairwise elevational overlaps were taken to be ratio of the intersection to the union for the output curves (Fig. 1.2); these were calculated using numerical integration. For each species, I also determined the central elevation as the 50th percentile value of the GAM curve.

I also generated a null expectation for the elevational overlap for a given pair of species. It is known that bird diversity in the Eastern Himalayas relates to elevation. I used a smoothing spline to estimate this relationship based on the average number of species observed per ten minute interval at each site. For both species being compared, I used this relationship to randomly draw an elevation of maximum suitability, and then shifted their actual habitat preference upslope or downslope accordingly and calculated the resulting overlap; I averaged this over 100 simulations to generate a null expectation.

Additionally, I observed that certain species overlapped in altitude, but were seldom found at the same point, which could be taken as further evidence of competition (Fig. 1.3). I therefore developed a simulation model to determine the expected number of points at which a given pair of species would be found together assuming no competition, based on the GAM models above. I interpreted the non-normalized GAM output for each species as the probability that a species would be detected at a given elevation during a single time interval. I used this probability as the basis to simulate a series of successful/unsuccessful detections at each survey point using a Monte Carlo approach; the length of the series at each site was based on the number of intervals that site was visited. I collapsed this series of detections into a single presence/absence value, with a species being considered present if there was at least one simulated detection at a site. This was done independently for both species being compared. The simulated presence-absence data for both species was then compared site by site in order to generate a predicted number of co-occurrences. From each simulation, I calculated a competition coefficient:

$$c_i = \sqrt{\frac{\text{Actual co - occurrences}}{\text{Expected co - occurrences}}}$$

The final value for the competition coefficient, c , was averaged over the c_i obtained from 5000 simulations.

Arunachal Pradesh has several major rivers and ridges; it is known that some of these features present geographical dispersal barriers. In order to avoid false negatives in my data, I divided Arunachal Pradesh into several subregions (Fig. 1.1b), and determined each species to either be present or absent in each subregion based on a combination of field guide maps and my own surveys. In subregions where a species was not present, the survey data was taken to be NA rather than a 0 for GAM fitting; I also avoided pairwise comparisons of congeners not found sympatrically in at least one subregion.

Trait and phylogenetic data:

I had two main sources of trait data. Measures of head length, tail length and overall length for all species were obtained from Rasmussen and Anderton 2015; measures of bill length/width/depth, tarsal thickness and wing chord for most passerine species were obtained from the supplemental material of Price et al 2014. These traits are known to correspond to functional aspects of a bird's ecology and foraging behaviour (Marchetti et al. 1995).

For phylogenetic data, I relied on global bird phylogeny created by Walter Jetz et al (Jetz et al. 2012). This phylogeny was generated by assigning species to a set of crown clades and generating trees for these clades, then combining them onto a set of backbone clades (Jetz et al. 2012). I downloaded a sample of 1000 trees from a pseudo-posterior distribution, including all species found during my surveys as tips (Jetz et al. 2012). From these, I calculated the pairwise patristic distance between all species. These distances were used to select a set of congeneric sister species (CSS) found during my surveys, as it is generally thought that the competition is strongest between closely related taxa; species belonging to a genus with only two representatives in my surveys were considered a part of the CSS set. It is worth noting that the sister taxon for the majority of Eastern Himalayan passerine species is extralimital (Price et al. 2014). Among the 210 species detected at 5 or more points, I were able to form 35 CSS pairs. From these, I excluded the aerial insectivores *Delichon nipalense* and *D. dasypus*, as their habit of foraging at

higher altitudes makes it difficult to interpret survey occurrences as being representative of their breeding ranges (Appendix B).

I based the taxonomy for this study on the IOC World List v. 7.1; all datasets describe above were reconciled to this taxonomy. One species pair, *Psittiparus ruficeps* & *P. bakeri*, was not found in the phylogenetic data and was therefore excluded from those analyses; the two taxa were considered conspecific until recently and are currently thought to exist only in allopatry.

Statistical and phylogenetic methods:

The available morphological variables were highly collinear, making direct interpretation complex. To overcome this, the morphological variables were log-transformed and a principal component analysis (PCA) was performed (Fig. 1.4). The first component, corresponding to overall size, explained over 78% of the variation in the data; the first three explained over 93% of the variation. Missing passerine data was predicted using the PCA fit from the passerine species in the Price et al dataset, based on values in the Rasmussen and Anderton dataset. I tested the relationship between morphological dissimilarity and range overlaps by regressing measures of range overlaps against the Euclidean distance between species in PC space. I also conducted a systematic empirical test of the hypothesis that closely related species compete more intensely by applying varying time cutoffs to the phylogeny, and examining the correlation between range overlaps and morphological similarity of all species pairs with a most recent common ancestor (MRCA) more recent than the cutoff.

I examined the effects of phylogenetics on traits using several methods. Moran's I is a measure of spatial autocorrelation, which gives the relationship between a matrix of pairwise differences of some quantity and a matrix of pairwise spatial distances between them (Moran 1950). However, it can be extended to use in a phylogenetic context by replacing spatial distances with phylogenetic distances (Gittleman and Kot 1990). Positive values of Moran's I indicate that closely related species are closer in trait space than would be expected; I generated the null expectation for Moran's I by using Brownian Motion (BM) simulations on my phylogeny. Abouheif's C_{mean} is a similar test that uses a distance matrix where the major diagonal can take on nonzero values (Pavoine et al. 2008). I calculated Moran's I and Abouheif's C_{mean} for morphology by assigning the values of PC1-PC4 as

continuous traits. I calculated these measures for the altitude occupied by treating the central altitude as a quantitative trait, and creating a pairwise distance matrix accordingly.

Software used:

All analyses, including simulation models, were carried out in R (R Core Team 2016). In addition to the base packages, I used functions from *ape*, *adephylo*, *geiger*, *missMDA*, *mgcv*, *phylobase* and *phytools* (Paradis et al. 2004, Harmon et al. 2008, Jombart and Dray 2008, Wood 2011, Revell 2012, Josse and Husson 2016, R Core Team 2016, R Hackathon et al 2016). Basic GIS processing (e.g. extracting the elevation of each survey point from a digital elevation model) was accomplished using QGIS v 2.18 (QGIS Development Team 2017).

RESULTS

For my 34 CSS species pairs, I found that neither the competition coefficients nor the raw degree of range overlap were correlated with morphological similarity. This is in part due to the fact that species with little range overlap also have low calculated competition coefficients, since they are not expected to co-occur. Additionally, species that appear to overlap broadly may in fact exclude each other at smaller spatial scales (Figs. 1.2-3).

I then applied the calculated competition coefficients to the raw range overlaps as a multiplicative factor to get a more accurate assessment of true spatial co-occurrences. The corrected range overlaps were found to be significantly correlated with the morphological difference between a species pair. (Fig. 1.5a; $t=2.59$, $df=32$, $p=0.014$, $r=0.41$). Species that differed more in morphology were expected to have greater altitudinal overlap, and vice versa. This is persuasive evidence that competition plays a role in setting the altitudinal ranges of species at short temporal scales.

Additionally, observed range overlaps were significantly different from the null expectation (paired student's t-test; $t=2.06$, $df=33$, $p=0.047$). This relationship between null and observed range overlaps was also significantly correlated with morphological similarity, with morphologically distinct species showing greater than expected overlap

(Fig. 1.5b; $t=2.42$, $p=0.021$, $r=0.38$). It is worth noting that many species show greater than expected altitudinal overlap. This is likely due to the relationship between elevation and overall diversity, which peaks at mid-elevations and is thought to be driven by arthropod abundances (Price et al. 2014). As a result, there is a significant benefit to birds at this elevation. This forced coexistence may therefore result in increased divergence along functional trait axes, allowing for stable coexistence.

It is generally thought that the strength of competition is higher amongst closely related taxa. When considering all pairwise congeneric comparisons, and not just sister taxa, corrected range overlaps were still significantly correlated to morphological difference, although the correlation was lower than when only CSS species were considered (Fig. 1.6; $t=3.89$, $df=153$, $p<0.005$, $r=0.29$). As I examined more distantly related species, this correlation declined, providing empirical evidence to suggest that distantly related species do not appear to affect each other's altitudinal ranges or functional traits (Fig. 1.7); the correlation falls off quickly with divergence time. This in turn suggests that ecological pressures have produced rapid, recent evolutionary diversification. Other studies have in fact found that much of the radiation of Eastern Himalayan avifauna is relatively recent, particularly in passerines (Päckert et al. 2012, Price et al. 2014).

I also found that when examining the entire phylogeny, there was evidence of non-Brownian evolution of both morphological traits and central elevation (Fig. 1.8). I created a consensus tree based on my set of 1000 phylogenies. I used the PCA values for morphology to calculate a distance from centroid for each species. For the consensus tree, observed values of Moran's I and Abouheif's C_{mean} , were significantly different from the results of 1000 randomizations for both morphology and central altitude. In each case, the results indicated that trait values were underdispersed, i.e. that related species are more similar than would be expected. To test whether phylogenetic uncertainty could affect these results, I calculated Moran's I and Abouheif's C_{mean} for 100 randomly selected trees in the original set. For every individual tree, the observed values of Moran's I and Abouheif's C_{mean} were significantly different from values generated by randomization, indicating that phylogenetic uncertainty is insufficient to alter the overall pattern. This pattern indicates that clades of species have evolved specialized morphologies corresponding to their ecological niches, foraging modes, etc. Underdispersion of central

elevations is likely to be driven by the previously mentioned bias towards mid-elevations (Price et al. 2014), causing those values to cluster.

For the consensus tree, when examining genera with at least 3 species independently, values of Moran's I were largely negative, indicating an overdispersion of traits (Fig. 1.9). The results for each genus were not significantly different from the Brownian expectation, likely due to the relatively paltry number of species per genus. However, a sign test indicates that the median value for Moran's I along both trait and altitudinal axes is significantly less than zero ($n=24$; for morphology, $s=2$, $p<0.0001$; for altitude, $s=2$, $p<0.0001$). This indicates more recent diversification along both trait and thermal tolerance axes. However, there was no indication of a tradeoff between divergence along each of these axes – in fact, there was a positive correlation between Moran's I for morphological traits and Moran's I for central elevation ($t=3.95$, $df=22$, $p<0.001$, $r^2=0.41$). Qualitatively similar results were obtained from an analysis of a random sample of 100 individual trees; for all 100, values of Moran's I clustered below zero for individual genera ($p<0.05$ for all 100 sign tests for PC1 and altitude). This may indicate that divergence along only one of these axes is insufficient to allow for stable coexistence of closely related species.

DISCUSSION

My results indicate that interspecific competition plays an important role in structuring the avian community of the Eastern Himalayas by causing altitudinal stratification. I interpret this result as occurring on multiple timescales. In the short term ('ecological time'), there is a significant effect of morphological dissimilarity on the extent of spatial co-occurrences exhibited by a species. Moreover, closely related species pairs are more segregated than would be expected under a null model. Among the morphologically similar species pairs, the reduced co-occurrence is generated by two seemingly different mechanisms. Some species pairs have distinctly different elevational ranges, with little overlap, and therefore co-occur rarely, with competition presumably playing a minor proximal role. Other species appear to overlap broadly in elevational space, but exclude each other at smaller spatiotemporal scales and so are rarely found together, more indicative of direct competition. Further research is required to understand what explains these different strategies. I found that phylogenetic relatedness does not

explain it – the age of a species pair’s most recent common ancestor does not predict the amount of co-occurrences relative to range overlap.

I also believe that competition has played a role on longer (‘evolutionary’) time scales. I hypothesize that species pairs that segregate to a large degree in elevational space, as discussed above, have evolved their ranges in response to competition. My interpretation is bolstered by my findings that species’ morphological traits and elevational ranges do not seem to have evolved at random. When considering the phylogeny as a whole, morphological traits and elevational ranges are underdispersed, suggesting the existence of optimal elevations, as well as one or more optimal clade-specific morphologies. However, the traits of individual clades are overdispersed, suggesting that there is selection for niche displacement along both morphological and thermal tolerance axes.

Older studies on passerine diversification in this region have emphasized the importance of interspecies competition and niche differentiation (Richman and Price 1992, Price 2010, Price et al. 2014). However, recent studies have underplayed the importance of competition in favor of abiotic considerations (Elsen et al. 2017, Srinivasan et al. 2018). My results suggest that these two viewpoints may be reconciled, in that the differences in abiotic preferences are themselves driven by the ghosts of competition past. My work further indicates that there is an evolutionary tradeoff between selection for optimal morphologies corresponding to a clade-specific fitness peak, and selection for divergent morphologies within a clade that push species away from that peak, spreading them into a ring around the summit. The same applies to elevational ranges, which are a proxy for thermal tolerance – there is a general preference for middle elevations, which have more abundant resources, but species are also forced away from that peak to allow for coexistence. In cases where species pairs show similar morphologies and elevational preferences, yet do not co-occur on smaller scales, further work may elucidate what mechanisms are responsible. Studies on Andean birds have shown that aggressive responses to heterospecific songs are important in setting elevational range limits, but no evidence of this exists in the Eastern Himalayas (Robinson and Terborgh 1995, Jankowski et al. 2008, Dingle et al. 2010); field observations suggest that responses to song playback are highly species specific. Songs may also reinforce range limits of species

pairs whose elevational ranges barely overlap, and in fact song traits may experience selection for this purpose (Brown Jr. and Wilson 1956).

In the coming century, anthropogenic climate change is expected to cause extensive perturbations to ecosystems and communities (Dirzo et al. 2014, Ceballos et al. 2017). Several attempts have been made to predict the responses of avian communities to this challenge (Chamberlain et al. 2013, Langham et al. 2015). One of the major challenges of these efforts is predicting the plasticity of species in their abiotic tolerances. However, there is some evidence that birds in montane environments tend to track their Grinnellian niches over time (Tingley et al. 2009). Additionally, several species in the Eastern Himalayan avian community track their Grinnellian niches during seasonal migration (Srinivasan et al. 2018). My results further indicate that thermal limits of many species are a product of continuing selection and are reinforced by interspecies competition. This suggests that many species may be challenged by climate change, as spatial range shifts may be countered by the presence of parapatric closely-related species. This may prevent species from shifting their ranges, thus subjecting them to rapid changes in their abiotic environment. Continuing selection on their abiotic preferences may hamper their ability to adapt to these changes.

Efforts to use species distribution modelling (SDM) techniques have become a commonly-used tool to estimate the change in species' spatial ranges in the face of climate change (Anderson 2013). However, these attempts are generally limited to consideration of changes in abiotic conditions alone. My results suggest that to accurately understand the effects of climate change on Himalayan avifauna, it is necessary to incorporate interspecies competition. This may further influence our understanding of the conservation status of species in this remarkable ecosystem, and aid in making conservation decisions over the next century.

FIGURES

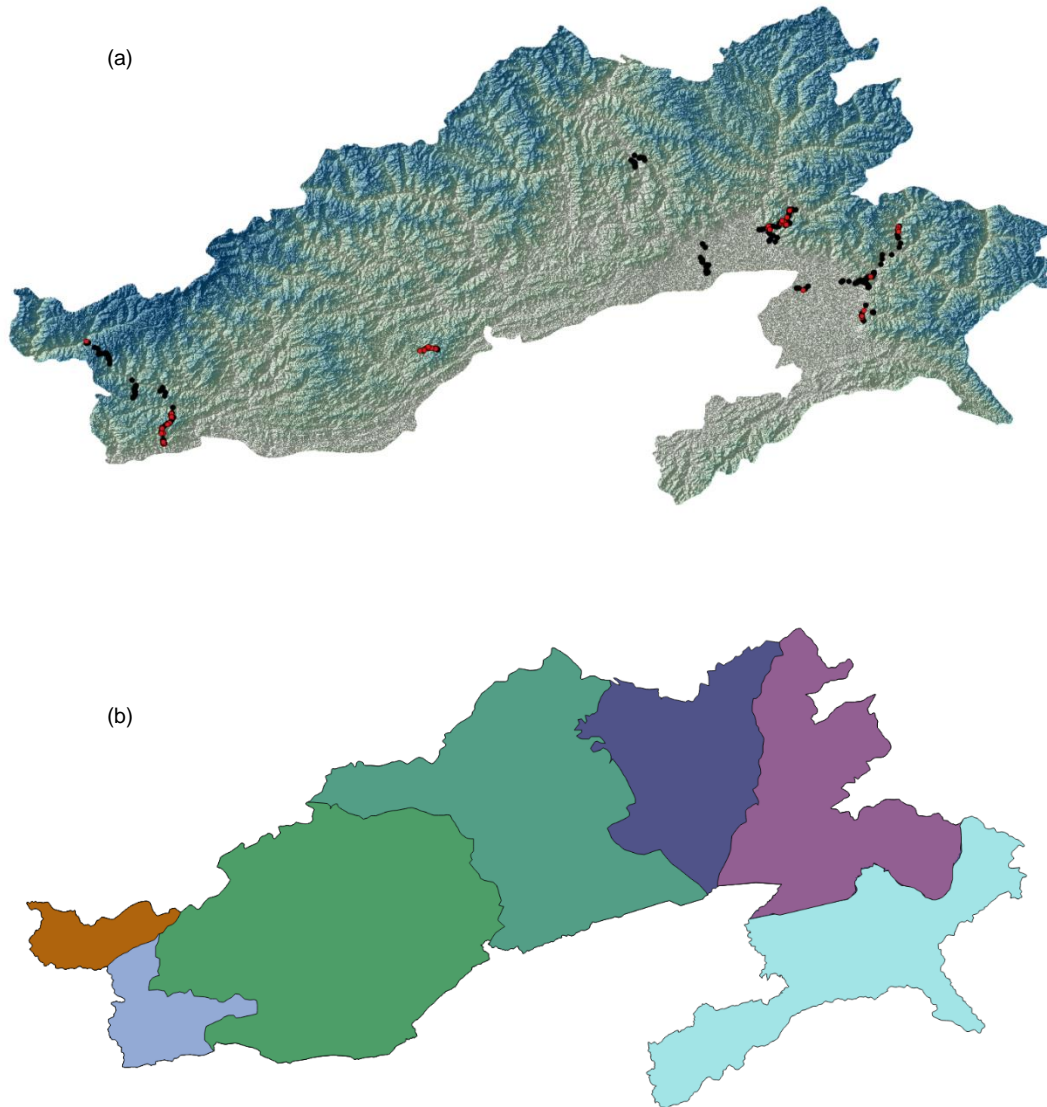


Fig. 1.1 (a) Digital elevation model of Arunachal Pradesh draped over a hillshade map. (b) Subregions used for the purpose of this study

(a) Regular survey points are in black; locations where species localities were collected opportunistically are in red. (b) From west to east, dividing lines between subregions are the Sela Massif, Kameng River, Subansiri River, Siang River, Dibang River and Lohit River.

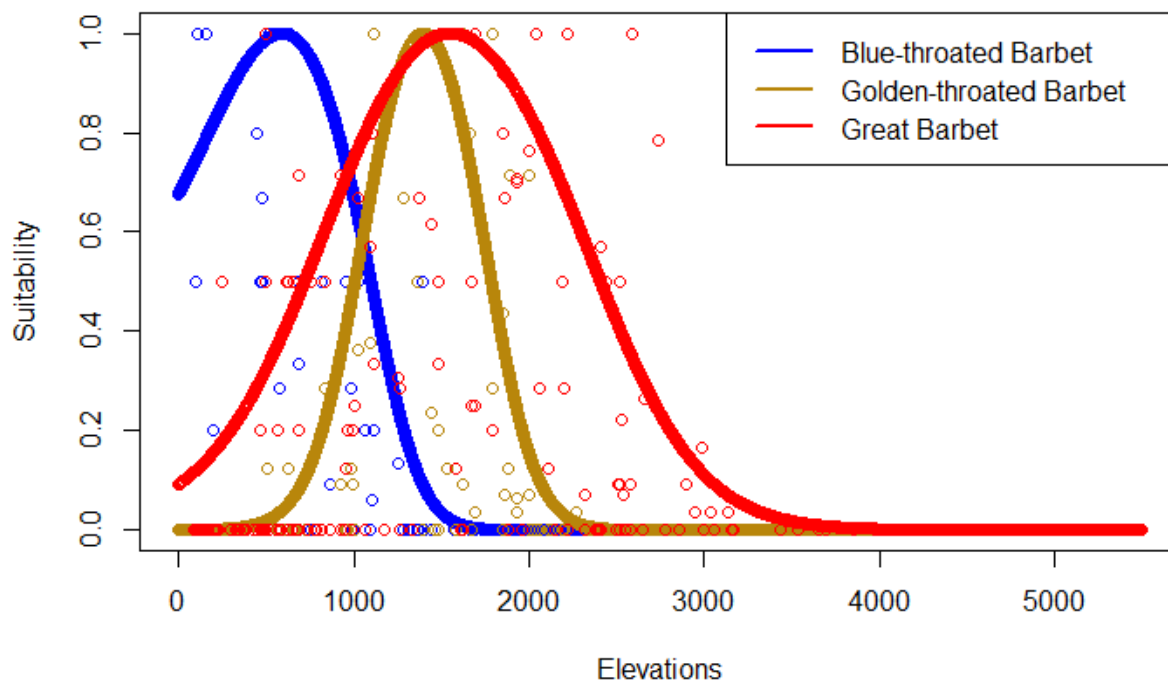


Fig. 1.2. Predicted habitat suitability relative to altitude for three species of *Psilopogon* barbet.

Solid lines represent the GAM predictions; open circles represent the proportion of surveys at a given location at which each species was detected. Notably, Blue-throated and Golden-throated Barbet are similarly sized and segregate altitudinally; Great Barbet, which is much larger, overlaps broadly with both.

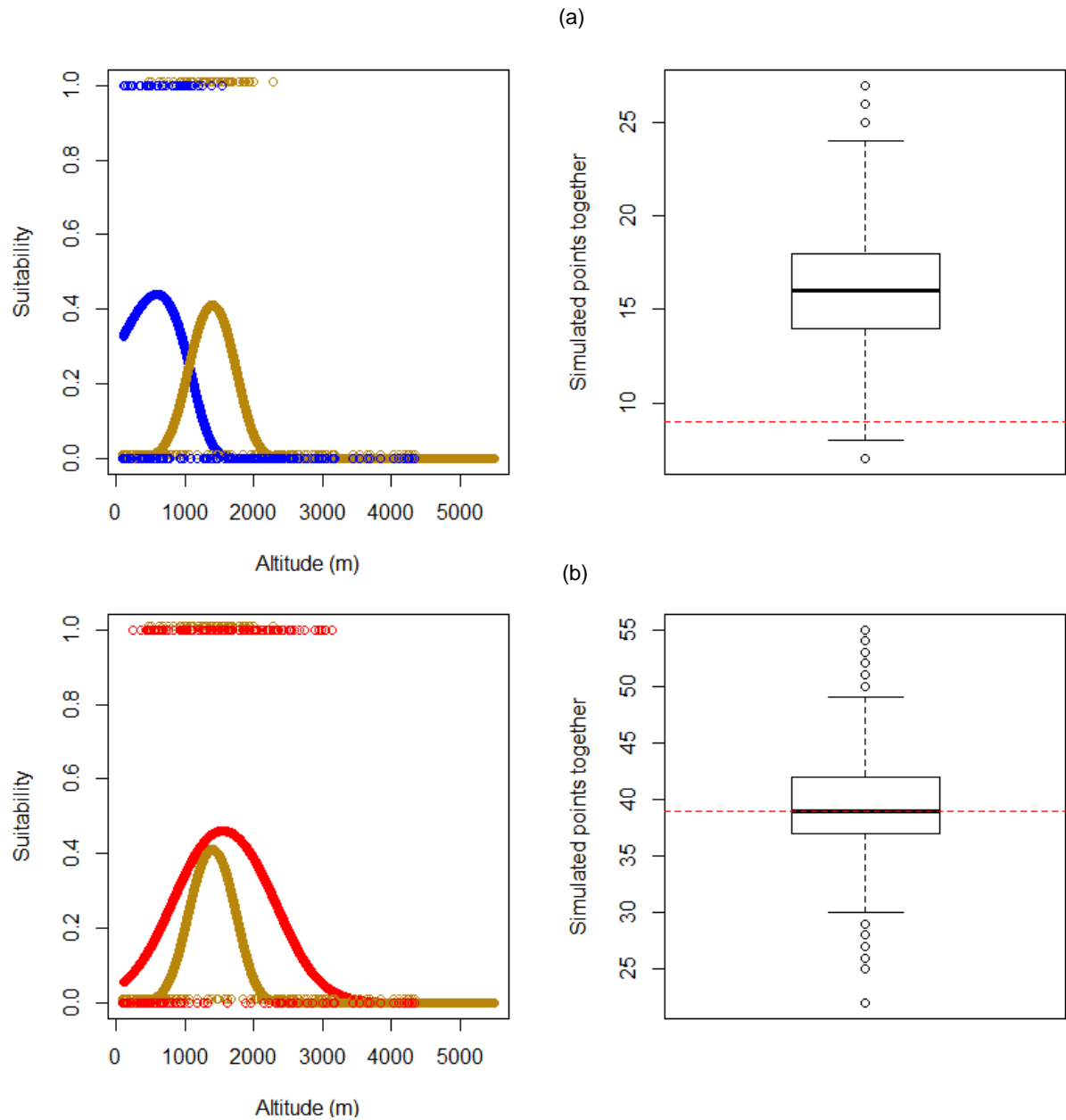


Fig. 1.3. Simulated vs. actual co-occurrence in *Psilopogon* barbets.

(a) Golden-throated (yellow) and Blue-throated Barbet (blue). (b) Golden-throated (yellow) and Great Barbet (red). Left figures show relationship between habitat suitability and elevation for each species; open circles represent presence/absence at each survey point. Right figures show box-and-whisker plots of simulated co-occurrences across 5000 simulations; red dashed line represents the actual number of co-occurrences during surveys. Golden-throated and Blue-throated Barbets are similar sized; Great Barbet is much larger.

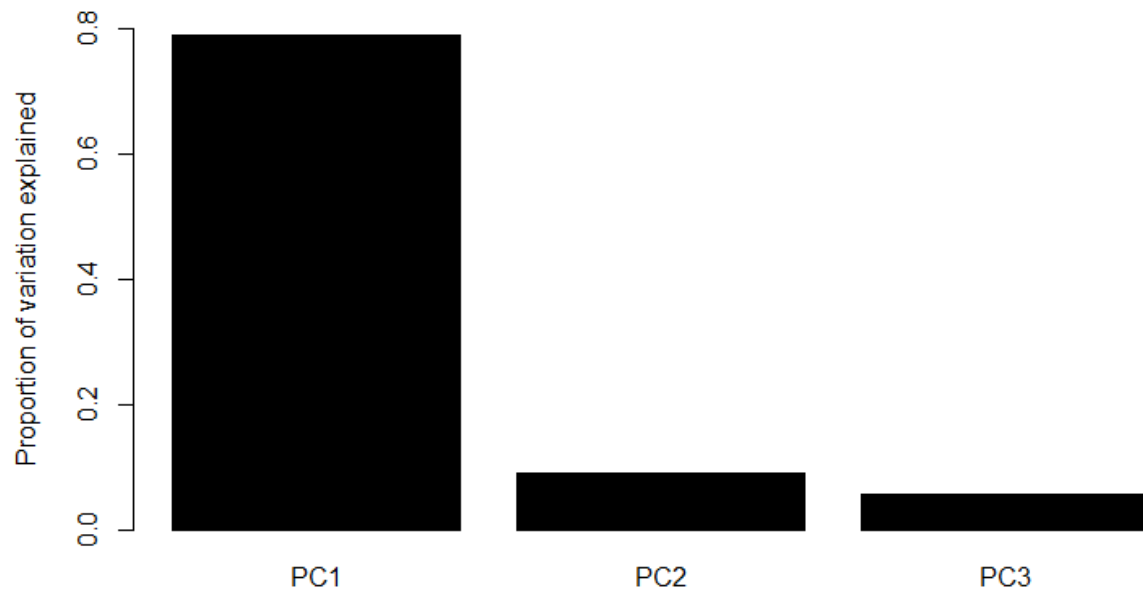


Fig. 1.4. Principal component analysis of morphological variance

PC1 explains the vast majority of the data, 78.9%; the first three principal components explain 93.6% of the data. PC1 broadly corresponds to overall body size; PC2 broadly corresponds to large-billedness, and PC3 corresponds to long-tailedness.

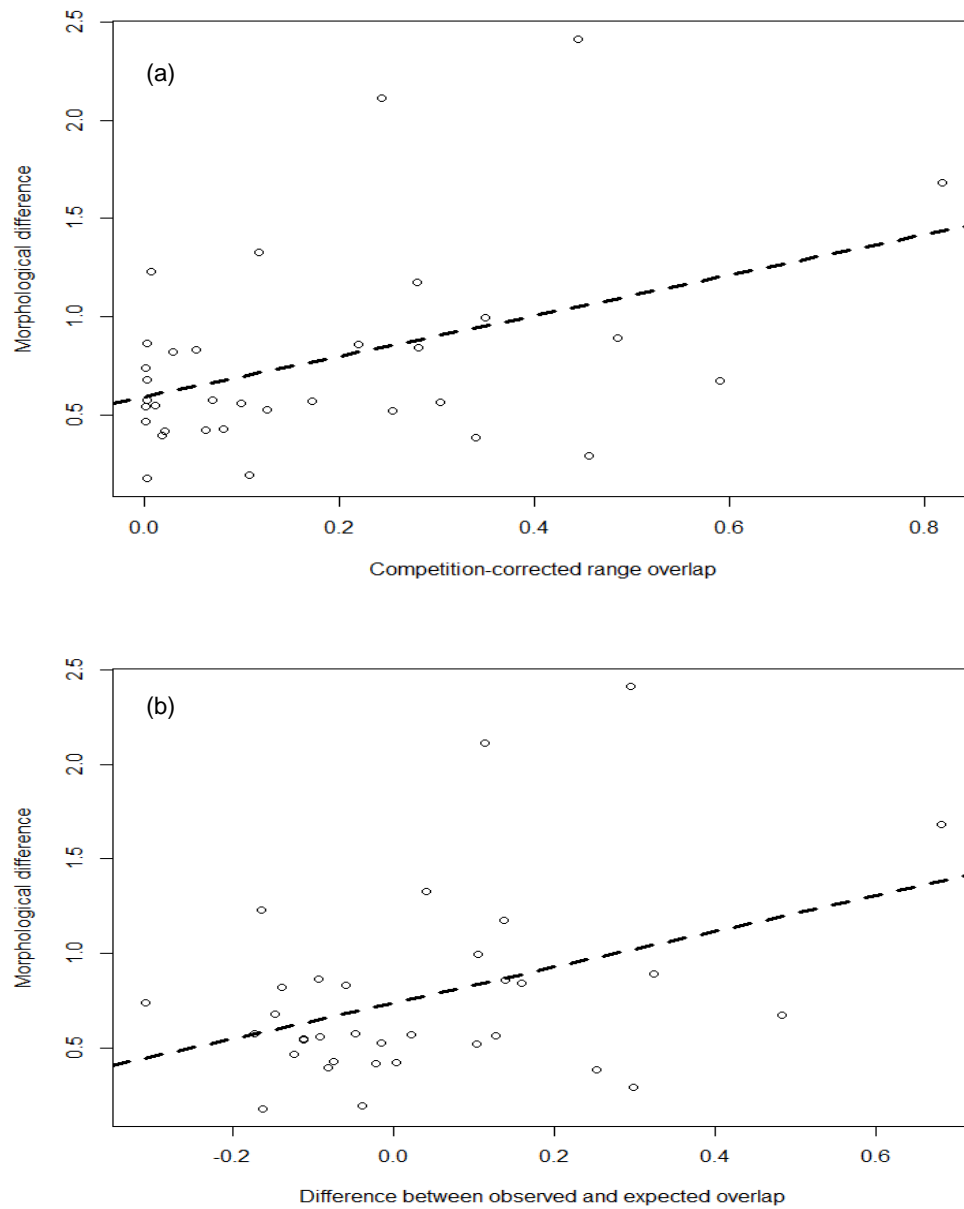


Fig. 1.5. Relationship between morphological difference and range overlaps, sympatric CSS pairs.

(a) Observed range overlaps corrected for interspecies competition; $t=2.59$, $df=32$, $p=0.014$, $r^2=0.17$.
 (b) Difference between corrected range overlaps and null expectation; $t=2.42$, $p=0.021$, $r^2=0.15$. In both cases, morphologically dissimilar species are expected to have greater overlaps in range. Open circles represent individual sympatric CSS pairs; dashed line indicates linear regression fit.

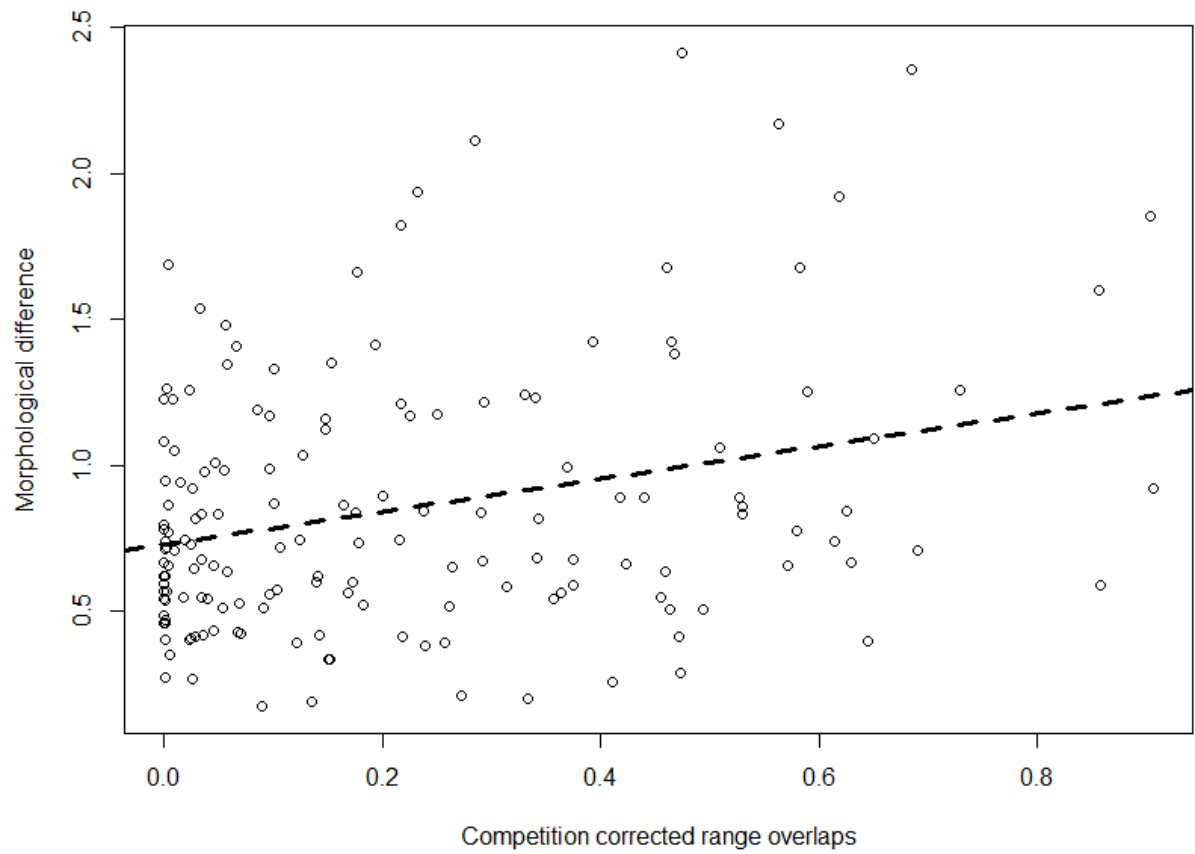


Fig. 1.6. Relationship between morphological difference and competition corrected range overlaps, all pairwise congeners

Open circles represent individual congeneric species pairs (159 pairs); dashed line represents the best-fit linear regression. $t=3.75$, $df=157$, $p<0.005$, $r^2=0.08$.

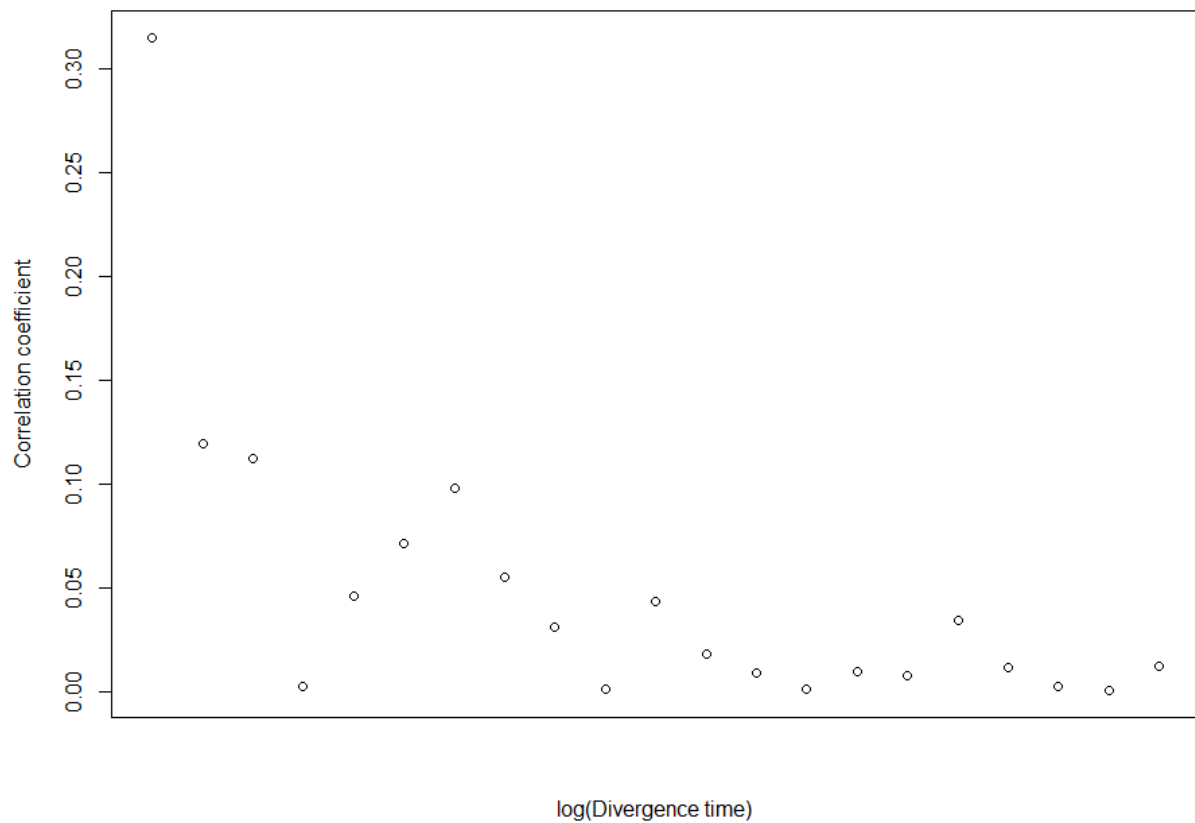


Fig. 1.7. Relationship between divergence time and the strength of the correlation between morphological difference and altitudinal overlaps.

Y-axis represents the r value for this correlation for all species pairs with a more recent MRCA than the X-axis value. As more and more distantly-related species pairs are added, the relationship ceases to explain any of the variation in the data.

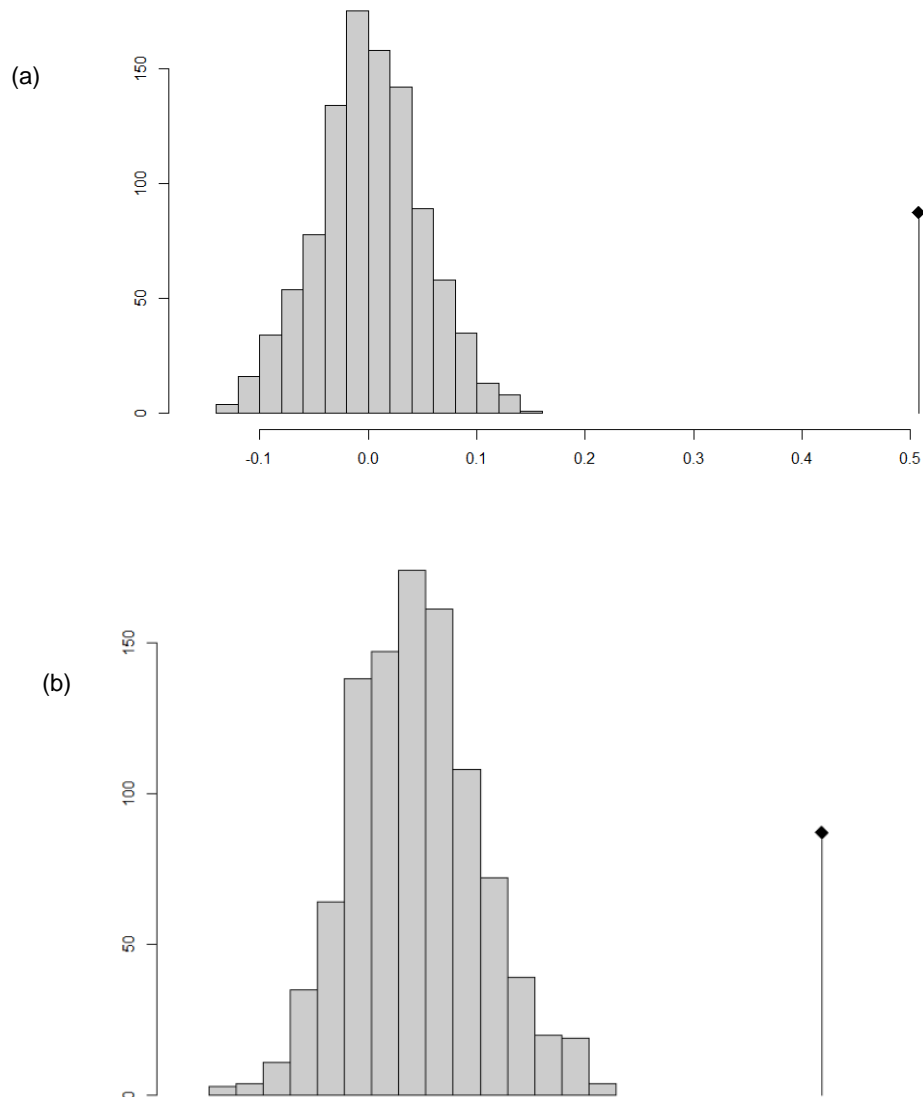


Fig. 1.8. Simulated and actual Moran's I, all species, for morphology and elevation.

(a) Morphology; the value for each species was taken to be its distance from centroid in principle component space after morphological variables. (b) Elevation; the value for each species was taken to be the central elevation occupied by that species. Bars represent number of simulations out of a thousand resulting in a given value of Moran's I; vertical line topped by diamond represents the observed value of Moran's I. Positive values of Moran's I indicate that species are more similar to their relatives than the null expectation.

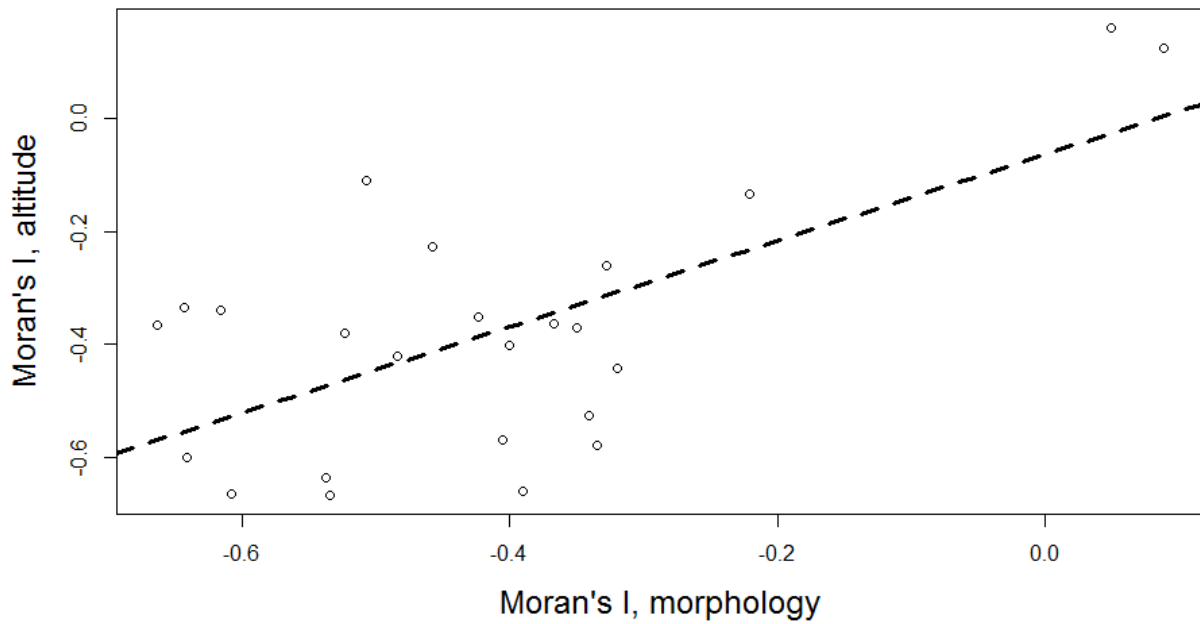


Fig. 1.9. Relationship between Moran's I for PC1 and Moran's I for central elevation.

Negative values of Moran's I indicate overdispersed traits, though all results are not significantly different from a null expectation. Open circles represent individual genera; dashed line indicates best fit linear regression ($t=3.95$, $df=22$, $p<0.001$, $r^2=0.41$).

Chapter 2 - The effects of climate change and species interactions on ranges of Eastern Himalayan birds

ABSTRACT

Biodiversity loss is an increasing threat to global ecosystems. Extinction rates have increased across the planet, to the point where it is currently debated that we are in the midst of a sixth mass extinction. The largest driver is habitat loss. Since a species' range is determined in large part by its Grinnellian niche, it follows that habitat loss is tantamount to a decrease in the spatial representation of a species' Grinnellian niche. This decrease in spatial area available can fuel the declines in populations that pull species into an extinction vortex. Climate change is another process which changes the spatial representation of a species' Grinnellian niche. Unlike habitat loss, climate change does not simply shrink and fragment ranges - it may in fact act to increase range sizes. Climate change also causes ranges to shift in space, in addition to the changes in size it creates. Climate change is therefore a potential driver of population changes, and has the resultant capacity to imperil biodiversity. Understanding the response of species and communities to climate change is therefore critical to better conserve them in the future. Here, I present an analysis of the breeding bird community of the Eastern Himalayas, a disproportionately understudied global biodiversity hotspot. The altitudinal range limits of this community are a result of complex interacting ecological and evolutionary pressures, making it less likely for species to mount a rapid adaptive or plastic response. I conducted surveys from 2013-2015 in Arunachal Pradesh, Northeast India, during the breeding season when altitudinal movements are minimal. I utilized a distribution modelling framework to understand the impacts of climate change on range sizes. I also use a simulation model to account for competitive species interactions between closely related pairs forced into sympatry. I find that on average, species' ranges will shrink by the year 2070 due to climate change, with larger declines expected for more extreme projections of global change. However, I do not find a clear elevational signature, with species moving upslope or downslope in response to temperature or precipitation pressures respectively. Overall, species projected to move upslope are expected to experience greater range contractions, as are species that will end up at higher altitudes. Species on the IUCN Red List show similar patterns, with more severe declines expected. Accounting for species interactions can change projections of

available habitat by ~10%; however, certain species are far more affected, with some species losing up to 80% of seemingly suitable habitat. My results highlight the dangers posed by climate change to biodiversity in the region, as well as the importance of planning for climate change when making conservation decisions.

INTRODUCTION

Biodiversity loss and climate change are two of the largest issues facing our world today. They are also inextricably intertwined. There has been considerable speculation, both in the scientific literature and in the popular press, that the Earth is currently experiencing a 6th mass extinction, and that climate change is exacerbating global extinction rates (Bellard et al. 2012, Dirzo et al. 2014, Ceballos et al. 2015, 2017). Extinction itself is preceded by a reduction in population size. Current changes in population sizes are caused by a variety of modalities, including poaching/overharvesting, pollution and invasive species (Soulé 1985, Kareiva and Marvier 2012). However, the most important driver is thought to be habitat loss through anthropogenic alteration of the environment (Tilman et al. 1994, Brooks et al. 2002).

The ecological niche of a species, in the Grinnellian sense, is the set of environmental requirements for that species to exist and reproduce at replacement level or above (Grinnell 1917, 1924). The Grinnellian niche thus plays a critical role in determining a species' spatial distribution (Guisan and Zimmermann 2000, Soberón 2007, Hargreaves et al. 2014). Habitat loss is essentially the decreased spatial representation of a species' Grinnellian niche, which thus reduces the area available to that species. Since the population density of many organisms is regulated by resource availability, it follows that a reduction in available area is tantamount to an eventual reduction in population (Lack 1954, Tilman et al. 1994). In turn, small populations are well known to be more susceptible to extinction (Soulé and Gilpin 1986, Brook et al. 2008). Along with habitat loss, anthropogenic climate change also changes the spatial realization of ecological niches, causing species' ranges to shift and change size (Parmesan and Yohe 2003, Parmesan 2006, Bellard et al. 2012). This has been well documented in multiple systems, particularly in areas with high-quality, long term species-specific monitoring data (Schloss et al. 2012, Tingley and Beissinger 2013, Langham et al. 2015). Understanding

the impacts of climate change on species' ranges is therefore critical in understanding the impacts climate change will have on conservation.

Tropical systems, despite being the highest-diversity areas on the planet, are disproportionately understudied (Collen et al. 2010, Feeley and Silman 2011). In particular, the potential effects of climate change on tropical systems are poorly understood (Feeley and Silman 2011). Moreover, in species-rich communities, complex networks of interspecies interactions may play a role in creating range limits. Specifically, antagonistic interspecies interactions may contribute to range contractions under various climate change scenarios (Urban et al. 2012, Gibson-Reinemer et al. 2015). However, these interactions are generally not considered in most climate change studies, generally due to a lack of understanding of the basic ecology of the system. This lack of knowledge of the severity of future threats is unfortunate given that the tropics, and particularly montane regions, are especially susceptible to climate change-related extinctions (Sekercioglu et al. 2008, Telwala et al. 2013).

I present an analysis of the likely effects of climate change on the avifauna of the Eastern Himalayas. The Eastern Himalayas are a global biodiversity hotspot (Myers et al. 2000, Mittermeier et al. 2011), and have the second-highest biodiversity density of any terrestrial region on the planet (Grenyer et al. 2006). Much of this diversity is created by the extreme altitudinal gradient, ranging from roughly sea level to over 8000 meters, and the resulting extreme diversity in habitat. Due to its remoteness, the area is very poorly studied, even compared to other tropical regions (Pawar et al. 2007). Despite its remoteness, however, the region is experiencing increased anthropogenic threats to habitat and wildlife (Chatterjee 2008, Datta et al. 2008, Dalvi et al. 2013). Additionally, it is known that ongoing climate change has already caused shifts in Himalayan plant communities (Telwala et al. 2013).

Birds are a useful model system when trying to understand the effects of climate change for a variety of reasons. Birds combine diversity, conspicuousness and ease of identification in a way that surpasses most other taxa, meaning that the same survey effort can generate more occurrence data. It is known that birds tend to closely track their Grinnellian niche over changes in climate (Tingley et al. 2009). In particular, Eastern Himalayan birds are thought to have a complex set of factors determining their range limits including interspecies competition, evolution of stratified thermal tolerances and dispersal

barriers (Price et al. 2014, Srinivasan et al. 2018). It is known that globally, birds are at risk of extinction due to climate change (Sekercioglu et al., 2008; for specific examples see e.g. Langham et al., 2015; Tingley and Beissinger, 2013). The spatial ecology of the avian community of the Eastern Himalayas may make them especially susceptible to climate change.

Species distribution models (SDMs) are a set of models that attempt to determine the range of a species by correlating species occurrence data to the environmental characteristics at those locations, and then projecting those relationships onto the landscape (Guisan and Thuiller 2005, Elith and Leathwick 2009, Miller 2010). SDMs use explanatory variables that aim to account for the biotic, abiotic and movement parameters that create a species' range (Soberon and Nakamura 2009). If projections for the explanatory variables into the future are available, the future range of a species can be estimated (Araújo and Guisan 2006, Elith et al. 2010, Anderson 2013). In practice, as biotic data is generally unavailable at a landscape scale and future projections are unavailable, most climate change projections rely on abiotic data alone (e.g. Nenzén and Araújo 2011, Franklin et al. 2013, Langham et al. 2015). SDMs thus provide an excellent framework within which to test the potential effects of climate change on species ranges.

METHODS

Surveys:

I focused my survey efforts in the Indian state of Arunachal Pradesh, which lies in the heart of the Eastern Himalayas, due to its relatively large size (83,743 square kilometers) making it representative of the region as a whole. Surveys consisted of point surveys conducted at 201 points across Arunachal Pradesh, India from May-July, 2013-2015 (Fig 1.1a.). In addition, coordinates for certain species (largely those of conservation concern) were obtained at an additional 65 points. These points ranged from 118-4354 meters in elevation, and included both protected and non-protected areas, as well as points along and away from the few paved roads. Efforts were made to spread surveys across varying habitat types. The time from May-July corresponds to the early-middle monsoon season, which is the peak breeding time for the majority of the region's avian species (Rasmussen and Anderton 2005). Additionally, species undergo minimal

altitudinal movements at this time, making survey data a more reliable indicator of breeding habitat suitability (Srinivasan et al. 2018).

At each point, two observers jointly compiled a list of all species either heard or seen at 10 minute intervals. Two observers were used in order to help reduce missed detections, as well as for safety in the field; one observer was present for all counts conducted. Points were visited over multiple days and multiple consecutive 10-minute interval lists were generated at each visit, creating a set of repeat surveys to assess detectability. A total of 375 bird species were recorded on these surveys; of these, 215 were detected at a minimum of 5 points, which I considered suitable for analysis (Appendix A). Additionally, 20 species are considered to be of conservation concern by the IUCN (IUCN 2017); 8 of these species were detected at a minimum of 5 points (Table 2.1). Additionally, two of these species are thought to be endemic to Arunachal Pradesh.

Modelling:

The chief sources of uncertainty in SDMs are the choice of explanatory variables, the occurrence data, the choice of statistical algorithm used to derive the relationships between those variables and the occurrence data, and the choice of a threshold used to discretize continuous habitat suitability maps into simple presence-absence maps (Liu et al. 2005, Diniz-Filho et al. 2009, Beale and Lennon 2012). Below, I describe my attempts to account for and/or minimize these sources of uncertainty.

I used the BIOCLIM dataset as my explanatory variables. The BIOCLIM variables, available through WorldClim, are a standard set of climate variables used for SDMs, both for current and future climates (e.g. Lamb et al. 2008, Gschweng et al. 2012, Langham et al. 2015). I used BIOCLIM version 1.4 for both current and future climate (Hijmans et al. 2005). I used the HadGEM3-ES circulation model, the successor of the widely used HadCM3 model, for future climate projections. Within this model, I considered four different future greenhouse gas concentration trajectories, ranging from optimistic (rcp2.6) to pessimistic (rcp8.5), as determined by the IPCC in their fifth report for the year 2070 (IPCC 2014). This helps account for uncertainty in climate change projections.

I converted my occurrence data to simple presence-absence data, with species being considered 'absent' at regular survey points where they were not detected. Incidental locations were considered 'not applicable' for species that were not specifically

noted to be present. I accounted for movement barriers by dividing the study area into 7 regions, demarcated by a set of rivers and high ridges/massifs (Fig. 1.1b) known to form species barriers (Rasmussen and Anderton 2005, Grimmer et al. 2012). I determined the extent of each species' range within the study area using maps from a recently published field guide (Grimmett et al. 2012); survey points from a region where a particular species is not thought to exist were considered 'not applicable', rather than absent, for that species in order to avoid miscategorizing potentially suitable habitat. For all species, models were fit across the entire study area; for a species absent from some set of subregions, those subregions were classified as absent post hoc, and considered absent for future climate scenarios as well.

Different modelling algorithms can create widely different modelled species ranges, even when using the same occurrence data and explanatory variables (Townsend Peterson et al. 2007, Elith and Graham 2009, Saupe et al. 2012). Ensemble forecasting, i.e. the process of combining the output from different modelling algorithms to create a consensus range map, has become a popular way of countering this source of uncertainty (Araújo and New 2007, Elith et al. 2010, Grenouillet et al. 2011). I used 4 different machine-learning methods – support vector machines (SVM), boosted regression trees (BRT), classification and regression trees (CART), and random forest (RF). Each of these were run 100 times per species with a 75-25 test-train split, and then averaged to create a single output for each algorithm. The outputs corresponding to present climate for each algorithm were normalized to have a maximum value of 1; the outputs for future climate scenarios were multiplied by the same constant corresponding to that algorithm. The area of the receiver operating characteristic curve (AUC) was calculated for each of these four maps, which represents a global accuracy for that model. The individual algorithm outputs were then averaged using those AUCs as a weight to generate a final ensemble output.

Threshold selection is a contentious issue, as it is known that different threshold criteria can result in differing qualitative patterns (Nenzén and Araújo 2011). I selected a threshold that maximizes the kappa statistic for the ensemble output (Liu et al. 2005, Freeman and Moisen 2008). The kappa statistic incorporates the false positive and false negative rate and attempts to optimize them, making it a superior measure to alternative thresholding criteria based on sensitivity or specificity alone (Liu et al. 2005, Miller 2010). These discretized maps will be referred to as presence-absence maps for the remainder

of the manuscript, to differentiate them from the continuous ensemble maps. The centroid of the range and the altitude corresponding to that centroid were determined for the ensemble maps, and the shift in centroid coordinates and elevation were calculated (Langham et al. 2015).

Finally, each species was categorized as being temperature-dependent or precipitation-dependent. This was done by classifying each BIOCLIM variable as being temperature-derived, precipitation-derived or both (Hijmans et al. 2005). The contribution of each variable in determining model output was ascertained as part of the model-fitting process in R (Naimi and Araujo 2016, R Core Team 2016). The contributions of temperature-derived and precipitation-derived variables were then summed to determine whether temperature or precipitation had a larger role in determining a species' distribution, each species being thus classified as temperature-dependent or precipitation-dependent.

Species interactions:

Competitive species interactions, especially among closely related species, are thought to be an important force in the structuring Eastern Himalayan avian community (Päckert et al. 2012, Price et al. 2014). I used a recent global phylogeny of extant bird species to identify pairs of congeneric species that are each other's closest relatives within the set of species present in the study area (Jetz et al. 2012, 2014); taxonomy was updated in accordance with the International Ornithological Congress's World Bird List version 7.3 (Gill and Donsker 2017). This generated 102 species pairs (out of 375 total species detected); of these, 34 pairs had at least 5 presences for both species and are thought to be sympatric in at least one study subregion (Appendix B).

In order to assess the strength of competitive species interactions for these species pairs, I created a simulation model to assess the number of survey points at which both species would be expected to co-occur, given their underlying habitat preferences (Fig. 1.3). I used a fine-scale digital elevation model (DEM) to extract the altitude for each survey point, and then created a generalized additive model (GAM) constrained to 3 knots, with a cubic spline smoothing function, to assess the binomial probability of detection of a species at a given altitude, using the success/failure data of each time interval spent at that site as independent trials. I then simulated survey data for both species in a given

pair, using the actual number of times each site was visited. If a species was simulated to occur at more points than it was actually found at, some of the presences were randomly converted to absences. Finally, the simulated number of co-occurrences was obtained, and compared to the actual number of co-occurrences. I ran 5000 simulations for each species pair. For each simulation, I calculated a competition coefficient c_i given by:

$$c_i = 1 - \sqrt{\frac{\text{Actual co-occurrences}}{\text{Expected co-occurrences}}}$$

The value of c for a given species pair was then calculated to be the mean of all 5000 c_i . The constant c was held constant across all cells in the landscape and then used to 'correct' the ensemble maps for both species:

$$S_1' = S_1 - (c * S_2)$$

where S_1' represents the corrected habitat suitability for species 1 in a given raster cell, and S_1 and S_2 represent the uncorrected habitat suitabilities for species 1 and 2 respectively. The ensemble output for species 2 was also corrected in the same way. I then evaluated the change in overall habitat suitability by summing the model output across all raster cells, and comparing this to the uncorrected value for each species.

Software:

All analyses were carried out in R (R Core Team 2016). SDMs were constructed using the package *sdm*, with following analyses conducted using the packages *raster*, *sdmTools* and *geosphere* (VanDerWal et al. 2014, Hijmans 2016a, 2016b, Naimi and Araujo 2016). The geoprocessing required to create SDMs was accomplished using packages *raster* and *rgdal* (Bivand et al. 2016), with some processing also done in QGIS 2.18 (QGIS Development Team 2017). GAM fits required for calculating competition coefficients were implemented using package *mgcv* (Wood 2011).

RESULTS

I found that species' range sizes, as determined by presence-absence maps, are expected to decrease relative to present (Fig. 2.1; Table 2.2a). This broad pattern holds

for the entire suite of 375 species, as well as the 215 species detected at a minimum of five points. For the climate scenarios (rcps 2.6, 4.5, 6.0 and 8.5), from the set of 215 species detected at a minimum of five points, 136, 144, 149 and 159 species are expected to undergo range contractions respectively; 69, 57, 84 and 108 species respectively are expected to undergo range contractions of greater than 50%. The remaining species are expected to undergo range expansions. When examining the smaller set of IUCN-listed species (Table 2.2b), the same general pattern holds, though the range contractions are expected to be more severe for species detected at a minimum of five points. Of the eight species of conservation concern detected at more than five points, five species are expected to undergo range contractions under all climate scenarios (*Paradoxornis flavirostris*, *Arborophila mandelli*, *Spelaeornis caudatus*, *Brachypteryx hyperythra* and *Harpactes wardi*). Only *H. wardi* is expected to experience range contractions of less than 50% under the two least severe climate scenarios, with the other four experiencing range contractions of more than 50% in all climate scenarios.

Additionally, I expect the centroid of species' ranges to shift by 7.8, 8.3, 9.5 and 11.2 kilometers on average for increasing magnitudes of climate change (Fig. 2.2). The direction of shift varies widely between species (Fig. 2.3), but the overall direction of shift is approximately due west for all climate scenarios. These results indicate that species will move in a consistent direction, but may have to move further as the magnitude of climate change increases.

The central elevation for each species is expected to increase on average, although there is significant variation (Fig. 2.4); many species are expected to decrease, rather than increase, their altitudinal range. I examined whether the direction of altitudinal shift for each species was explained by whether the species' distribution was controlled more by precipitation or temperature. I conducted a Pearson's chi square test on the number of species expected to move upslope or downslope after classifying them as either precipitation-controlled or temperature-controlled, as described above in Methods: Modelling. I found that disproportionately more species expected to move downslope are responsive to precipitation rather than temperature (Fig. 2.5); these results were significant for two of the four climate scenarios and near-significant for a third (df=1; rcp 2.6 – $X^2=3.99$ & $p=0.046$, rcp 4.5 - $X^2=6.70$ & $p=0.0097$, rcp 6.0 - $X^2=3.43$ & $p=0.064$, rcp 8.5 - $X^2=0.97$ & $p=0.32$).

I also examined the relationship between changes in relative range size and changes in central altitude. Species that are expected to move upslope are also more likely to undergo range contractions under all climate scenarios (Fig. 2.6). Likewise, species that are expected to end up at high altitudes are also more likely to undergo range contractions. However, the relationship between current elevation and future changes in range size is less clear, with a significant relationship found only in the rcp 4.5 emissions scenario.

When accounting for interspecies competition, I found small decreases in the amount of modelled suitable habitat for most species both under present and future climate conditions (Fig. 2.7). The median decrease in projected available habitat was ~8%. However, there are several species expected be more affected by interspecies competition, with six species expected to be excluded from over 50% of their climatically suitable range under at least one climate scenario – *Aethopyga gouldiae*, *Anthus roseatus*, *Arborophila torqueola*, *Brachypteryx hyperythra*, *Copsychus malabaricus* and *Horornis brunescens*. Of particular note is *B. hyperythra*, a range-restricted species considered Near Threatened by the IUCN and expected to decline by ~70% due to climate change according to my models. The amount of suitable habitat is expected to further decrease by 44%-55% when accounting for competition with its widespread sister species *B. leucophris*. This finding may warrant a re-examination of its conservation status. Another species, *H. brunescens*, is a Himalayan endemic found at higher elevations, and though currently listed as least concern its population is decreasing (IUCN 2017).

I also determined whether the specific climate scenario had a significant effect on the results discussed above (change in range size, distance and direction of shift in range centroid, change in central elevation, and change in range size when accounting for species competition). I used univariate repeated-measures Analyses of Variance (ANOVAs). For variables where climate scenario was found to have a significant effect, I performed a post-hoc Tukey test with a Bonferroni correction applied for multiple comparisons.

I found that climate change scenarios did not have a significant effect on the expected change in range size (univariate repeated measures ANOVA, $p=0.301$). However, when I separately analyzed species expected to experience range contractions and species expected to experience range expansions, I found significant effects. When

analyzing the species expected to undergo range contractions ($p < 0.0001$), the largest contractions were found under rcp 8.5, followed by rcp 6.0, rcp 2.6 and rcp 4.5. The degree of climate change also affects the expected range expansion ($p = 0.003$), with an rcp 8.5 scenario causing larger expansions than rcp 2.6/4.5; rcp 6.0 was not distinguishable from other scenarios.

The effect of climate change scenario on the projected distance of range shift is significant ($p < 0.0001$). The largest shifts are projected to occur with rcp 8.5, followed by rcp 6.0 and then rcp 2.6/4.5, which were not distinguishable from each other. However, there was no effect on the direction of the range shift ($p = 0.241$).

Climate change scenarios have a significant effect on the degree of elevational movement ($p < 0.0001$ for species moving upslope and for species moving downslope). For species expected to move upslope, the largest shifts are projected under rcp 4.5/8.5, followed by rcp 6.0 and then rcp 2.6. For species expected to move downslope, the largest shifts are expected for rcp 4.5, followed by rcp 2.6 and then rcp 6.0; rcp 8.5 was not distinguishable from either rcp 2.6 or rcp 6.0.

Finally, I found a significant effect of climate change scenario on the effects of competition on range size ($p = 0.023$). Competition is expected to exert a larger effect under rcp 8.5 compared to rcp 2.6/4.5, with rcp 6.0 indistinguishable from the other three scenarios.

DISCUSSION

My results show that a significant proportion of Eastern Himalayan avian diversity may be imperiled by climate change; by extension, this has significant implications for Eastern Himalayan biodiversity as a whole. In particular, it should be noted that my results are conservative, as they assume that birds are not dispersal-limited and can access all climatically suitable habitat. Additionally, my results do not include a time lag for vegetation changes, and assume that all climatically suitable habitat will also be biotically suitable. It is therefore likely that the true extent of range contractions in response to climate change will be greater than that described here. In addition to changes in range sizes, ranges will also shift in response to climate change, highlighting the importance of habitat connectivity.

While the average decrease in range size is noteworthy, it should be highlighted that there is significant variation in the way species are expected to respond to climate change. In particular, there is a complex relationship between a species' ecological requirements and the projected changes in its elevational range and overall range size. It may seem counterintuitive that a large percentage of species is expected to move downslope in the face of changing climates. However, this pattern has in fact been documented in the Sierra Nevada mountains of the Western United States, thanks to the availability of high-quality historical data allowing for the quantification of the effects of climate change that have already taken place (Tingley et al. 2009, 2012). Those studies also showed that complex altitudinal movements in response to climate change can be explained by birds tracking either temperature or precipitation, in order to maintain their Grinnellian niche. This is in accord with the results presented here. There appear to be concordant mechanisms behind the altitudinal responses of birds to climate change across widely different geographical regions and biomes. When considering species-specific conservation strategies, these results highlight the importance of the target species' natural history in predicting its response to climate change.

My results suggest that accounting for competition does not affect the range projections for most species, with some notable exceptions. However, there are difficulties associated with fully appreciating the extent of competition through the simulation modelling approach used. My approach was based on the ratio of actual co-occurrences to predicted co-occurrences, which was used as a competition coefficient. That said, many species have segregated altitudinal ranges with little overlap, meaning that both the predicted and actual co-occurrences are zero. This means that the strength of pairwise competitive interactions cannot be easily calculated. However, it is thought that this altitudinal segregation is itself a result of competition operating on evolutionary timescales (Price et al. 2014). Interspecies interactions may therefore have a larger effect than presented here, and one that is difficult to predict. Nevertheless, certain species pairs do overlap extensively in their spatial ranges, and therefore have their range projections significantly altered by accounting for competition (see also Results from Chapter 1). The species expected to be most affected by competition include at least one species thought to be of conservation concern, *Brachypteryx hyperythra*. Moreover, I found that the effects of competition are greatest for the most severe projections of climate change. Further

research is required to refine our understanding of the ecological effects on range limits, as the mechanistic differences between species pairs with large altitudinal overlaps but few fine-scale co-occurrences, and pairs with little altitudinal overlap, are yet unknown.

In addition to interspecies variation, there is significant variation in the expected response to climate change within a species, depending on the climate change scenario used. The distance of range shifts, extent of changes in range size, and changes in elevation ranges are all affected by the extent of predicted warming. The relationship between climate scenario and species' responses is complicated. For example, the intermediate rcp 4.5 scenario is expected to cause larger changes in elevation than either the most optimistic (rcp 2.6) or pessimistic (rcp 8.5) scenarios. Similarly, range contractions are actually expected to be larger under rcp 2.6 than they are under rcp 4.5. The spatial realizations of the niche spaces of organisms, as analyzed through an SDM framework, do not easily lend themselves to mechanistic explanations where more warming leads to greater change. However, my models agree that the rcp 8.5 scenario will result in the largest changes in range size, as well as the longest range shifts. These results may be viewed as a challenge, in that we do not precisely know how greenhouse gas concentrations will change over the next 50 years or where they will end up by the year 2070 and beyond. As a result, this makes precise assessments of the threats faced by individual species difficult. On the other hand, these results may also be viewed as an opportunity, as climate change mitigation efforts will provide tangible benefits to species and ameliorate some of the threats they face.

My results also have implications for protected area design. Protected areas are a cornerstone of conservation efforts in the Eastern Himalayas, and particularly in India, as they provide a legal framework to combat the rampant poaching and overexploitation of forest resources (Chatterjee 2008, Harrison et al. 2016). However, protected areas in the region were generally created for the preservation of charismatic megafauna, and the degree to which those protected areas serve to protect overall biodiversity is poorly understood (Pawar et al. 2007). Moreover, this system of reserves was not designed with any consideration to climate change resiliency. As such, these results need to be taken into consideration when prioritizing areas for future protection in a systematic conservation planning framework (Margules and Pressey 2000).

More generally, this study highlights the potential impacts of climate change on tropical ecosystems, which has been poorly quantified. The majority of the Earth's biodiversity is located in the tropics, and most conservation efforts have failed to explicitly include the effects of climate change (Pimm 2008). As landscapes become increasingly fragmented and protected lands become islands in a sea of inhospitable regions, dispersal becomes more and more difficult. As a result, changes to climate that render current protected areas climatically inhospitable can severely threaten global biodiversity. These results therefore highlight the necessity of explicitly using climate change projections in conservation efforts, as well as incorporating information on natural history and ecology in creating those predictions. In order to allow for ranges to shift over time, it is also critical to allow for dispersal between protected areas through habitat corridors. In this way, the future of tropical biodiversity may be secured despite the upcoming challenges of the next century.

FIGURES AND TABLES

Common name	Scientific name	IUCN status	Number of points
Bugun Liocichla*	<i>Liocichla bugunorum</i>	CR	2
Swamp Prinia	<i>Laticilla cinerascens</i>	EN	3
Beautiful Nuthatch	<i>Sitta formosa</i>	VU	4
Marsh Babbler	<i>Pellorneum palustre</i>	VU	4
Rufous-necked Hornbill	<i>Aceros nipalensis</i>	VU	6
Blyth's Tragopan	<i>Tragopan blythii</i>	VU	6
Rusty-throated Wren-Babbler*	<i>Spelaeornis badeigularis</i>	VU	8
Chestnut-breasted Partridge	<i>Arborophila mandellii</i>	VU	9
Jerdon's Babbler	<i>Chrysomma altirostre</i>	VU	9
Black-breasted Parrotbill	<i>Paradoxornis flavirostris</i>	VU	10
Blyth's Kingfisher	<i>Alcedo hercules</i>	NT	1
Great Hornbill	<i>Buceros bicornis</i>	NT	1
River Lapwing	<i>Vanellus duvaucelii</i>	NT	1
Sikkim Wedge-billed Babbler	<i>Sphenocichla humei</i>	NT	1
Spot-billed Pelican	<i>Pelecanus philippensis</i>	NT	1
Grey-headed Parakeet	<i>Psittacula finschii</i>	NT	4
Rusty-bellied Shortwing	<i>Brachypteryx hypertyra</i>	NT	8
Cachar Wedge-billed Babbler	<i>Sphenocichla roberti</i>	NT	12
Ward's Trogon	<i>Harpactes wardi</i>	NT	14
Rufous-throated Wren-Babbler	<i>Spelaeornis caudatus</i>	NT	17

Table 2.1. List of species of conservation concern detected during the course of this study, their IUCN status and the number of points they were detected at.

Under IUCN classification, CR denotes Critically Endangered, EN Endangered, VU Vulnerable, and NT Near Threatened. * denote species that thought to be endemic to the study area.

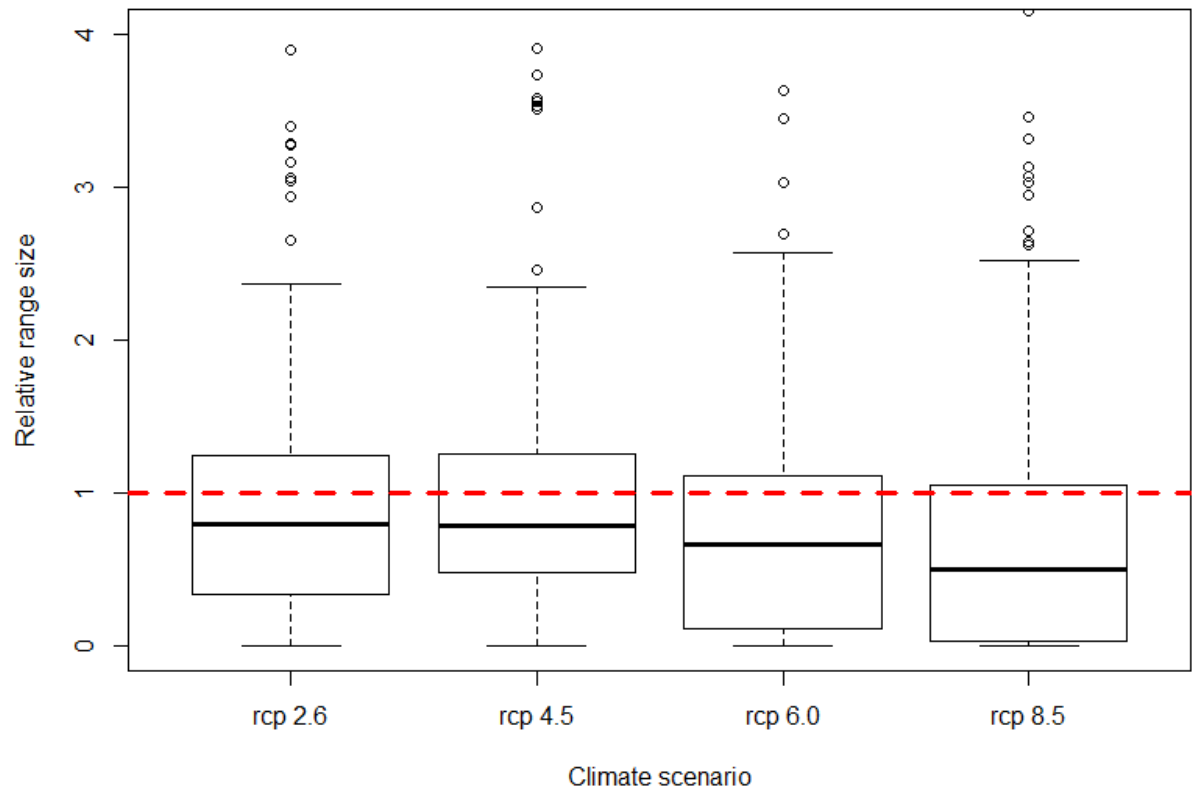


Fig. 2.1. Relative range sizes for thresholded SDMs

Predicted range sizes decrease due to climate change, with a larger effect as the magnitude of climate change increases. Boxes represent the 25% and 75% quartiles, and the bold line represents the median. Whiskers are 1.5 times the interquartile distance. A value of 1 (red dashed line) indicates no change in range size relative to the present. Values greater than 4 have been omitted from the plot for visual clarity, but are contained in the calculations of quartiles and medians.

(a)

Climate scenario	Relative range size, species detected at 5 or more points (n=215)	Relative range size, all species (n=375)
rcp 2.6	0.792	0.780
rcp 4.5	0.788	0.807
rcp 6.0	0.663	0.609
rcp 8.5	0.498	0.424

(b)

Climate scenario	Relative range size, species detected at 5 or more points (n=8)	Relative range size, all species (n=20)
rcp 2.6	0.524	1.426
rcp 4.5	0.680	1.639
rcp 6.0	0.364	0.750
rcp 8.5	0.238	0.766

Table 2.2. Median changes in relative range size for (a) the entire species pool and (b) species of conservation concern.

Models based on species detected at more than 5 points are considered to be more reliable.

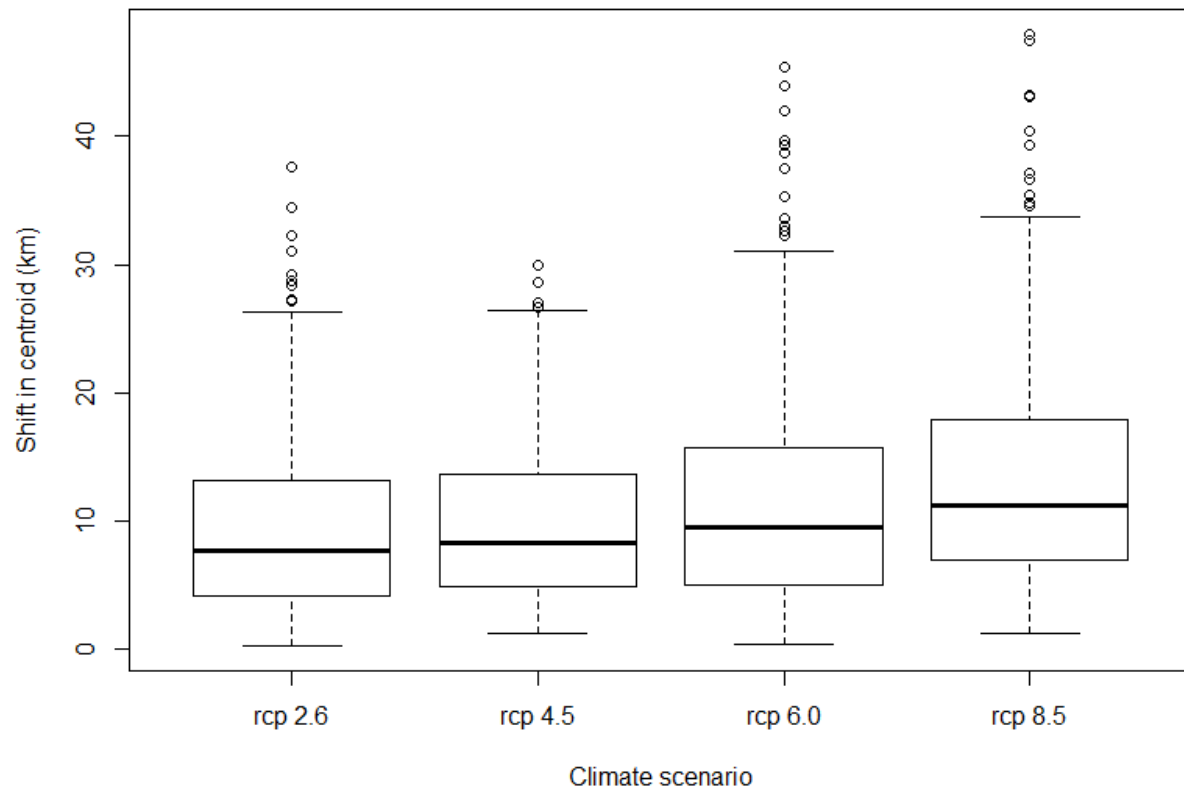


Fig. 2.2. Distance of shift in range centroid (in kilometers) for different climate change scenarios.

Boxes represent the 25% and 75% quartiles, bold lines represent the medians and whiskers extend 1.5 times the interquartile distance.

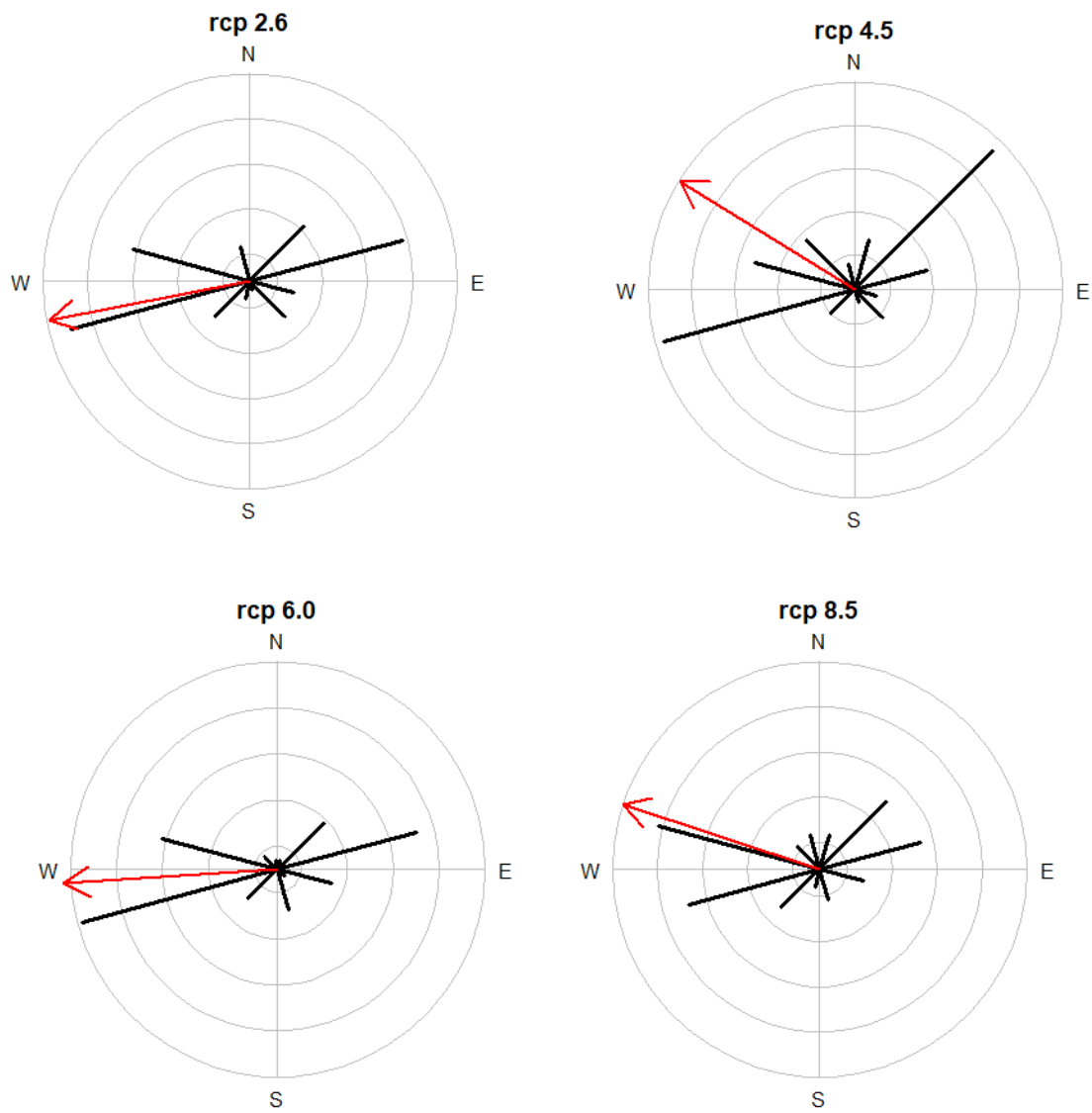


Fig. 2.3. Barplot representing the direction of shift in range centroid for different climate change scenarios.

The length of the bars represent the number of species moving in a particular direction; the red arrows indicate the direction of the vector sum of the shift in range centroid for all species. The overall direction of shift is relatively stable between different climate scenarios.

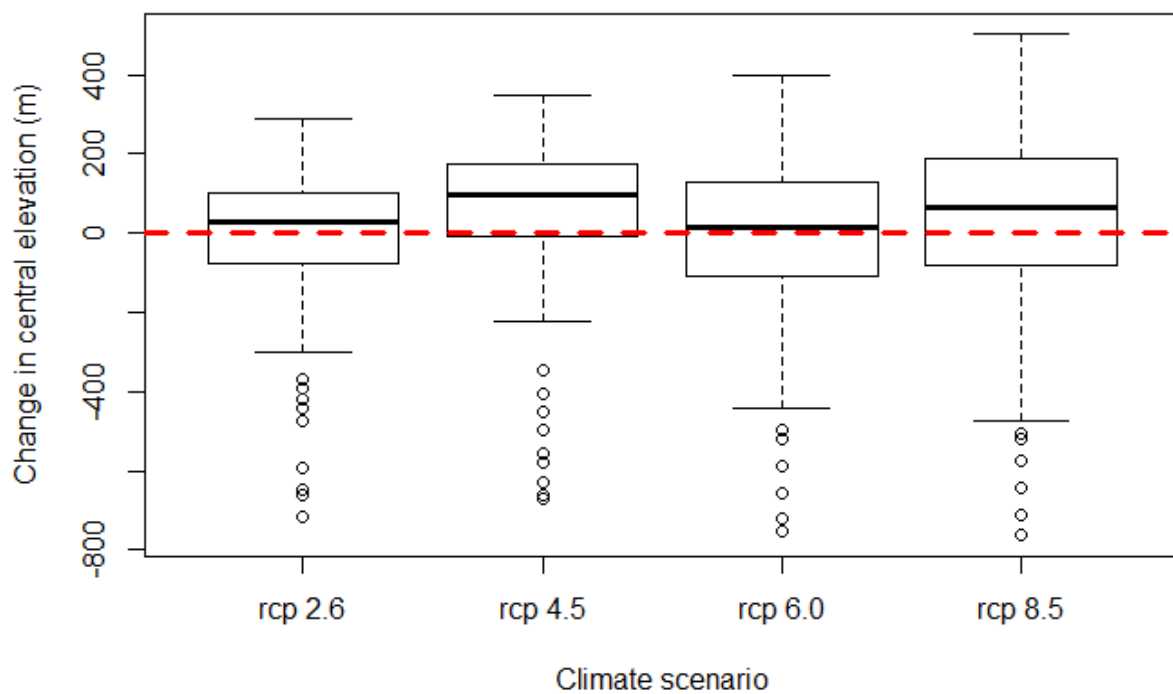


Fig. 2.4. Box and whisker plots representing the change in central elevation of species ranges (in meters) relative to the present.

The red dashed line represents no change in elevation.

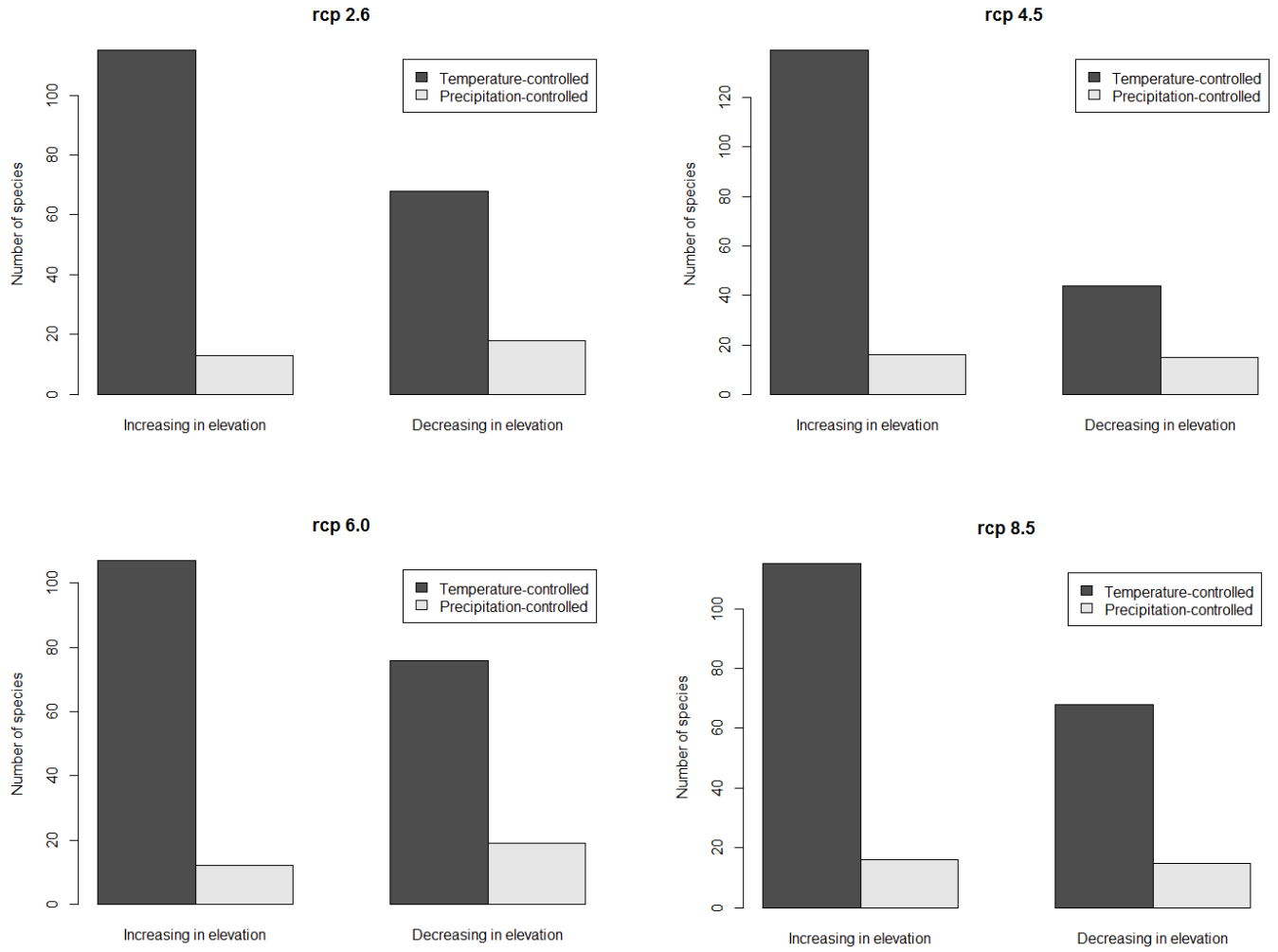


Fig. 2.5. Barplot depicting the number of temperature-controlled and precipitation-controlled species expected to increase and decrease in elevation under each climate scenario.

Far more species are temperature-controlled than are precipitation-controlled. Pearson chi squared tests ($df = 1$) are significant for rcp 2.6 and rcp 4.5, and are near-significant for rcp 6.0

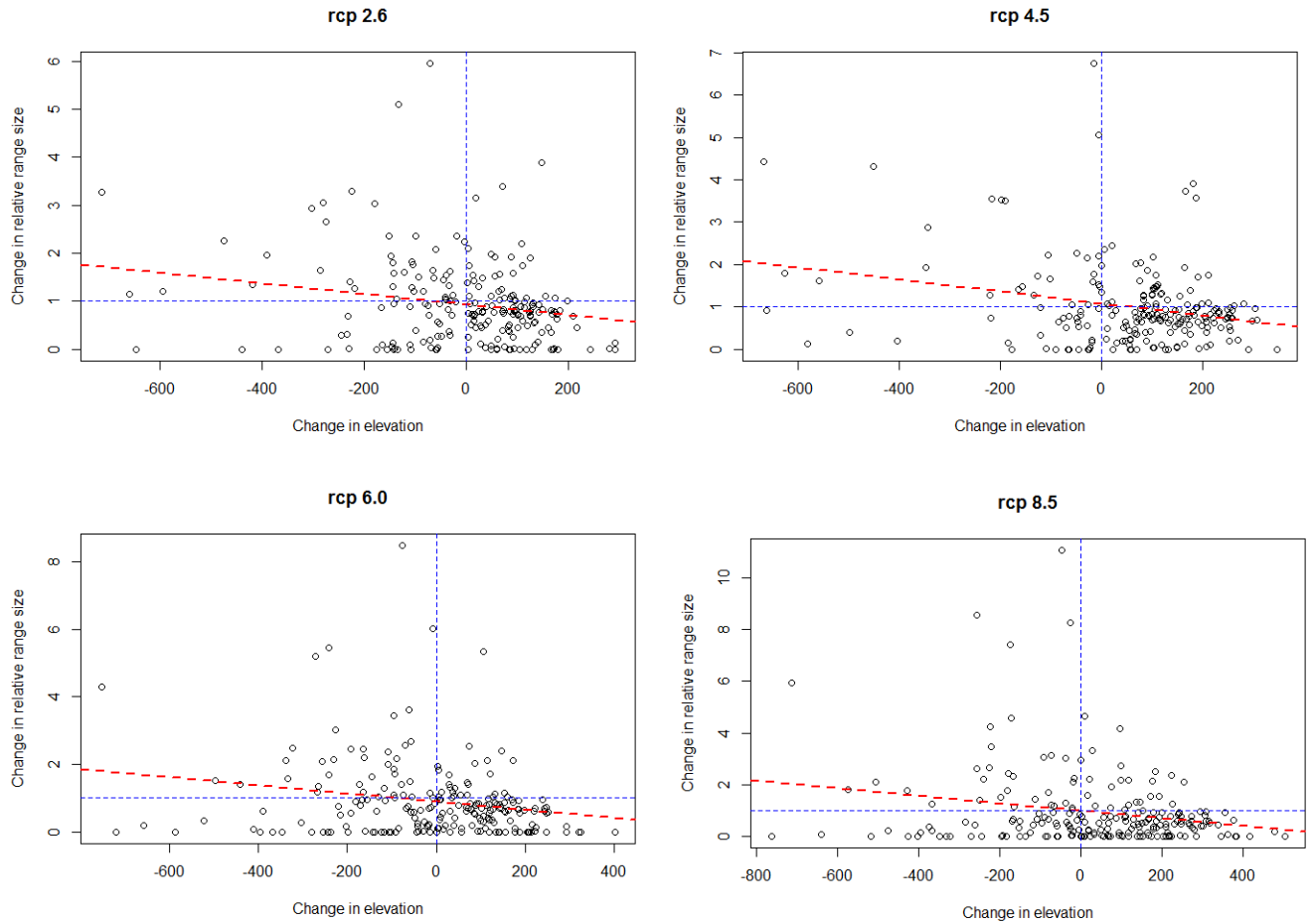


Fig. 2.6. Species predicted to increase in their central elevation are predicted to undergo range size contractions under all climate scenarios.

Red dashed lines represent the best-fit linear regression; dashed blue lines represent no change in central elevation and no change in range size. $p < 0.005$ for each climate scenario.

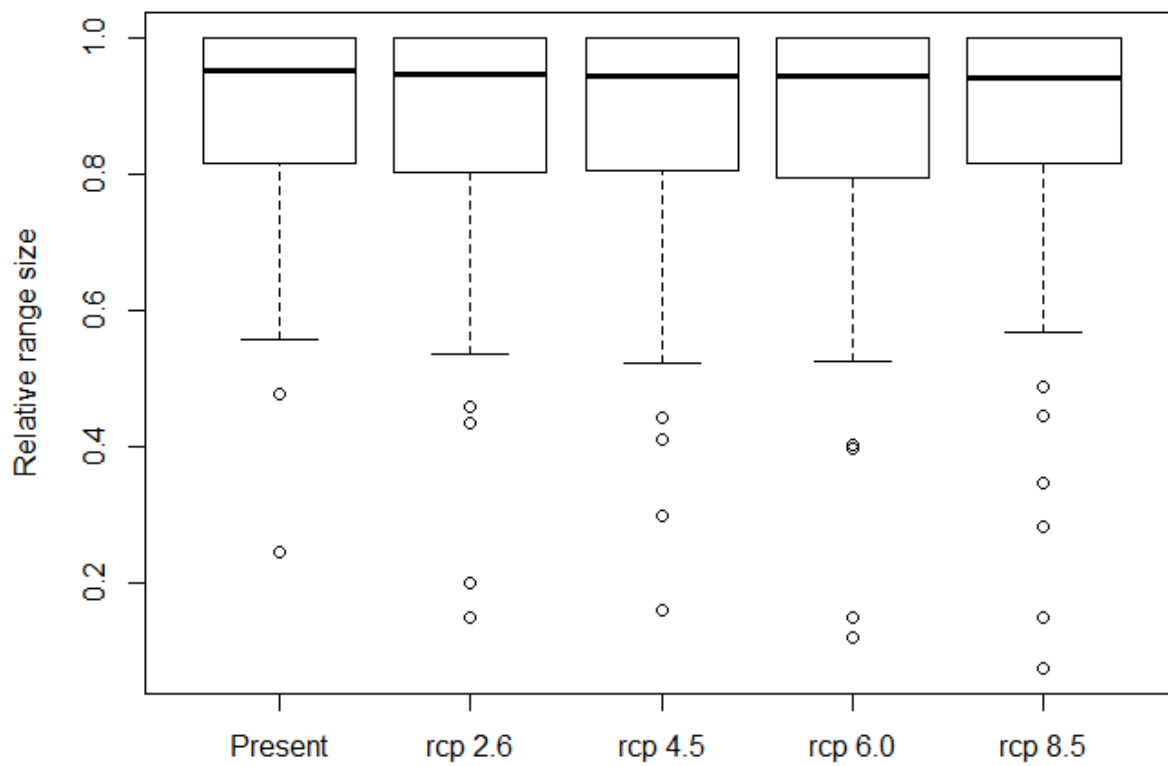


Fig. 2.7. Box and whisker plot representing change in modelled habitat availability after correcting for interspecies competition under all climate scenarios.

The median difference is ~5%; however, several species show much larger decreases in habitat availability.

Chapter 3 - Systematic conservation planning for Eastern Himalayan birds

ABSTRACT

Biodiversity loss is an ongoing global crisis, with many studies concluding that the world is in the throes of a sixth mass extinction largely caused by anthropogenic activity. Habitat destruction and climate change are major drivers of biodiversity loss, particularly in tropical/subtropical montane regions where terrestrial biodiversity is highest. Most conservation management strategies are based in extensive knowledge of the ecology and natural history of the system those strategies are designed to protect. However, tropical regions are systematically underrepresented in the ecological literature, and therefore effective management strategies are difficult to formulate for most taxa and ecotypes. Systematic conservation planning (SCP) provides a spatially explicit framework for conservation decision-making given a paucity of ecological information. I utilize the SCP framework on the breeding bird community of the Eastern Himalayas, a global biodiversity hotspot. I conducted surveys in Arunachal Pradesh, Northeast India, for three summers to collect occurrence data for the breeding bird community. 375 species were detected during these surveys, 20 of which are thought to be of conservation concern by the IUCN; 215 species were detected at a minimum of five points. The survey data was used to create species distribution models (SDMs) based on both current climate and future projections of climate change for the year 2070. Species were given weights based on IUCN status, with additional considerations for endemism. Spatial prioritizations were implemented using Zonation, a widely used software in SCP efforts. I used two different algorithms; the additive benefit function (ABF) values alpha diversity while core area zonation (CAZ) prioritizes individual rare species. I examined three target coverages – 12.2% (the proportion of protected areas in Arunachal Pradesh), 20% and 35%. I found that the current network of protected areas differs significantly from the ideal network based on Zonation output. However, there is significant overlap (~71%) between prioritizations made with no constraints and prioritizations created with current protected areas as a mandatory inclusion, suggesting that current protected areas may provide complementarity to areas identified as high priority by Zonation. CAZ and ABF model outputs are relatively congruent, with ~68% overlap. The poor performance of current

protected areas may partially be explained by underrepresentation of elevations from ~0-3000 metres, where both alpha and beta diversity are highest. My results provide a spatially explicit path forward for conservation in the region. In particular, they highlight the need for conservation action in northwestern and eastern Arunachal Pradesh. I call for these analyses to be utilized in order to create tangible impacts on the ground. However, I caution against overinterpretation of these results, as current protected areas may have value that is not apparent from a study of birds alone.

INTRODUCTION

The world is rapidly losing biodiversity, with serious consequences for global ecosystems (Hooper et al., 2012). It is increasingly clear that we are in the midst of a 6th mass extinction, and that rapid action is required to ameliorate its effects (see e.g. Ceballos et al., 2017; Dirzo et al., 2014). The root cause of biodiversity loss is anthropogenic (Kerr and Currie 1995, Brook et al. 2008). The precise drivers of biodiversity vary, but at a global scale disturbances related to habitat loss are the most important (Brooks et al. 2002). Anthropogenic climate change is expected to have major impacts to ecosystems throughout the world over the coming century (e.g. Parmesan and Yohe, 2003; Parmesan, 2006). The perturbations caused by climate change are expected to exacerbate preexisting anthropogenic threats to biodiversity, accelerating the global rate of extinction (Thomas et al. 2004, Bellard et al. 2012).

Conservation biology has been defined as a crisis discipline since its inception (Soulé 1985). Over the last few decades, several advances in the field have given conservation biologists a flexible and diverse toolkit to achieve conservation goals (Kareiva and Marvier 2012). These tools may be broadly separated into species-level and ecosystem-level strategies. However, in either case, extensive natural history information is required in order to develop specific management strategies.

Tropical and subtropical mountain regions are the highest-diversity terrestrial areas on our planet (Connell 1978). As such, there is far more biodiversity to lose from these areas, and the stakes are correspondingly higher. However, tropical biodiversity conservation involves several specific challenges. To begin with, these areas are

underrepresented in biological research, and there is a corresponding lack of basic ecological information (Collen et al. 2010); gathering this information would be extremely time-consuming, require significant resources, and would in many cases pose major logistical challenges. This has created difficulties in accurately assessing the status of individual species and ecosystems, which in turn creates issues for formulating strategies and prioritizing action (Collen et al. 2010, Feeley and Silman 2011). Tropical/subtropical areas are also home to a large percentage of the world's human population, and are subjected to ever-increasing anthropogenic pressures. Finally, climate change is expected to be a major threat to such regions (Malcolm et al. 2006, Gibson-Reinemer et al. 2015).

Systematic conservation planning (SCP) is a framework that may be utilized as a decision-making tool for conservation action (Margules and Pressey 2000). The SCP framework can be adapted as a purely spatial process, thereby mitigating the lack of ecological information available and allowing for approximate solutions to conservation problems to be found in the short term. This framework has been widely utilized across geographic regions and taxonomic zones (see e.g. Levin et al., 2013; Pawar et al., 2007; Wu et al., 2014; Zeydanlı et al., 2012 for examples of utilizing this framework). Briefly, the SCP process involves understanding the spatial distributions of the taxa involved, prioritizing them or otherwise setting conservation goals, and then using this to identify areas that should be prioritized for future conservation action. This is a relatively tractable and flexible process that can accommodate a wide variety of taxa.

I address each step of the SCP process as follows (details below in Methods). Spatial distributions were obtained using species distribution models (SDMs), a class of correlative models relating occurrence data generated by surveys to the biotic and abiotic characteristics of their environment (see e.g. Elith and Leathwick, 2009; Guisan and Zimmermann, 2000; Soberon and Nakamura, 2009 for a comprehensive review of these models). I based species prioritizations off the IUCN Red List (IUCN, 2017), with additional considerations for endemism (Rasmussen and Anderton 2005, Grimmer et al. 2012). Finally, I conducted spatial prioritizations using Zonation, a software program designed for use in creating spatially optimized conservation area networks (Moilanen 2007).

The Eastern Himalayas are a global biodiversity hotspot (Myers et al. 2000b, Mittermeier et al. 2011). They have the second-highest concentration of terrestrial biodiversity on the planet (Grenyer et al. 2006). They are also remarkably understudied,

even relative to other tropical areas; several conspicuous new vertebrate taxa have recently been described from the region (Pawar et al., 2007; for examples of newly described vertebrate taxa see e.g. Alström et al., 2016; Kamei et al., 2012; Li et al., 2015). The Eastern Himalayas are also thought to be particularly threatened by habitat loss (Brooks et al. 2002), and are expected to be among the high-diversity areas most affected by climate change (Malcolm et al. 2006). They are also subjected to other anthropogenic pressures, most notably hunting (Velho et al. 2012, Dalvi et al. 2013, Harrison et al. 2016). Formally protected areas therefore play a crucial role in conservation in this region, as both habitat loss and poaching can be more easily prevented in such areas through the legal system. However, most protected areas in the Eastern Himalayas, especially in India, were primarily created for the protection of charismatic megafauna. It is not known whether these protected areas serve to protect overall biodiversity.

I chose the Eastern Himalayan bird community as a system for my SCP analysis. I selected birds for a variety of reasons. First, bird diversity in the region is high; in particular, the density of passerine bird diversity is the highest on the planet (Price et al. 2014). Second, birds can be identified in the field and their taxonomy is well understood (Rasmussen and Anderton 2005, Grimmett et al. 2012, Jetz et al. 2012). Third, birds are found across all habitat types, thereby potentially providing a useful 'umbrella' for overall biodiversity conservation (Roberge and Angelstam 2004, Breckheimer et al. 2014). Birdwatching is also an increasingly popular activity and a source for ecotourism money, which can assist in conservation action (Glowinski 2007, Mohan and Athreya 2011). Lastly, birds, particularly in montane areas, are projected to be imperiled by climate change (Pimm 2008, Sekercioglu et al. 2008, Chamberlain et al. 2013). For these reasons, this community is particularly well suited to an SCP analysis, and an SCP analysis would be particularly useful for this community.

METHODS

Surveys:

I selected the state of Arunachal Pradesh (AP), India as my study region. AP contains the majority of the Eastern Himalayan region. The altitude varies from ~100-6800

meters; as Eastern Himalayan biodiversity largely stems from the steep altitudinal gradient, this indicates that AP's biota is representative of the region as a whole. AP is 83,743 square kilometers in area, making it possible to collect sufficient survey data for a comprehensive analysis. However, it is also large enough that conservation action here will have a significant impact on conservation in the Eastern Himalayas.

Surveys were conducted across AP from May-June 2013-2015. This period coincides with the monsoon, when breeding activity is at its peak and altitudinal movements are minimal (Rasmussen and Anderton 2005, Srinivasan et al. 2018). 201 points were selected, ranging from 118-4354 metres in elevation (Fig. 1.1a). Survey points within and outside protected areas were included; surveys were conducted both along and away from roads. At each point, two observers jointly compiled a list of all species seen and/or heard. Multiple observers were used to increase overall survey efficiency; points were visited multiple times to assess species detectability. Every survey involved one constant observer. Efforts were made to select points with different vegetation types within an altitudinal band.

In addition to the regular surveys, opportunistic data was also collected, mostly for species listed 'Near Threatened' or above by the IUCN (IUCN 2017) (Fig. 1.1a). Those locations were not used in the SDMs for species not specifically noted at those points. This opportunistic collection helped increase the available sample size for rare species of conservation concern, precisely the species that are important for an SCP analysis but which often must be omitted for lack of data (Pawar et al. 2007).

Overall, I recorded 375 species during my surveys. Of these, 215 were detected at a minimum of five points and were used as the basis for the following analyses (Appendix A). I also recorded 20 species thought to be of conservation concern; of these, 8 were recorded at five or more points (Table 2.1).

Species distribution models:

Species distribution models are a widely-used class of correlative models that create spatially explicit maps of predicted species distributions (Elith and Leathwick 2009, Miller 2010). The chief sources of uncertainty in an algorithm may be classified as relating to one of the following four factors: predictor data, response data, modelling algorithm and threshold selection (Diniz-Filho et al. 2009, Beale and Lennon 2012). Explicitly minimizing

and accounting for uncertainty is a major part of the distribution modelling process, and requires informed decision-making (Guisan and Zimmermann 2000, Miller 2010). Below, I summarize the decisions made to account for uncertainty arising from each potential source.

I used the BIOCLIM (v. 1.4) variables from the WorldClim dataset for my predictor variables (Hijmans et al. 2005). These variables are widely used in SDM applications for present and future climates (for widely disparate examples see e.g. Gschwend et al., 2012; Lamb et al., 2008; Langham et al., 2015). To account for uncertainty in future climate projections, I used 4 different potential trajectories for global climate as defined by the 5th IPCC report (IPCC 2014); I used the HadGEM3-ES circulation model for each trajectory. These range from rcp2.6 at the most optimistic, to rcp8.5 at the least optimistic.

Absence data is a fraught issue in the SDM process. Several studies use pseudoabsences, or randomly-generated absences, in order to avoid false negatives from survey data. However, pseudoabsence choice itself is a major source of uncertainty, with different choices leading to different model outcomes (VanDerWal et al. 2009, Lobo et al. 2010). I therefore chose to interpret my surveys as indicating true absences, except for opportunistically collected data, which I justify in part due to repeat surveys helping to account for imperfect detection.

The relationship between occurrence data and a given predictor variable can be calculated in a wide variety of ways, all of which can result in very different spatial predictions (Elith and Graham 2009, Saupe et al. 2012). Recent studies have indicated that ensemble forecasting, i.e. combining the output from multiple algorithms into one overall output, improves model accuracy (Araújo and New 2007, Grenouillet et al. 2011). I used four different algorithms – support vector machines, classification and regression trees, boosted regression trees, and random forest – which are known to be robust, and are also suitable for projecting future distributions under changed climates (Elith et al. 2010). Each model was run 100 times with a 75-25 test-train split, and the outputs were normalized and averaged using the area under the ROC curve (AUC), a global accuracy metric, as a weight (Liu et al. 2011).

Threshold selection is another hotly-disputed topic in the SDM literature. Briefly, there are multiple criteria for threshold selection, which can give rise to very different model outputs and predictions (Liu et al. 2005, Freeman and Moisen 2008, Nenzén and Araújo

2011). I avoided this by using only the continuous threshold outputs without discretizing them. In part, thresholded results may predict the extirpation of certain species (as indeed is the case with my models); however, those predictions of extirpation may not come to pass due to plasticity, adaptation or other factors. Using continuous output allows for those species to be included in my spatial prioritization analyses.

Spatial prioritization:

I utilized Zonation to conduct spatial prioritizations. Zonation is a software program that was developed as a tool to aid in conservation decision-making (Moilanen 2007). It is extremely flexible, with a variety of options available to customize solutions based on the precise goals of a given analysis (Moilanen 2007, Lehtomäki and Moilanen 2013). Zonation has been widely utilized for SCP across many taxa and in many geographical areas (for recent examples see e.g. Brum et al., 2017; Liang et al., 2018; Pollock et al., 2017). The full details of Zonation have been well explained in the prior references; here, I focus on an explanation of those features most pertinent to my analyses.

Zonation uses a set of biodiversity raster features, in my case SDMs, as its primary input. For each raster, cell values are recalculated to represent the fraction of the overall habitat within that cell, i.e. each cell's value is divided by the sum of the entire raster. If some features are more important than others, weights can be applied; I applied a set of weights to my species (see next section for details). Cells are then removed iteratively from the landscape based on a variety of algorithms; after each iteration, the values of the remaining cells are recalculated. I used two different removal algorithms, Core Area Zonation (CAZ) and the Additive Benefit Function (ABF). In CAZ, the *maximum* value across all biodiversity features at a given cell is used as the value of the landscape; in ABF, the *sum* of all biodiversity features is used. As such, the CAZ algorithm may favor cells with a few rare species over many common species; the ABF algorithm will do the opposite, although the weights applied will affect this. These may be thought of as two philosophical alternatives to conservation planning, minimizing extinction or maximizing overall diversity respectively.

Another useful feature of Zonation is its ability to account for reserve connectivity and compactness. This can be implemented in a variety of ways, some feature-specific and some based on the entire landscape. I used a landscape method in my analysis,

specifically a boundary length penalty that attempts to minimize the perimeter to area ratio. As my SDM outputs were continuous, and the landscape is topographically complex, I deemed feature-specific smoothing algorithms unsuitable for my purposes.

Finally, Zonation allows for specified areas to be included in prioritization analyses – those areas are automatically given the highest priority on the landscape. I created a digitized map of current PAs as an optional inclusion (WII 2015) (Fig. 3.1, Table 3.1). This allowed us to understand the additions that would best complement current PAs, as well as understanding how an optimized reserve network might differ from the existing one if it was freed of those constraints.

The primary Zonation output is a raster where each cell is ranked by removal order. The current PAs in AP covers ~12.2% of the landscape. The ideal coverage of protected areas is an actively debated topic, with recent proposals calling for up to 50% of global land area to be set aside for conservation purposes – the so-called Half Earth initiative. While this seems impractical, it should be noted that AP's population density is quite low, especially compared to the rest of India, and expansion of the PA system is therefore achievable. I selected two coverage goals, a pessimistic 20% and an optimistic 35%.

Conservation prioritizations:

I assigned weights to each species based on estimates of conservation status and global range size. Zonation treats weights as increasing the value of each cell in a given biodiversity feature multiplicatively. Weights scale linearly, so a weight of 3 gives half the importance of a weight of 6 on a cell by cell basis. For my weighting, I initially assigned each species a base weight of one. After this, I used the IUCN Red List to set initial prioritizations. The IUCN classifies species as Least Concern, Near Threatened, Vulnerable, Endangered or Critically Endangered. Species received one point per level above Least Concern. I also assessed whether species were endemic to India (+1), to the Himalayas (+0.5), to the Eastern Himalayas (+1), or to Arunachal Pradesh (+2); species falling into multiple categories were given the highest value. Species ranges were estimated through a combination of field guides and maps from the IUCN and BirdLife International (BirdLife International, 2018; IUCN, 2017).

RESULTS

The Zonation output indicates that current protected areas are not optimally located to conserve avian diversity (Fig. 3.3; Table 3.2). When examining models based on current distributions, only 13.4% (ABF) and 15.0% (CAZ) of the most valuable 12.2% of cells, i.e. the area covered by the current PAs, overlaps with those PAs. If the PA network had been selected at random, I would expect a 12.2% overlap, indicating that current coverage is barely an improvement. These numbers are somewhat improved when considering prioritizations based on future climates. When considering the top 12.2% of cells from a combined prioritization based on present and possible future distributions, the overlap with the current PAs is 20.2% (ABF) and 16.8% (CAZ) respectively. However, this means that ~80% of the area within the PA network is located outside areas systematically identified by Zonation as high priority. When the number of Zonation cells selected was increased, the overlap with current PAs increased non-linearly (Table 3.2, Fig. 3.4). When considering present and future distributions, a 20th percentile cutoff overlaps 42.3% (ABF) and 40.5% (CAZ) with current PAs. A 35th percentile cutoff gains even further, with 50.9% (ABF) and 48.9% (CAZ) of current PAs falling within the selected cells.

I also created spatial prioritizations that forced the inclusion of current PAs, essentially by setting them as the highest value cells on the landscape. The overlaps between these maps, and maps created with no constraints, were relatively high (Table 3.3, Fig. 3.5). For example, at 20% coverage, when considering present and all future distributions, the overlap was 71.8% (ABF) and 70.9% (CAZ) respectively. The majority of the differences in these maps comes from the omission of Mouling National Park, Yordi-Rabe Supe Wildlife Sanctuary and the Kamlang-Namdapha complex from virtually all unconstrained prioritizations. Of interest, Yordi-Rabe Supe is the most recently designated protected area in the region, though the precise justifications for its creation are unclear.

Since CAZ and ABF cell removal rules can be said to represent different conservation philosophies (see Methods: Spatial Prioritization), I also examined the overlap between prioritizations based on each of these rules at different coverage levels (Table 3.4, Fig. 3.6). When considering all current and future distributions, the overlap is 68.3% for a coverage of 20%, and 68.2% for a coverage of 35%. The CAZ rule prioritizes areas in southern AP and far eastern AP. The ABF rule exchanges this for a band of

habitat in the northern/central part of the state. It should be noted that none of the above areas selected by the CAZ and ABF algorithms were extensively surveyed, and may therefore merit further investigation. Both algorithms prioritize the eastern Dibang drainage, the lower Siang drainage and the high-altitude regions of Tawang province.

While 375 species were detected during my surveys, the above results were generated using the 215 species detected at a minimum of five points. I also created a set of prioritizations based on all 375 species and examined the difference this made in selecting areas for conservation action. I found that the differences were quite large (Table 3.5, Fig. 3.7), with an overlap of only 64.4% (ABF) or 62.3% (CAZ) for a coverage level of 20% and 73.1% (ABF) and 78.1% (CAZ) for a coverage level of 35% when considering current and future distributions. Some of this difference arises from the inclusion of the Bugun Liocichla, *Liocichla bugunorum*, a Critically Endangered AP endemic only known from the edge of Eaglenest Wildlife Sanctuary, and Swamp Prinia *Laticilla cinerascens*, an Endangered species found in grasslands at low elevations (Rasmussen and Anderton 2005). Including these species increases the value of areas in western and southern AP, with the entire Western Kameng drainage becoming high priority due to the possible presence of suitable habitat for the Liocichla. Eaglenest Wildlife Sanctuary in particular increases dramatically in value.

I also investigated potential reasons for the poor performance of current protected areas. My survey data was taken inside and outside protected areas (Table 3.1, Figs. 1.1a, 3.1). I therefore used a generalized additive model (GAM) to examine whether average diversity in protected areas was significantly different from average diversity outside protected areas. As elevation nonlinearly affects alpha diversity (Price et al. 2014), I included it as a term in the GAM (Fig. 3.8). I found that average diversity is significantly lower inside protected areas than it is outside protected areas ($z = -2.796$, $p = 0.005$), independent of the effects of elevation. Additionally, I examined the elevational distribution of protected areas, compared to the overall landscape. Protected areas underrepresent low-mid elevations, from 0-2750 metres, while overrepresenting high-elevation areas (Fig. 3.9); peak diversity occurs at ~1600 metres.

I also looked at species turnover relative to elevation by calculating the Sørensen-Dice dissimilarity index between adjacent elevational bands. The Sørensen-Dice index is a measure of beta diversity. Between a pair of elevations, it is given by: $\beta =$

$\frac{b+c}{(2*a)+b+c}$, where a is the number of species found at both elevations, and b and c are the number of species found uniquely at each elevation. A high value indicates that the community at a given location has a high proportion of unique species relative to its neighbours. In the context of conservation decision-making, sites with low beta diversity have similar species composition and hence may be redundant. I assigned species to elevational bands by draping the SDMs for each species over a digital elevation model. A species was considered to be present in an elevational band if at least 20% of its distribution lay within that band. I found that beta diversity peaks at low elevations and again at ~2000 metres, areas that are underrepresented in the current PA network (Fig. 3.10). Conversely, the current PA network overrepresents areas with low beta diversity.

Finally, I analyzed the value provided by individual protected areas by examining the overlap of high-priority cells with all PAs, and breaking this down by individual PA. If all PAs contributed equally, I would expect the number of overlapping cells in an individual PA to be proportional to the area of that PA, relative to the overall PA network. I found that three reserves – Eaglenest/Sessa, Dibang Biosphere Reserve and D'Ering Wildlife Sanctuary – consistently outperform the null expectation by over 50%, across different coverage levels and cell removal rules (Table 3.6). On the other hand, Mouling National Park and Yordi-Rabe Supe Wildlife Sanctuary consistently fail to provide any value.

DISCUSSION

My results indicate that the current placement of PAs does not adequately protect Eastern Himalayan avifauna in AP, especially under climate change scenarios. However, the value provided by individual protected areas is highly variable, with protected areas such as Eaglenest Wildlife Sanctuary being a critical to regional conservation goals. The overall pattern is unsurprising, as most PAs were designed for the protection of a small number of charismatic megafauna, meaning that they do not represent all habitat types. In addition, current PAs were not designed with the goal of climate resiliency. While my results may be unsurprising, they are also disappointing, in that they indicate a failure of charismatic megafauna to provide a broad umbrella for overall biodiversity conservation in the region.

It additionally appears that current PAs underrepresent certain elevations, and it is at precisely those elevations are where both alpha diversity and beta diversity peak. This underrepresentation is likely to be a major driver of my finding that an optimized PA networks would not greatly overlap with the current network. Moreover, when correcting for the effects of altitude, protected areas apparently harbor lower avian diversity than non-protected areas. I urge caution against overinterpreting this result, as degraded/urbanized locales in non-protected areas were not chosen for surveys. This choice is justifiable, as degraded urbanized areas were *a priori* excluded from all spatial prioritizations presented here. However, including agricultural fields and market streets being used as survey points might have caused protected areas to appear more diverse. It is certainly worth noting all the same that in relatively good habitat, protected status is at best irrelevant to diversity, indicating that current management strategies do not provide a general benefit to birds.

The disjunction between optimized and current protected areas is driven by a lack of value contributed by certain PAs, most notably Yordi-Rabe Supe Wildlife Sanctuary and Mouling National Park. Yordi-Rabe Supe is a particularly intriguing case, as it is the most recently created protected area (WII 2015). However, there is very little easily accessible information regarding this PA, and there is virtually no analysis presented as to why it should have been designated over any other part of AP. Once again, however, I urge caution in interpreting these results. As a salutary lesson, I note that the Kamlang/Namdapha complex of protected areas appears to provide little value in my analyses (Table 7). However, this is misleading, as the critically endangered White-bellied Heron *Ardea insignis* and the near-endemic Snowy-throated Babbler *Stachyris oglei* are known to occur there, to say nothing of other vertebrates of conservation concern. They are not represented in my surveys as I were unable to access the majority of the two PAs during the monsoon due to impassable roads. As a result. The perceived value of Kamlang/Namdapha is misleadingly low. Nevertheless, I feel confident in concluding that Eaglenest Wildlife Sanctuary and the Dibang Biosphere Reserve provide the highest benefits to bird conservation.

A previous SCP analysis was conducted in AP and the rest of Northeast India, based on amphibian species (Pawar et al. 2007). My study extends this work, since the previous study did not account for climate change; additionally, birds are found across a

wider range of habitats, especially at high altitude above the treeline. There are some intriguing qualitative differences between the results of the 2007 study and the one presented here. The most consequential difference is that the amphibian study identified areas of eastern AP to be the highest priority. No regions in western AP were selected as high priority. By contrast, my studies emphasize the importance of western AP, especially around the Eaglenest Wildlife Sanctuary, and particularly when accounting for climate change. It is difficult to speculate what exactly is driving this difference in outcomes. However, it does make it clear that considering only one set of taxa in an SCP analysis can lead to results that are not optimal for overall biodiversity.

My analyses generally show that the largest gaps in conservation are in two different areas – the northwestern part of AP (around the district of Tawang) and the eastern part (around the district of Anjaw) (Fig. 3). There are coherent biogeographical reasons for this. In western AP, the Sela Massif and the Kameng River together create a formidable high-low barrier for birds with narrow altitudinal ranges (Fig. 1). Several species such as the Rufous Sibia *Heterophasia annectans* are only found in the small region to the west of the Kameng River (Rasmussen and Anderton, 2005; my own surveys confirm this as well). As a result, the bird community there has several species that are found nowhere else in AP. The eastern part of AP, on the other hand, is across Lohit River and is therefore not separated from Myanmar and the Northeast Indian Hills like the rest of AP. Again, this results in a relatively unique community, with species like White-tailed Blue Flycatcher *Cyornis concretus* that are not found further west (Rasmussen and Anderton, 2005; again, my own surveys confirm this). Neither region has a PA – there is a large gap north of Eaglenest and west of Yordi-Rabe Supe, and likewise northeast of Kamlang (Fig. 2).

While my analyses provide an assessment of the spatial areas that should be a priority for action, it is necessary for this to translate into action on the ground. There has been a long-observed gap between ‘academic’ conservation and ‘practical’ conservation (Whitten et al. 2001, Knight et al. 2008). The SCP process provides a powerful framework for bringing scientific best practices to bear on conservation decision making, as demonstrated here. However, this means very little in and of itself unless implemented. In particular, I would like to emphasize that Zonation indicates the most important cells for conservation action in a landscape; it does not necessarily convey anything about the

management of those areas. As mentioned earlier, protected areas are important for conservation in the Indian context, in part because they provide a legal framework for combating overhunting, as well as forms of habitat loss such as unsustainable logging. However, these goals may be accomplished outside a formal legal framework. AP has a complex political history, especially as it pertains to the Indian government. Community conserved areas and other forms of protected status may serve the needs of community as well as meeting conservation goals. Flexibility in the management of areas identified as being high priority is a powerful tool to advance conservation goals in those areas. It is my hope that by working with local stakeholders and being responsive to community needs, the results presented here will serve as a guide to future conservation work in this unique and irreplaceable landscape.

FIGURES AND TABLES

Protected area	Size (sq km)
D'Ering Memorial Wildlife Sanctuary	190
Dibang Biosphere Reserve	4149
Eaglenest Wildlife Sanctuary	217
Itanagar Wildlife Sanctuary	140
Kamlang Wildlife Sanctuary	783
Kane Wildlife Sanctuary	31
Mehao Wildlife Sanctuary	281
Mouling National Park	483
Namdapha National Park	1808
Pakhui Tiger Reserve	862
Sessa Orchid Sanctuary	100
Tale Valley Wildlife Sanctuary	337
Yordi-Rabe Supe Wildlife Sanctuary	397

Table 3.1. List of protected areas, Arunachal Pradesh, along with their size in square kilometers.

Bold text indicates protected areas that were surveyed.

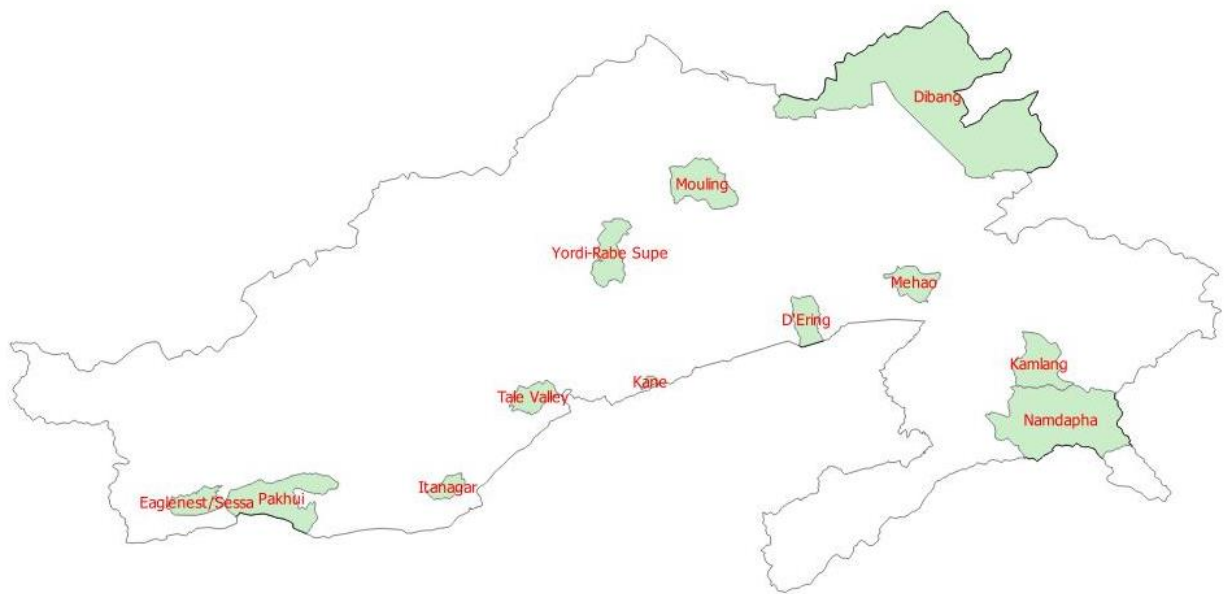


Fig. 3.1. Map of protected areas of Arunachal Pradesh.

Labels correspond to names in Table 3.1. Eaglenest Wildlife Sanctuary and Sessa Orchid Sanctuary (extreme southwest) are contiguous (see Table 1); Kamlang Wildlife Sanctuary and Namdapha National Park are nearly so.

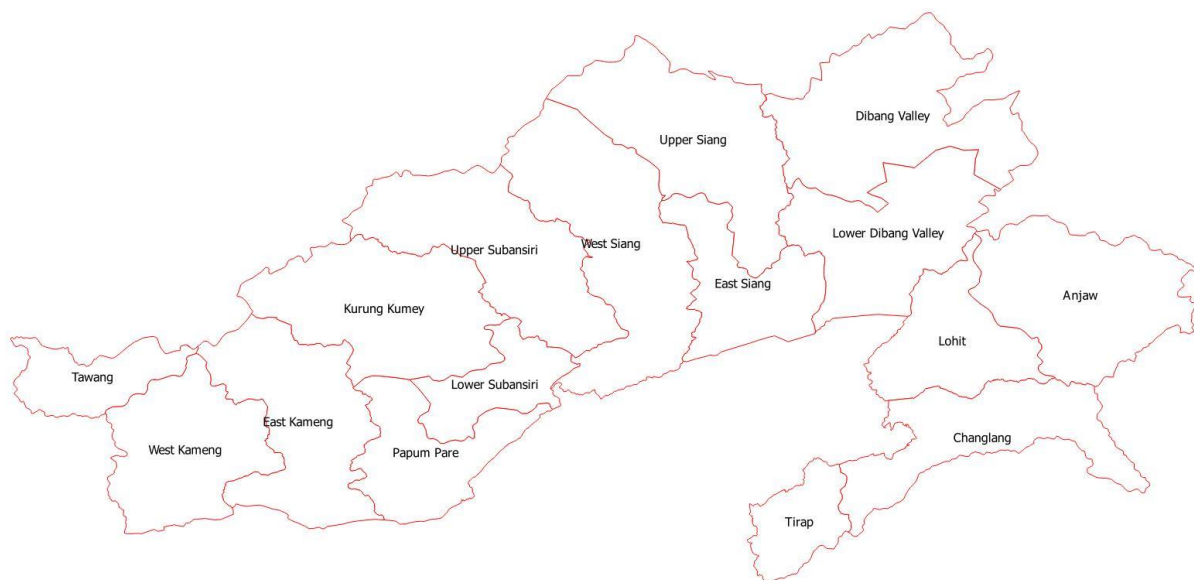


Fig. 3.2. Map of districts of Arunachal Pradesh.

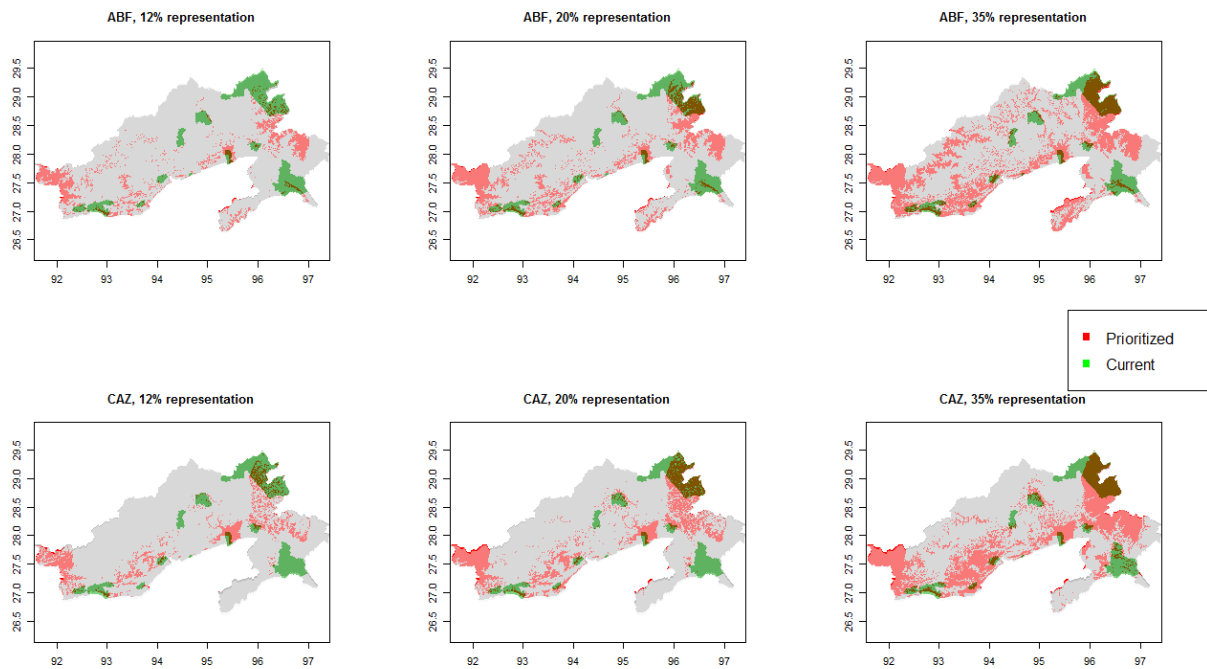


Fig. 3.3. Zonation output for present species distributions (red), overlaid with map of current protected areas (green) for three different levels of coverage.

Current protected areas cover 12.2% of land area. Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. The overlap between current protected areas, and areas identified as being of high conservation priority, are relatively low, especially for the 12% target (see table 3.2)

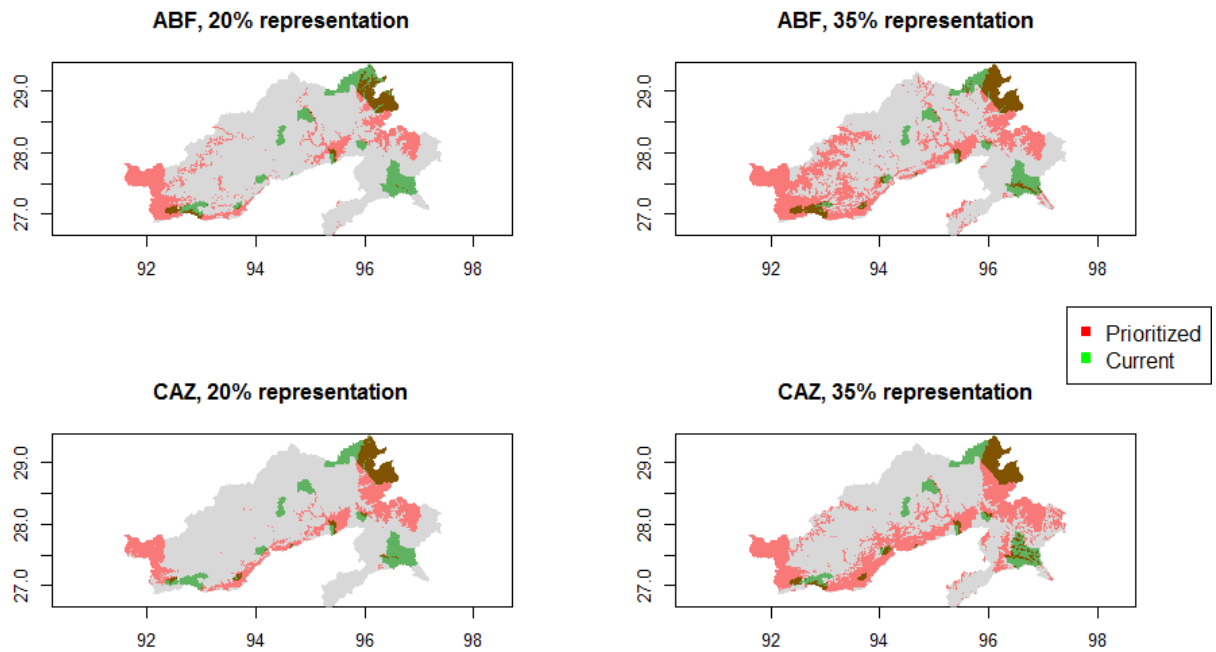


Fig. 3.4. Zonation output summed across present climate and all future climate scenarios (red), overlaid with map of current protected areas (green) for two different levels of coverage.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. See also Table 3.2

Cell removal	Climate scenario	Target Representation		
(ABF/CAZ)		12.2%	20%	35%
ABF	Present	0.108	0.282	0.465
ABF	rcp 2.6	0.155	0.264	0.468
ABF	rcp 4.5	0.170	0.294	0.504
ABF	rcp 6.0	0.163	0.285	0.453
ABF	rcp 8.5	0.115	0.286	0.477
ABF	Combined	0.174	0.319	0.500
CAZ	Present	0.173	0.350	0.503
CAZ	rcp 2.6	0.077	0.243	0.457
CAZ	rcp 4.5	0.092	0.332	0.485
CAZ	rcp 6.0	0.111	0.288	0.512
CAZ	rcp 8.5	0.150	0.387	0.522
CAZ	Combined	0.114	0.366	0.500

Table 3.2. Overlap of maps with current protected areas, for different target coverages.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. Each target representation gives that quantile of cells, based on a ranking of conservation value – for example, the 12.2% target representation are the top 12.2% of cells. Combined climate scenarios are derived from summing the rankings of each cell for both current and future and then calculating the respective quantiles. The proportion of current protected areas included increases non-linearly, indicating that current protected areas are not optimally located but provide complementarity to optimal areas.

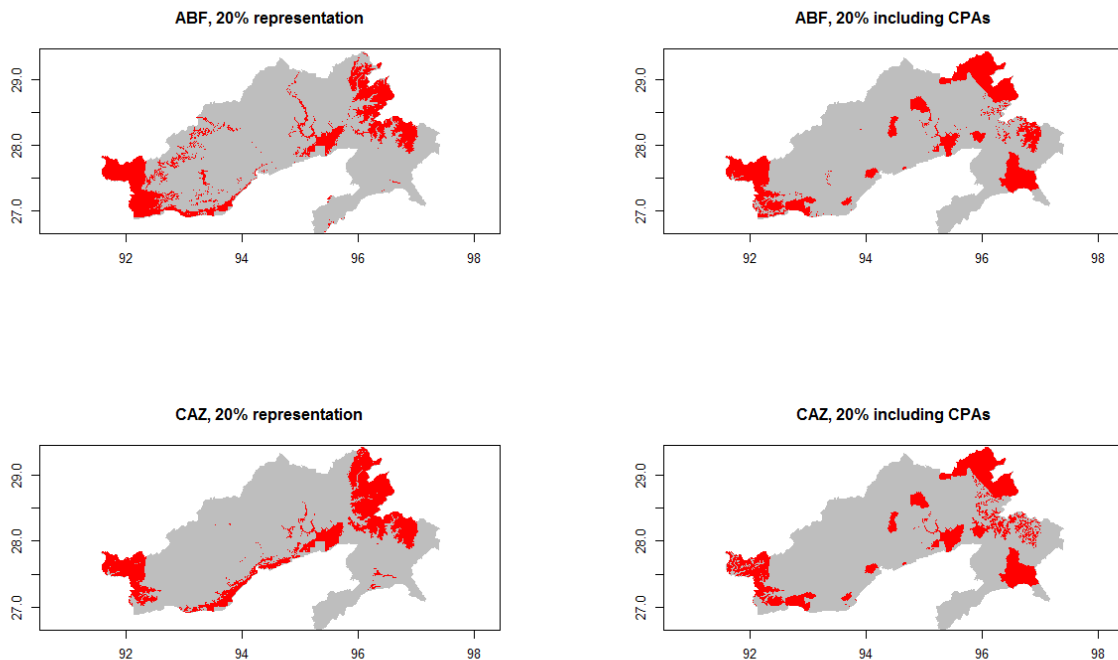


Fig. 3.5. Zonation output summed across present climate and all future climate scenarios (red), overlaid with map of current protected areas (green) for two different levels of coverage.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. Left panels represent output with no constraints; right panels include current protected areas within their coverage. See also Table 3.3.

Cell removal (ABF/CAZ)	Climate scenario	Target Representation	
		20%	35%
ABF	Present	0.561	0.813
ABF	rcp 2.6	0.550	0.814
ABF	rcp 4.5	0.569	0.827
ABF	rcp 6.0	0.563	0.809
ABF	rcp 8.5	0.564	0.817
ABF	Combined	0.584	0.825
CAZ	Present	0.603	0.826
CAZ	rcp 2.6	0.537	0.810
CAZ	rcp 4.5	0.592	0.820
CAZ	rcp 6.0	0.565	0.830
CAZ	rcp 8.5	0.625	0.833
CAZ	Combined	0.612	0.825

Table 3.3. Overlap of maps with and without including current protected areas, for different levels of coverage.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. Each target representation gives that quantile of cells, based on a ranking of conservation value – for example, the 12.2% target representation are the top 12.2% of cells. Combined climate scenarios are derived from summing the rankings of each cell for both current and future and then calculating the respective quantiles. At the 35% target representation, there is a large overlap between conservation prioritizations constrained to include protected areas, and prioritizations without that constraint.

Climate scenario	Target representation	
	20%	35%
Present	0.613	0.706
rcp 2.6	0.679	0.696
rcp 4.5	0.640	0.698
Rcp 6.0	0.672	0.718
Rcp 8.5	0.652	0.644
Combined	0.756	0.695

Table 3.4. Overlap of Core Area Zonation (CAZ) and Additive Benefit Function (ABF) maps for different levels of coverage, protected areas not explicitly included.

ABF cell removal prioritizes range-weighted diversity; CAZ cell removal uses the most valuable biodiversity feature for each cell. Each target representation gives that quantile of cells, based on a ranking of conservation value – for example, the 12.2% target representation are the top 12.2% of cells. Combined climate scenarios are derived from summing the rankings of each cell for both current and future and then calculating the respective quantiles. For both target representations, there is a significant difference between the prioritizations generated.

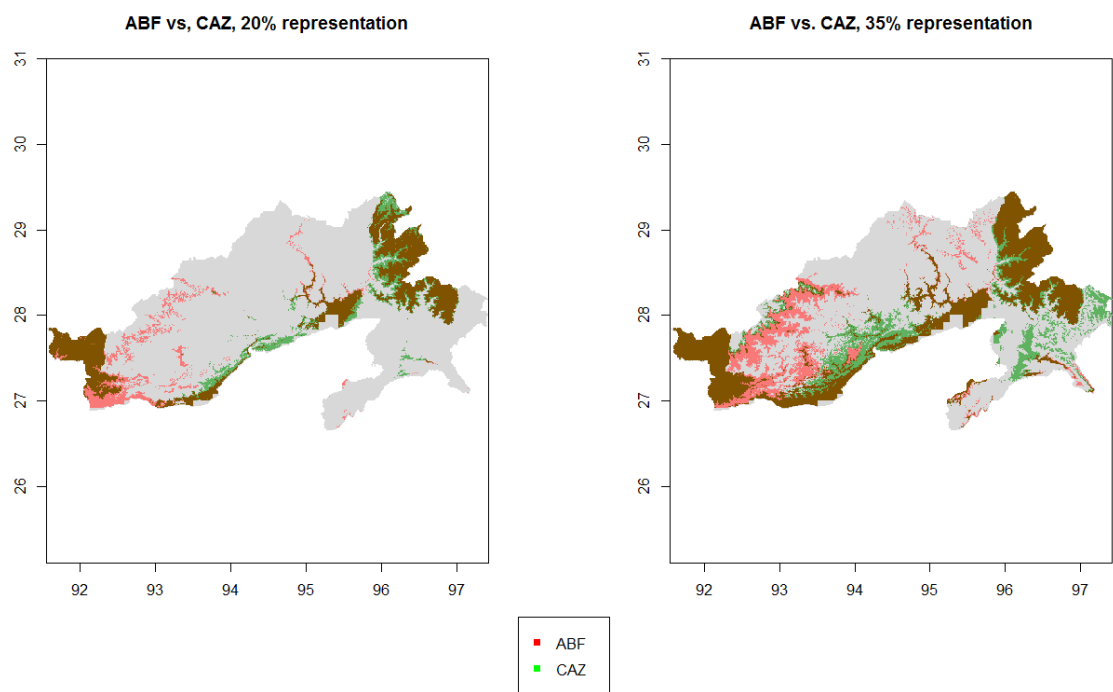


Fig. 3.6. Zonation output summed across present climate and all future climate scenarios using ABF removal (red) and CAZ removal (green), for 20% and 35% coverage.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. See also Table 3.4.

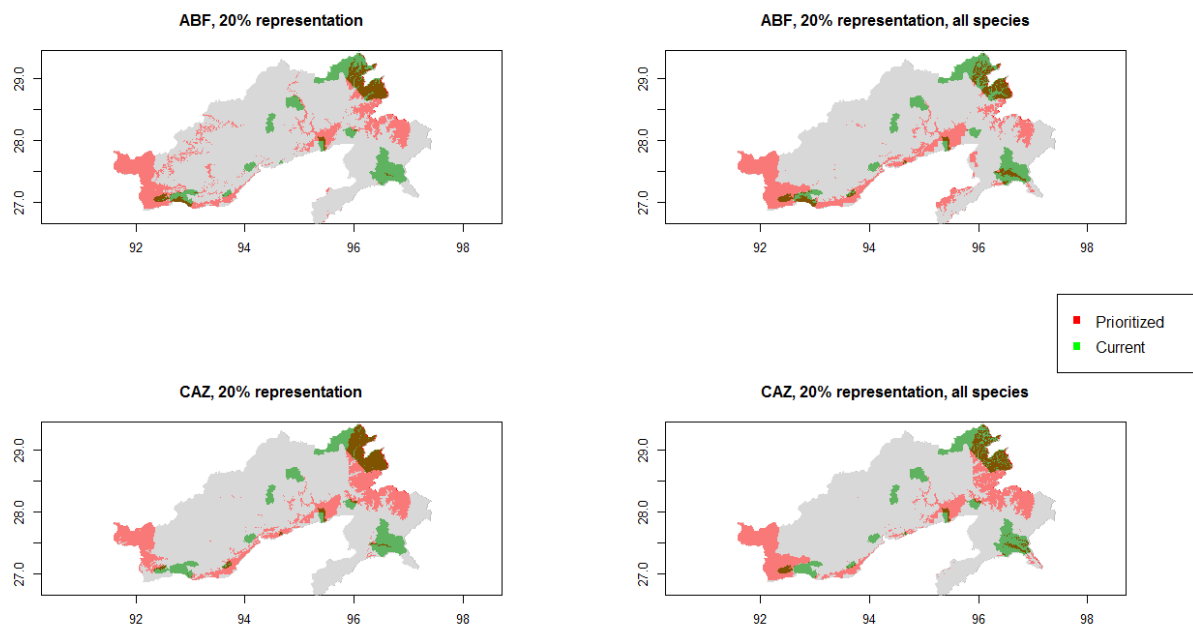


Fig. 3.7. Zonation output summed across present climate and all future climate scenarios (red), overlaid with map of current protected areas (green).

ABF cell removal prioritizes range-weighted diversity; CAZ cell removal uses the most valuable biodiversity feature for each cell. Left panels show prioritizations based on set of 215 species detected at a minimum of five points; right panels show prioritizations based on all 375 species detected. See also Table 3.5.

Cell removal (ABF/CAZ)	Climate scenario	20%	35%
ABF	Present	0.502	0.686
ABF	rcp 2.6	0.516	0.713
ABF	rcp 4.5	0.542	0.701
ABF	Rcp 6.0	0.524	0.710
ABF	Rcp 8.5	0.525	0.680
ABF	Combined	0.556	0.708
CAZ	Present	0.519	0.719
CAZ	Rcp 2.6	0.463	0.721
CAZ	Rcp 4.5	0.549	0.722
CAZ	Rcp 6.0	0.478	0.776
CAZ	Rcp 8.5	0.531	0.777
CAZ	Combined	0.516	0.749

Table 3.5. Overlap of results for all species vs. set of 215 species detected at a minimum of five survey points.

Additive Benefit Function (ABF) cell removal prioritizes range-weighted diversity; Core Area Zonation (CAZ) cell removal uses the most valuable biodiversity feature for each cell. Each target representation gives that quantile of cells, based on a ranking of conservation value – for example, the 12.2% target representation are the top 12.2% of cells. Combined climate scenarios are derived from summing the rankings of each cell for both current and future and then calculating the respective quantiles. There is a significant difference in the spatial prioritizations derived from including those species with the most data, and including rare species without sufficient data available data.

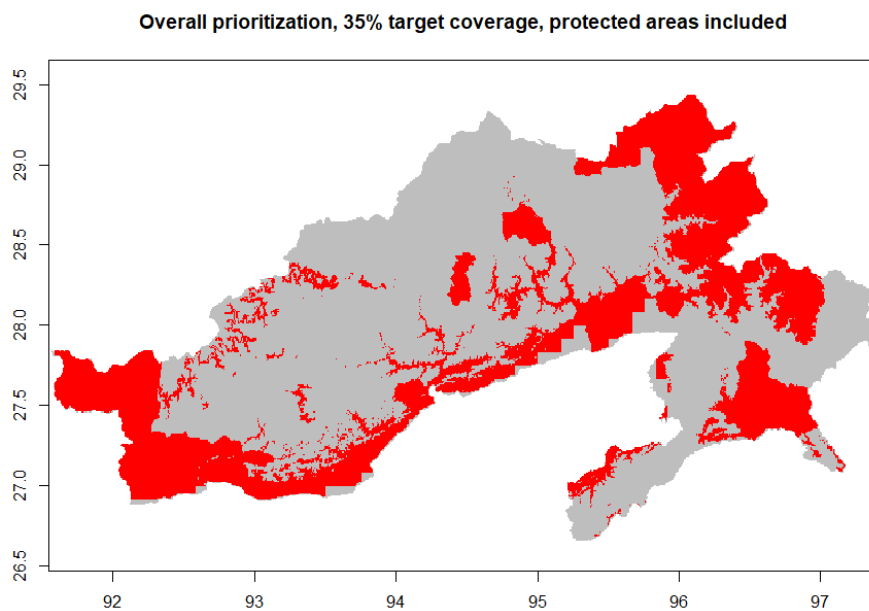
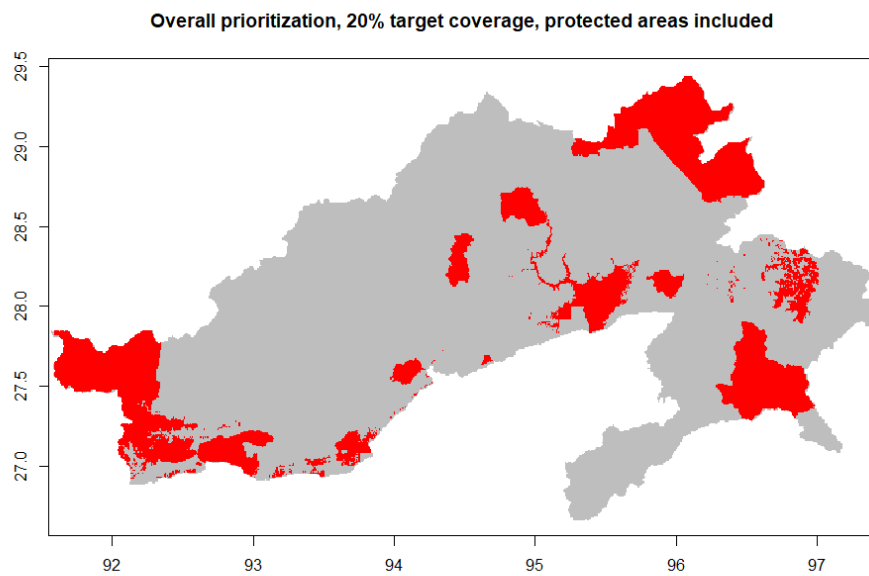


Fig. 3.8. Zonation output summed across present and all future climate scenarios, both Core Area Zonation (CAZ) and Additive Benefit Function (ABF) cell removal, for 215 species with the most data and for all 375 species.

Maps are based on summed rankings for both cell removal rules.
Maps explicitly include protected areas.

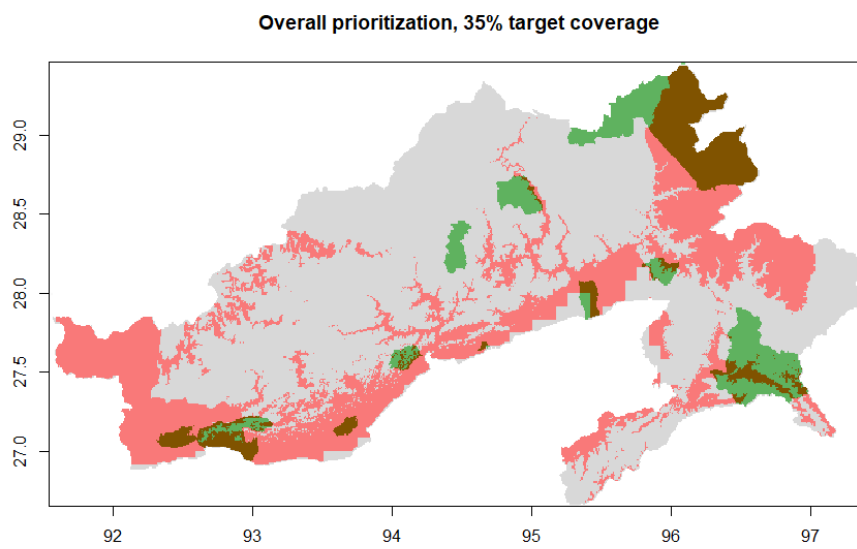
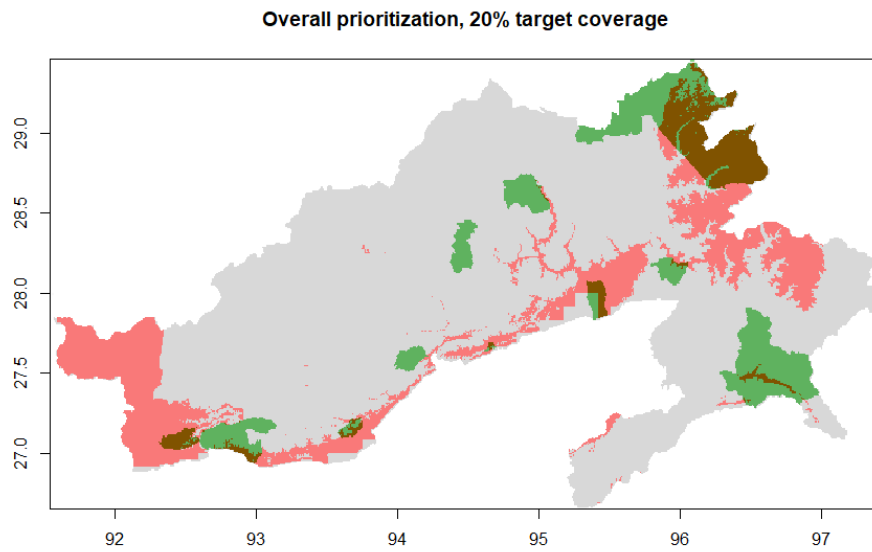


Fig. 3.9. 'Master prioritizations' from Zonation output (see Fig. 9) without explicitly including protected areas.

Zonation output shown in red; current protected areas shown in green.

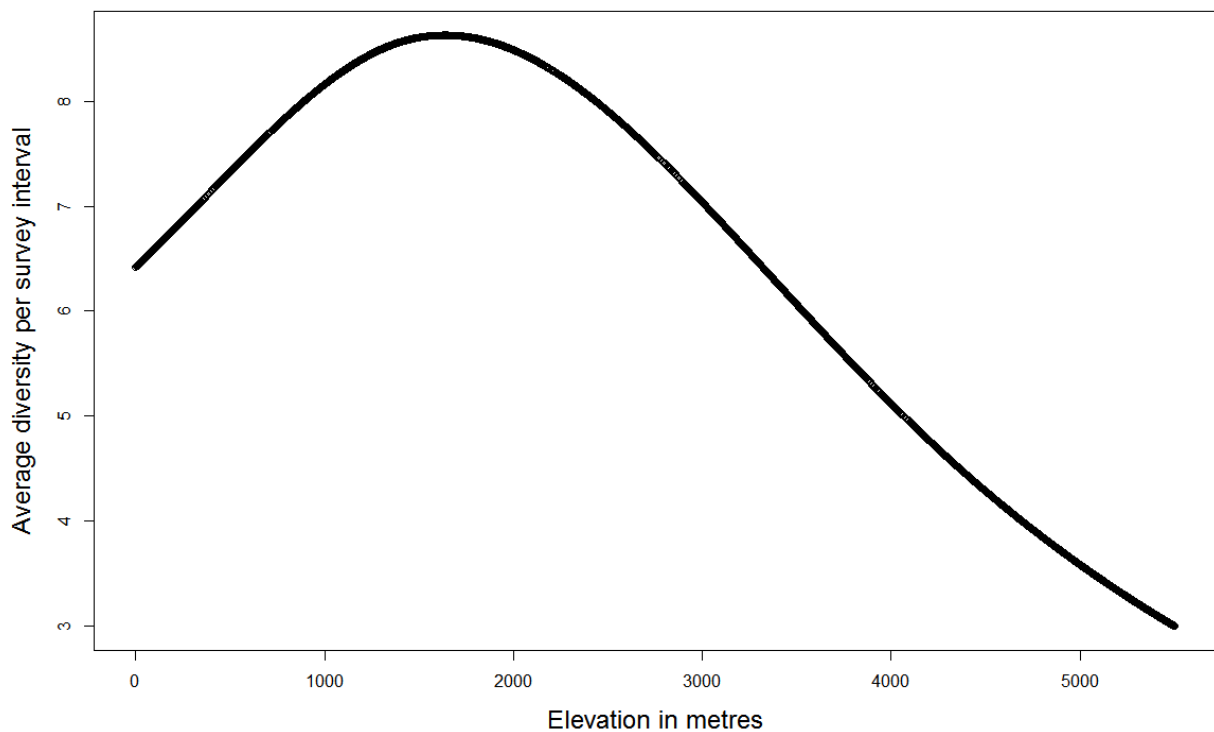


Fig. 3.10. Relationship of overall (alpha) diversity to elevation

Predicted diversity based on a cubic smoothing GAM with three knots of Poisson family, calculated on the average number of species per survey interval found at each survey point. The maximum predicted diversity occurs at 1637 meters.

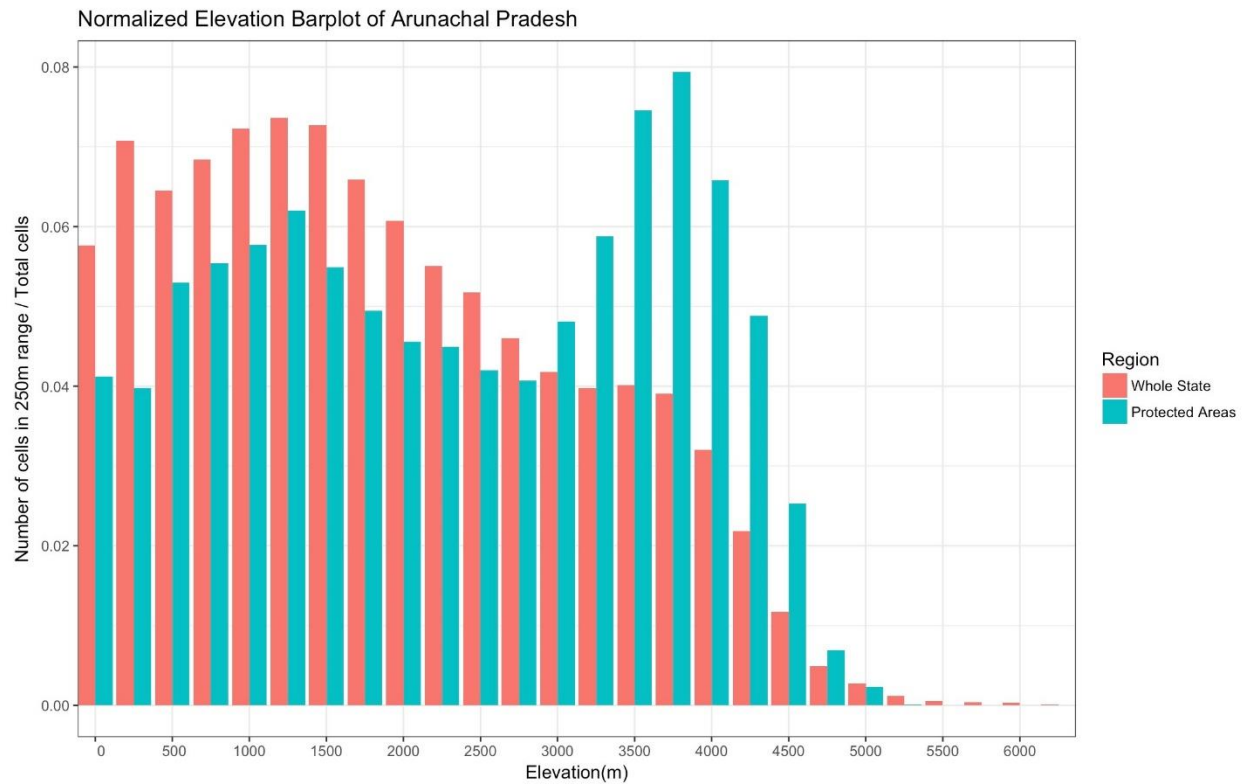


Fig. 3.11. Proportion of Arunachal Pradesh falling into different elevational bands.

Red – whole state, blue – protected areas. Protected areas underrepresent elevations from 0-3000 meters, while overrepresenting higher elevations. Note that elevations underrepresented by protected areas have the lowest diversity (Fig. 3.10) and highest beta diversity (Fig. 3.12).

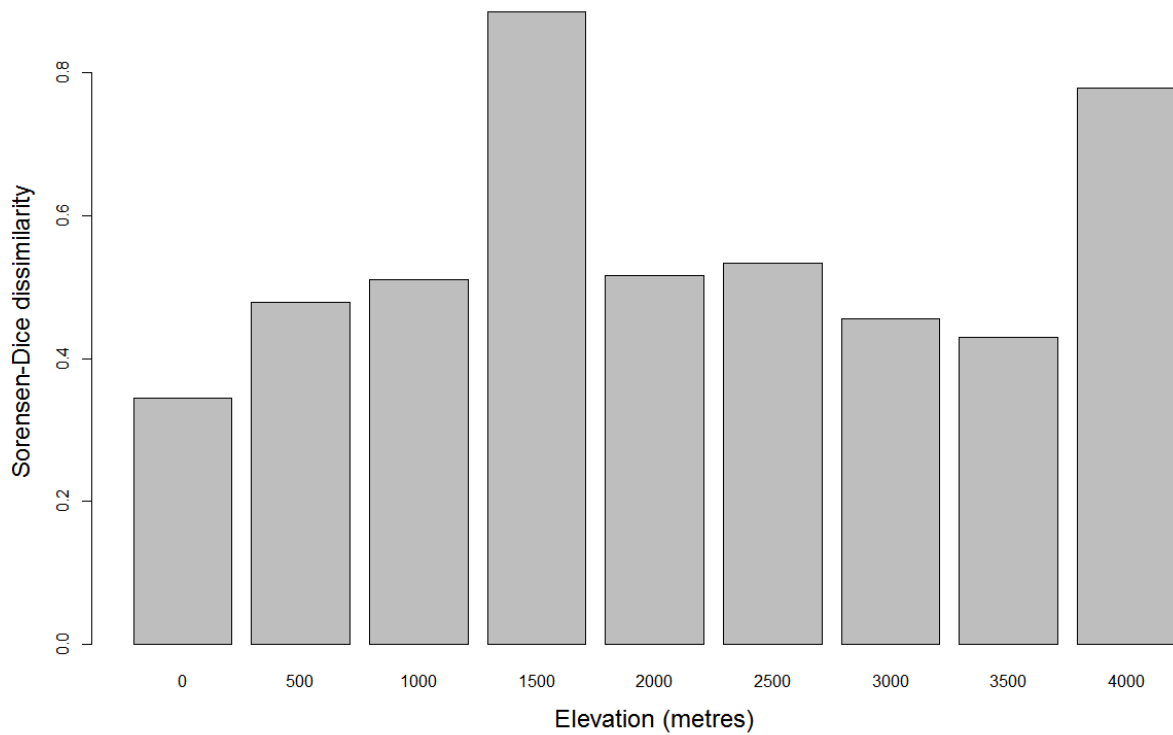


Fig. 3.12. Sørensen-Dice dissimilarity index for different elevational bands.

Larger values indicate more species turnover between adjacent elevations, i.e. more unique community composition in a given band. Beta diversity peaks at ~1500 metres. The peak at 4000 metres reflects high turnover at the treeline; however, it involves far fewer species (Fig. 9).

Protected area	Proportion of area	ABF, 12%	ABF, 20%	ABF, 35%	CAZ, 12%	CAZ, 20%	CAZ, 35%
D'Ering	0.029	0.080	0.055	0.037	0.161	0.050	0.037
Dibang	0.452	0.753	0.747	0.648	0.719	0.844	0.643
Eaglenest/Sessa	0.027	0.099	0.080	0.054	0.064	0.025	0.042
Itanagar	0.014	0.000	0.006	0.026	0.016	0.032	0.029
Kamlang	0.052	0.000	0.000	0.000	0.000	0.000	0.032
Kane	0.003	0.000	0.000	0.004	0.000	0.006	0.005
Mehao	0.029	0.003	0.007	0.011	0.038	0.014	0.019
Mouling	0.057	0.013	0.011	0.010	0.000	0.001	0.008
Namdapha	0.186	0.001	0.009	0.054	0.002	0.022	0.094
Pakhui	0.087	0.052	0.085	0.138	0.001	0.004	0.057
Tale Valley	0.025	0.000	0.000	0.017	0.000	0.002	0.035
Yordi-Rabe Supe	0.041	0.000	0.000	0.000	0.000	0.000	0.000

Table 3.6. Proportion of overlap between Zonation prioritizations based on current and future distributions and current PA network, broken down by individual PA.

Second column represents the proportion of total PA area for each individual protected area – the largest, Dibang Biosphere Reserve, accounts for over 40% of all protected land. Remaining columns represent the fraction of the overlap between a prioritization and the current PA network contained within each PA; columns therefore sum to 1. Bolded values highlight reserves contributing at least 1.5 times the null expectation (the proportional contribution to land area).

Conclusions

SUMMARY OF FINDINGS

Chapter 1 - Altitudinal limits of Eastern Himalayan birds are created by competition past and present

My findings indicate that competition acts on multiple time scales to structure the ranges of species. In the short term, morphologically similar species co-occur less than do morphologically dissimilar species, indicating that divergence along some niche axis is required for stable coexistence. Moreover, species pairs overlap less than would be predicted by a null model, with a greater difference in morphologically similar species. However, this pattern only applies to closely related species, indicating that distantly related species behave as though they are competitively neutral.

In the long term, there is evidence of competition-mediated selection on traits. When examining the entire phylogeny, there is evidence of underdispersal of morphological traits, i.e. closely related species being more morphologically similar than would be expected. The same applies to altitudinal traits, with species tending to prefer middle elevations due to higher resource availability. However, when examining individual clades, traits appear to be overdispersed. This is evidence of a tradeoff between selection pressures. On the one hand, selection optimizes morphologies of clades for different Eltonian niches. On the other hand, selection forces species away from their optimal morphologies in order to allow for coexistence with closely related sympatric species.

Chapter 2 – The effects of climate change and species interactions on ranges of Eastern Himalayan birds

Climate change is expected to have a profound effect on the ranges of species over the next 50 years. The majority of species are expected to experience range contractions, with several species experiencing declines of over 50%. However, there is significant variation between species. The precise climate change scenario anticipated has a significant effect on the expected degree of range contraction or expansion.

Species are also expected to shift their ranges in addition to changes in range size. The more extreme the expected degree of climate change, the further species are expected to move. However, the direction of range shift is constant between climate

change scenarios. There is also significant variation as to whether species will move upslope or downslope, some of which can be explained by whether species' distributions are more controlled by temperature or precipitation. Species whose distributions are controlled by temperature are significantly more likely to move upslope than species whose distributions are controlled by precipitation. In addition, species that are anticipated to move upslope are more likely to experience range contractions, whereas species that are anticipated to move downslope are more likely to experience range expansions. Similarly, species that are expected to end up at higher elevations are more likely to experience range contractions.

Incorporating the effects of interspecies competition affects projections of changes in species' ranges. The median change in predicted range size is ~4.5%, as many species overlap minimally and hence do not affect each other's ranges to a significant degree. However, several species show far larger effects of competition. The effects of competition are largest under the most severe projections of climate change, where 6 species out of 35 tested are expected to have ranges over 50% smaller than would be predicted without taking competition into account.

Chapter 3 – Systematic conservation planning for Eastern Himalayan birds

The current system of protected areas in Arunachal Pradesh is insufficient to meet conservation targets. When examining the highest-value areas for conservation in Arunachal Pradesh, the overlap with current protected areas is barely more than would be expected if current protected areas had been placed at random. However, current protected areas only cover 12.2% of the land area of Arunachal Pradesh, a level of coverage that can be increased. When examining the overlap of current protected areas with the top 20% and top 35% highest-value areas for conservation, it was much higher, indicating that current protected areas may form an adequate base for an expanded conservation network.

I used two different algorithms to create spatial prioritizations, one that favoured overall diversity (ABF) and one that favoured individual rare species (CAZ). Maps created using both algorithms overlapped by ~60%. Similarly, I created spatial prioritizations that forced the inclusion of current protected areas. Those prioritizations overlapped with prioritizations created with no constraints by ~70%. Finally, I created maps using all

species found during surveys, as well as only those species found at a minimum of five sites. Those maps overlapped by ~55%. These results indicate that the subjective choices made during the modelling process can create different outcomes, and that those choices should be considered carefully before making irrevocable decisions.

I also examined potential reasons for the underperformance of current protected areas. Bird alpha diversity peaks at middle elevations (~1500-1750 metres). However, elevations from 0-3000 metres are underrepresented in the current protected area system relative to their representation in Arunachal Pradesh as a whole. Moreover, it is not just alpha diversity that peaks at these elevations – beta diversity does so as well, meaning that species turnover is greater in adjacent elevational bands and there is less redundancy. These factors both adequately explain the underperformance of the current network.

Finally, I examined the conservation value of individual protected areas, as well as regions where future conservation action is required. The Dibang Biosphere Reserve, Eaglenest Wildlife Sanctuary and D'Ering Wildlife Sanctuary all provide a disproportionate amount of value, whereas Yordi-Rabe Supe Wildlife Sanctuary and Mouling National Park provide almost no value. In order to fully meet conservation goals, more conservation action is required in the northwestern (Tawang) and eastern (Anjaw/Changlang) parts of Arunachal Pradesh.

IMPLICATIONS OF FINDINGS

The results presented here make several important contributions to the existing literature. As has been discussed earlier, the degree to which competitive species interactions structure communities has been debated for decades. Studies on the relationship between range overlaps and ecological traits have often involved detailed mechanistic analyses on a small number of species (for some representative examples see e.g. Gatz Jr 1979, Hindar and Jonsson 1982, Fauth et al. 1990, Churchfield et al. 1999, Arlettaz 1999). However, relatively few studies have examined entire guilds of species at the landscape scale. Moreover, few studies have combined studies of competition with studies of evolutionary dynamics to produce a cohesive explanation for the effects of competition.

Our results also have specific implications for the literature on the bird community on the Eastern Himalayas. It has long been assumed that competitive species interactions are important in this community, despite the high diversity. Mechanistic studies have been carried out on individual genera, the results of which have supported the community hypothesis (Johansson et al. 2007, Price 2010, Price et al. 2014). On the other hand, studies of larger numbers of species have proposed that biotic limitations are less important than abiotic limitations in structuring the bird community. (Elsen et al. 2017, Srinivasan et al. 2018). My results suggest a way that these divergent viewpoints can be reconciled. On the one hand, there is evidence that in the short term, competitive interactions reduce species co-occurrences even when the species have relatively large altitudinal overlaps. On the other hand, the extent of the altitudinal overlaps between species is itself a product of competition playing out over evolutionary timescales, with evidence that the evolution of species' functional morphologies and thermal tolerances have been shaped by interspecies interactions. Reconciling diverging views on the importance of competition in this diverse community provides a holistic view of the processes that shape it. In turn, this allows us to better understand how changing environments in the coming decades will alter and affect this community.

As has been discussed elsewhere, there is significant evidence that global biodiversity will be imperiled by climate change (Thomas et al. 2004, Malcolm et al. 2006, Hooper et al. 2012). Birds are no exception to this rule, especially in montane communities (Pimm 2008, Sekercioglu et al. 2008, Tingley and Beissinger 2013, Langham et al. 2015). However, understanding the effects of climate change on high-diversity tropical and subtropical environments is complicated by a lack of detailed data (Collen et al. 2010, Feeley and Silman 2011). Moreover, the traditional approach to understanding the effects of climate change is to create species distribution models (SDMs) and project those models into the future (Kearney and Porter 2009, Elith et al. 2010, Anderson 2013). SDMs generally attempt to model distributions by accounting for biotic, abiotic and movement limitations on species (Soberón and Townsend Peterson 2005). However, in practice, abiotic variables are given the most attention (Araújo and Guisan 2006, Anderson 2013). This can be an issue in communities such as the Eastern Himalayas, where competition affects species distributions intimately, and where furthermore there is reason to suspect

dispersal limitations further help account for large-scale patterns of diversity (Srinivasan et al. 2014).

My effort to understand the effects of climate change on an entire guild of species is, I believe, the most detailed such effort undertaken in a tropical or subtropical community. Moreover, I explicitly included both biotic factors and movement limitations in addition to changes in climate in my analyses. These results can therefore be extrapolated with some confidence onto other Eastern Himalayan taxa, as well as onto other tropical and subtropical montane regions. The sharp declines projected for many species, including several of conservation concern, are discouraging on their face. On the other hand, forewarning of the challenges that species will face gives us more time to plan for their future. Additionally, there is some reason for optimism, as several species including some of conservation concern are expected to expand their ranges. I also provide evidence that accounting for biological interactions influences the projections of future species distributions, which will hopefully incentivize such analyses in other regions.

Finally, spatial prioritization analyses are a commonly used tool, and have been carried out in a wide variety of regions and on a wide variety of taxa (Moilanen 2007; for recent examples see e.g. Wu et al. 2014, Brum et al. 2017, Liang et al. 2018). A spatial prioritization based on amphibians and reptiles was previously carried out for parts of the Himalayas, along with other contiguous areas in Northeast India (Pawar et al. 2007). However, that study had several limitations. The occurrence data gathered was presence-only, which contributed to uncertainty in predicting the distributions of the species involved (VanDerWal et al. 2009, Elith and Leathwick 2009). The amphibian/reptile community is also less diverse, and is more strongly limited by environmental constraints, meaning that higher altitudes are relatively free of these species and hence are undervalued. Moreover, data on some of the rarest species, which presumably would be the highest priority for conservation, was lacking and those species were excluded from analyses. Finally, the prioritizations failed to account for the potential changes in distributions due to climate change. By contrast, the study I present involves more certain data on a larger set of species distributed across more habitats, with the potential effects of climate change explicitly accounted for.

Using the systematic conservation planning (SCP) framework (Margules and Pressey 2000), I was therefore able to identify parts of Arunachal Pradesh that would most

benefit from some type of conservation action. I was also able to identify the currently existing reserves that are critical for protecting overall biodiversity, as well as individual rare species. I was also able to identify those reserves that do not appear to contribute towards biodiversity protection. These results may provide a basis for political decision making, for example in the relative funding that different reserves are given, while also serving as a guide for the creation of future reserves.

FUTURE DIRECTIONS

Science begets science. As new hypotheses are tested and supported or rejected, so new questions arise. The findings and their implications summarized above create natural lines of enquiry for future researchers.

As discussed, there is a significant relationship between morphological dissimilarity and spatial co-occurrences among closely related species pairs. Morphologically similar species show very little overlap. However, different species pairs appear to handle this tradeoff differently. Some species show very little overlap in their elevational ranges; however, within that narrow zone, they co-occur about as often as would be expected. Other species have broadly overlapping elevational ranges but are rarely found together. Currently, I do not have an explanation for this difference. There is no effect of phylogenetic relatedness – the age of the most recent common ancestor of a given species pair does not predict which of the two strategies that species pair will follow. Clearly, more research is required to understand the ecological and evolutionary dynamics at play. Birds that have narrow elevational ranges with limited overlap may have narrowly defined physiological limits while species that do overlap broadly may have developed secondary mechanisms that prevent them from co-occurring more broadly, thereby reinforcing competition.

For example, species may have enhanced aggressive responses to the territorial songs of heterospecific competitors, thereby adding a component of interference competition to their interactions. There is some evidence for this in the tropical Andes (Robinson and Terborgh 1995, Jankowski et al. 2008, Dingle et al. 2010), but this has not yet been studied in the Eastern Himalayas. My own field experience suggests that responses to song playback is highly species-specific. However, a systematic investigation of call responses from conspecific and heterospecific species along an

elevation gradient would be a valuable contribution to this system. A further improvement would involve selecting multiple species pairs, some of which overlap extensively in altitudinal range and others of which barely overlap. This could also be combined with an analysis of the ways of song traits have evolved, and whether there is selection for more distinctive songs where species' ranges come together – essentially a test of character displacement (Brown Jr. and Wilson 1956).

Further investigations of the impacts of climate change are also critical. My survey data provides a baseline for bird distributions. Unfortunately, historical data from the Eastern Himalayas is sparse, meaning that we cannot yet ascertain whether climate change has already affected species. However, going forward, monitoring the bird community closely will allow us to determine whether the projected changes to the community are happening in real time. Moreover, we can try to understand whether there is variation in how species respond, and what the sources of variation are. For example, the ability of species to adapt rapidly to environmental change is likely to differ between species. Identifying which species can and cannot adapt will further refine our understanding of the conservation status of individual species. Moreover, we may be able to predict the ability of species to respond based on their traits, which can then be applied to regions outside the Eastern Himalayas.

Moreover, I established that competitive species interactions affect projections of species' future ranges. However, the measure of the strength of competition I used was derived from spatial patterns of coexistence and are not mechanistically derived. Especially for species pairs where incorporating competition makes a large difference in projected ranges, an enhanced mechanistic understanding of the strength of competition would be invaluable. Moreover, as species ranges begin to shift, these interactions could be studied in real time to determine whether the strength of competition between species changes. Again, such studies would be widely applicable outside the Eastern Himalayas.

Finally, there is the matter of applying my results to achieve practical, tangible conservation goals on the ground. The value of academic conservation research has been a subject of debate. It has been argued that such work does nothing to actually enhance conservation efforts (Whitten et al. 2001, Knight et al. 2008). While basic research is critical in the conservation decision-making process, it is necessary to translate that into action, especially in a region that has high diversity and yet faces a variety of challenges

(Soulé 1985, Chatterjee 2008, Kareiva and Marvier 2012). My results suggest a clear, spatially explicit path forward. In order to implement it, it will be necessary to work with a wide variety of people – state and central governments, non-governmental organizations and most important local stakeholders – to develop conservation strategies in highlighted regions that are powerful and yet flexible. The management strategies chosen cannot be one-size-fits-all. It is necessary to tailor them both to the individual ecosystems being protected, as well as the particular groups of people living in the places where conservation action is being mooted. Differences between the distinct indigenous cultures in the region must be carefully considered (Velho et al. 2012, Velho and Laurance 2013). If the research presented here results in successful conservation interventions, then it may serve as a framework for future efforts in other imperiled parts of our planet.

Appendices

APPENDIX A: LIST OF SPECIES DETECTED

Below are the species detected during my surveys, along with their IUCN status and taxonomic classification. Species in bold were detected at least 5 times. Under status, LC=Least Concern, NT = Near Threatened, VU = Vulnerable, EN = Endangered, CR = Critically Endangered.

Order	Family	Scientific name	Common name	Status	Points
Accipitriformes	Accipitridae	<i>Accipiter badius</i>	Shikra	LC	1
Accipitriformes	Accipitridae	<i>Accipiter trivirgatus</i>	Crested Goshawk	LC	2
Accipitriformes	Accipitridae	<i>Accipiter virgatus</i>	Besra	LC	1
Accipitriformes	Accipitridae	<i>Buteo burmanicus</i>	Himalayan Buzzard	LC	2
Accipitriformes	Accipitridae	<i>Ictinaetus malayensis</i>	Black Eagle	LC	11
Accipitriformes	Accipitridae	<i>Lophotriorchis kienerii</i>	Rufous-bellied Hawk-Eagle	LC	2
Accipitriformes	Accipitridae	<i>Pernis ptilorhynchus</i>	Crested Honey Buzzard	LC	7
Accipitriformes	Accipitridae	<i>Spilornis cheela</i>	Crested Serpent Eagle	LC	7
Apodiformes	Apodidae	<i>Aerodramus brevirostris</i>	Himalayan Swiftlet	LC	27
Apodiformes	Apodidae	<i>Apus leuconyx</i>	Blyth's Swift	LC	9
Apodiformes	Apodidae	<i>Apus nipalensis</i>	House Swift	LC	1
Apodiformes	Apodidae	<i>Hirundapus caudacutus</i>	White-throated Needletail	LC	2
Bucerotiformes	Bucerotidae	<i>Buceros bicornis</i>	Great Hornbill	NT	1
Caprimulgiformes	Podargidae	<i>Batrachostomus hodgsoni</i>	Hodgson's Frogmouth	LC	1
Charadriiformes	Charadriidae	<i>Vanellus duvaucelii</i>	River Lapwing	NT	1
Charadriiformes	Charadriidae	<i>Vanellus indicus</i>	Red-wattled Lapwing	LC	2

Ciconiiformes	Ciconiidae	<i>Anastomus oscitans</i>	Asian Openbill	LC	1
Columbiformes	Columbidae	<i>Chalcophaps indica</i>	Common Emerald Dove	LC	9
Columbiformes	Columbidae	<i>Columba leuconota</i>	Snow Pigeon	LC	1
Columbiformes	Columbidae	<i>Columba livia</i>	Rock Dove	LC	3
Columbiformes	Columbidae	<i>Columba pulchricollis</i>	Ashy Wood Pigeon	LC	3
Columbiformes	Columbidae	<i>Ducula aenea</i>	Green Imperial Pigeon	LC	2
Columbiformes	Columbidae	<i>Ducula badia</i>	Mountain Imperial Pigeon	LC	17
Columbiformes	Columbidae	<i>Macropygia unchall</i>	Barred Cuckoo-Dove	LC	31
Columbiformes	Columbidae	<i>Spilopelia chinensis</i>	Spotted Dove	LC	8
Columbiformes	Columbidae	<i>Streptopelia orientalis</i>	Oriental Turtle Dove	LC	9
Columbiformes	Columbidae	<i>Treron apicauda</i>	Pin-tailed Green Pigeon	LC	13
Columbiformes	Columbidae	<i>Treron bicinctus</i>	Orange-breasted Green Pigeon	LC	1
Columbiformes	Columbidae	<i>Treron sphenurus</i>	Wedge-tailed Green Pigeon	LC	42
Coraciiformes	Alcedinidae	<i>Alcedo atthis</i>	Common Kingfisher	LC	1
Coraciiformes	Alcedinidae	<i>Alcedo hercules</i>	Blyth's Kingfisher	NT	1
Coraciiformes	Alcedinidae	<i>Halcyon coromanda</i>	Ruddy Kingfisher	LC	3
Coraciiformes	Alcedinidae	<i>Halcyon smyrnensis</i>	White-throated Kingfisher	LC	4
Coraciiformes	Alcedinidae	<i>Megaceryle lugubris</i>	Crested Kingfisher	LC	1
Coraciiformes	Bucerotidae	<i>Aceros nipalensis</i>	Rufous-necked Hornbill	VU	2
Coraciiformes	Cerylidae	<i>Ceryle rudis</i>	Pied Kingfisher	LC	2
Coraciiformes	Meropidae	<i>Nyctyornis athertoni</i>	Blue-bearded Bee-eater	LC	2
Cuculiformes	Cuculidae	<i>Cacomantis merulinus</i>	Plaintive Cuckoo	LC	7
Cuculiformes	Cuculidae	<i>Cacomantis sonneratii</i>	Banded Bay Cuckoo	LC	2
Cuculiformes	Cuculidae	<i>Centropus bengalensis</i>	Lesser Coucal	LC	7
Cuculiformes	Cuculidae	<i>Centropus sinensis</i>	Greater Coucal	LC	1
Cuculiformes	Cuculidae	<i>Clamator coromandus</i>	Chestnut-winged Cuckoo	LC	5
Cuculiformes	Cuculidae	<i>Cuculus canorus</i>	Common Cuckoo	LC	23
Cuculiformes	Cuculidae	<i>Cuculus micropterus</i>	Indian Cuckoo	LC	61

Cuculiformes	Cuculidae	<i>Cuculus poliocephalus</i>	Lesser Cuckoo	LC	48
Cuculiformes	Cuculidae	<i>Cuculus saturatus</i>	Himalayan Cuckoo	LC	27
Cuculiformes	Cuculidae	<i>Eudynamys scolopaceus</i>	Asian Koel	LC	1
Cuculiformes	Cuculidae	<i>Hierococcyx nisicolor</i>	Hodgson's Hawk-Cuckoo	LC	16
Cuculiformes	Cuculidae	<i>Hierococcyx sparveroides</i>	Large Hawk-Cuckoo	LC	68
Cuculiformes	Cuculidae	<i>Phaenicophaeus tristis</i>	Green-billed Malkoha	LC	2
Cuculiformes	Cuculidae	<i>Surniculus dicruroides</i>	Fork-tailed Drongo-Cuckoo	LC	41
Falconiformes	Falconidae	<i>Falco subbuteo</i>	Eurasian Hobby	LC	1
Falconiformes	Falconidae	<i>Falco tinnunculus</i>	Common Kestrel	LC	1
Galliformes	Phasianidae	<i>Arborophila mandellii</i>	Chestnut-breasted Partridge	VU	9
Galliformes	Phasianidae	<i>Arborophila rufogularis</i>	Rufous-throated Partridge	LC	13
Galliformes	Phasianidae	<i>Arborophila torqueola</i>	Hill Partridge	LC	32
Galliformes	Phasianidae	<i>Bambusicola fytchii</i>	Mountain Bamboo Partridge	LC	1
Galliformes	Phasianidae	<i>Lophophorus impejanus</i>	Himalayan Monal	LC	1
Galliformes	Phasianidae	<i>Lophura leucomelanos</i>	Kalij Pheasant	LC	1
Galliformes	Phasianidae	<i>Polyplectron bicalcaratum</i>	Grey Peacock-Pheasant	LC	3
Galliformes	Phasianidae	<i>Tragopan blythii</i>	Blyth's Tragopan	VU	2
Galliformes	Phasianidae	<i>Tragopan temminckii</i>	Temminck's Tragopan	LC	1
Gruiformes	Rallidae	<i>Porzana bicolor</i>	Black-tailed Crane	LC	1
Passeriformes	Aegithalidae	<i>Aegithalos concinnus</i>	Black-throated Bushtit	LC	12
Passeriformes	Aegithalidae	<i>Aegithalos iouschistos</i>	Rufous-fronted Bushtit	LC	1
Passeriformes	Aegithinidae	<i>Aegithina tiphia</i>	Common Iora	LC	3
Passeriformes	Campephagidae	<i>Coracina macei</i>	Large Cuckooshrike	LC	2
Passeriformes	Campephagidae	<i>Coracina melaschistos</i>	Black-winged Cuckooshrike	LC	30
Passeriformes	Campephagidae	<i>Pericrocotus brevirostris</i>	Short-billed Minivet	LC	25
Passeriformes	Campephagidae	<i>Pericrocotus ethologus</i>	Long-tailed Minivet	LC	2
Passeriformes	Campephagidae	<i>Pericrocotus roseus</i>	Rosy Minivet	LC	3
Passeriformes	Campephagidae	<i>Pericrocotus solaris</i>	Grey-chinned Minivet	LC	10

Passeriformes	Campephagidae	<i>Pericrocotus speciosus</i>	Scarlet Minivet	LC	24
Passeriformes	Certhiidae	<i>Certhia discolor</i>	Sikkim Treecreeper	LC	4
Passeriformes	Certhiidae	<i>Certhia hodgsoni</i>	Hodgson's Treecreeper	LC	1
Passeriformes	Certhiidae	<i>Certhia nipalensis</i>	Rusty-flanked Treecreeper	LC	1
Passeriformes	Cettiidae	<i>Abroscopus albogularis</i>	Rufous-faced Warbler	LC	29
Passeriformes	Cettiidae	<i>Abroscopus schisticeps</i>	Black-faced Warbler	LC	15
Passeriformes	Cettiidae	<i>Abroscopus superciliaris</i>	Yellow-bellied Warbler	LC	14
Passeriformes	Cettiidae	<i>Cettia brunnifrons</i>	Grey-sided Bush Warbler	LC	9
Passeriformes	Cettiidae	<i>Cettia castaneocoronata</i>	Chestnut-headed Tesia	LC	22
Passeriformes	Cettiidae	<i>Cettia major</i>	Chestnut-crowned Bush Warbler	LC	1
Passeriformes	Cettiidae	<i>Horornis brunnescens</i>	Hume's Bush Warbler	LC	9
Passeriformes	Cettiidae	<i>Horornis fortipes</i>	Brown-flanked Bush Warbler	LC	37
Passeriformes	Cettiidae	<i>Phyllergates cuculatus</i>	Mountain Tailorbird	LC	33
Passeriformes	Cettiidae	<i>Tesia cyaniventer</i>	Grey-bellied Tesia	LC	28
Passeriformes	Cettiidae	<i>Tesia olivea</i>	Slaty-bellied Tesia	LC	15
Passeriformes	Cettiidae	<i>Tickellia hodgsoni</i>	Broad-billed Warbler	LC	10
Passeriformes	Chloropseidae	<i>Chloropsis aurifrons</i>	Golden-fronted Leafbird	LC	1
Passeriformes	Chloropseidae	<i>Chloropsis cochinchinensis</i>	Blue-winged Leafbird	LC	1
Passeriformes	Chloropseidae	<i>Chloropsis hardwickii</i>	Orange-bellied Leafbird	LC	20
Passeriformes	Cinclidae	<i>Cinclus pallasii</i>	Brown Dipper	LC	2
Passeriformes	Cisticolidae	<i>Cisticola exilis</i>	Golden-headed Cisticola	LC	5
Passeriformes	Cisticolidae	<i>Orthotomus sutorius</i>	Common Tailorbird	LC	25
Passeriformes	Cisticolidae	<i>Prinia atrogularis</i>	Black-throated Prinia	LC	10
Passeriformes	Cisticolidae	<i>Prinia crinigera</i>	Striated Prinia	LC	1
Passeriformes	Cisticolidae	<i>Prinia flaviventris</i>	Yellow-bellied Prinia	LC	15
Passeriformes	Cisticolidae	<i>Prinia gracilis</i>	Graceful Prinia	LC	5
Passeriformes	Cisticolidae	<i>Prinia hodgsonii</i>	Grey-breasted Prinia	LC	2
Passeriformes	Cisticolidae	<i>Prinia inornata</i>	Plain Prinia	LC	2

Passeriformes	Corvidae	<i>Cissa chinensis</i>	Common Green Magpie	LC	5
Passeriformes	Corvidae	<i>Corvus leuallantii</i>	Eastern Jungle Crow	LC	16
Passeriformes	Corvidae	<i>Corvus macrorhynchos</i>	Large-billed Crow	LC	19
Passeriformes	Corvidae	<i>Dendrocitta formosae</i>	Grey Treepie	LC	33
Passeriformes	Corvidae	<i>Dendrocitta frontalis</i>	Collared Treepie	LC	1
Passeriformes	Corvidae	<i>Dendrocitta vagabunda</i>	Rufous Treepie	LC	1
Passeriformes	Corvidae	<i>Garrulus glandarius</i>	Eurasian Jay	LC	5
Passeriformes	Corvidae	<i>Nucifraga caryocatactes</i>	Spotted Nutcracker	LC	9
Passeriformes	Corvidae	<i>Pyrrhocorax pyrrhocorax</i>	Red-billed Chough	LC	2
Passeriformes	Corvidae	<i>Urocissa flavirostris</i>	Yellow-billed Blue Magpie	LC	12
Passeriformes	Dicaeidae	<i>Dicaeum ignipectus</i>	Fire-breasted Flowerpecker	LC	38
Passeriformes	Dicaeidae	<i>Dicaeum melanoxanthum</i>	Yellow-bellied Flowerpecker	LC	3
Passeriformes	Dicaeidae	<i>Dicaeum minullum</i>	Plain Flowerpecker	LC	8
Passeriformes	Dicruridae	<i>Dicrurus aeneus</i>	Bronzed Drongo	LC	17
Passeriformes	Dicruridae	<i>Dicrurus hottentottus</i>	Hair-crested Drongo	LC	23
Passeriformes	Dicruridae	<i>Dicrurus leucophaeus</i>	Ashy Drongo	LC	69
Passeriformes	Dicruridae	<i>Dicrurus macrocercus</i>	Black Drongo	LC	1
Passeriformes	Dicruridae	<i>Dicrurus paradiseus</i>	Greater Racket-tailed Drongo	LC	4
Passeriformes	Dicruridae	<i>Dicrurus remifer</i>	Lesser Racket-tailed Drongo	LC	6
Passeriformes	Elachuridae	<i>Elachura formosa</i>	Spotted Elachura	LC	6
Passeriformes	Estrildidae	<i>Lonchura atricapilla</i>	Chestnut Munia	LC	3
Passeriformes	Estrildidae	<i>Lonchura striata</i>	White-rumped Munia	LC	2
Passeriformes	Eurylaimidae	<i>Psarisomus dalhousiae</i>	Long-tailed Broadbill	LC	4
Passeriformes	Fringillidae	<i>Carpodacus edwardsii</i>	Dark-rumped Rosefinch	LC	1
Passeriformes	Fringillidae	<i>Carpodacus puniceus</i>	Red-fronted Rosefinch	LC	1
Passeriformes	Fringillidae	<i>Carpodacus sipahi</i>	Scarlet Finch	LC	11
Passeriformes	Fringillidae	<i>Carpodacus thura</i>	Himalayan White-browed Rosefinch	LC	7
Passeriformes	Fringillidae	<i>Chloris spinoides</i>	Yellow-breasted Greenfinch	LC	14

Passeriformes	Fringillidae	<i>Leucosticte nemoricola</i>	Plain Mountain Finch	LC	4
Passeriformes	Fringillidae	<i>Mycerobas melanozanthos</i>	Spot-winged Grosbeak	LC	3
Passeriformes	Fringillidae	<i>Procarduelis nipalensis</i>	Dark-breasted Rosefinch	LC	7
Passeriformes	Fringillidae	<i>Pyrrhoptes epauletta</i>	Golden-naped Finch	LC	6
Passeriformes	Fringillidae	<i>Pyrrhula erythrocephala</i>	Red-headed Bullfinch	LC	2
Passeriformes	Fringillidae	<i>Pyrrhula nipalensis</i>	Brown Bullfinch	LC	18
Passeriformes	Hirundinidae	<i>Delichon dasypus</i>	Asian House Martin	LC	6
Passeriformes	Hirundinidae	<i>Delichon nipalense</i>	Nepal House Martin	LC	5
Passeriformes	Hirundinidae	<i>Hirundo rustica</i>	Barn Swallow	LC	1
Passeriformes	Hirundinidae	<i>Riparia chinensis</i>	Grey-throated Martin	LC	1
Passeriformes	Laniidae	<i>Lanius schach</i>	Long-tailed Shrike	LC	2
Passeriformes	Laniidae	<i>Lanius tephronotus</i>	Grey-backed Shrike	LC	1
Passeriformes	Leiothrichidae	<i>Actinodura egertoni</i>	Rusty-fronted Barwing	LC	28
Passeriformes	Leiothrichidae	<i>Actinodura waldeni</i>	Streak-throated Barwing	LC	14
Passeriformes	Leiothrichidae	<i>Cutia nipalensis</i>	Himalayan Cutia	LC	12
Passeriformes	Leiothrichidae	<i>Garrulax caerulatus</i>	Grey-sided Laughingthrush	LC	20
Passeriformes	Leiothrichidae	<i>Garrulax leucolophus</i>	White-crested Laughingthrush	LC	36
Passeriformes	Leiothrichidae	<i>Garrulax ocellatus</i>	Spotted Laughingthrush	LC	10
Passeriformes	Leiothrichidae	<i>Garrulax pectoralis</i>	Greater Necklaced Laughingthrush	LC	15
Passeriformes	Leiothrichidae	<i>Garrulax ruficollis</i>	Rufous-necked Laughingthrush	LC	4
Passeriformes	Leiothrichidae	<i>Garrulax rufogularis</i>	Rufous-chinned Laughingthrush	LC	1
Passeriformes	Leiothrichidae	<i>Garrulax striatus</i>	Striated Laughingthrush	LC	57
Passeriformes	Leiothrichidae	<i>Heterophasia annectans</i>	Rufous-backed Sibia	LC	10
Passeriformes	Leiothrichidae	<i>Heterophasia capistrata</i>	Rufous Sibia	LC	2
Passeriformes	Leiothrichidae	<i>Heterophasia picaoides</i>	Long-tailed Sibia	LC	6
Passeriformes	Leiothrichidae	<i>Heterophasia pulchella</i>	Beautiful Sibia	LC	61
Passeriformes	Leiothrichidae	<i>Leiothrix argentauris</i>	Silver-eared Mesia	LC	43
Passeriformes	Leiothrichidae	<i>Leiothrix lutea</i>	Red-billed Leiothrix	LC	26

Passeriformes	Leiothrichidae	<i>Liocichla bugunorum</i>	Bugun Liocichla	VU	1
Passeriformes	Leiothrichidae	<i>Liocichla phoenicea</i>	Red-faced Liocichla	LC	13
Passeriformes	Leiothrichidae	<i>Minla cyanouroptera</i>	Blue-winged Minla	LC	23
Passeriformes	Leiothrichidae	<i>Minla ignotincta</i>	Red-tailed Minla	LC	23
Passeriformes	Leiothrichidae	<i>Minla strigula</i>	Bar-throated Minla	LC	21
Passeriformes	Leiothrichidae	<i>Trochalopteron affine</i>	Black-faced Laughingthrush	LC	18
Passeriformes	Leiothrichidae	<i>Trochalopteron erythrocephalum</i>	Chestnut-crowned Laughingthrush	LC	42
Passeriformes	Leiothrichidae	<i>Trochalopteron imbricatum</i>	Bhutan Laughingthrush	LC	10
Passeriformes	Leiothrichidae	<i>Trochalopteron squamatum</i>	Blue-winged Laughingthrush	LC	14
Passeriformes	Leiothrichidae	<i>Trochalopteron subunicolor</i>	Scaly Laughingthrush	LC	3
Passeriformes	Leiothrichidae	<i>Turdoides earlei</i>	Striated Babbler	LC	3
Passeriformes	Locustellidae	<i>Locustella luteoventris</i>	Brown Bush Warbler	LC	5
Passeriformes	Locustellidae	<i>Locustella mandelli</i>	Russet Bush Warbler	LC	4
Passeriformes	Monarchidae	<i>Hypothymis azurea</i>	Black-naped Monarch	LC	8
Passeriformes	Monarchidae	<i>Terpsiphone paradis</i>	Indian Paradise Flycatcher	LC	14
Passeriformes	Motacillidae	<i>Anthus hodgsoni</i>	Olive-backed Pipit	LC	11
Passeriformes	Motacillidae	<i>Anthus roseatus</i>	Rosy Pipit	LC	7
Passeriformes	Motacillidae	<i>Anthus rufulus</i>	Paddyfield Pipit	LC	1
Passeriformes	Motacillidae	<i>Motacilla alba</i>	White Wagtail	LC	3
Passeriformes	Muscicapidae	<i>Anthipes monileger</i>	White-gorgeted Flycatcher	LC	19
Passeriformes	Muscicapidae	<i>Brachypteryx hyperythra</i>	Rusty-bellied Shortwing	NT	6
Passeriformes	Muscicapidae	<i>Brachypteryx leucophris</i>	Lesser Shortwing	LC	22
Passeriformes	Muscicapidae	<i>Brachypteryx montana</i>	White-browed Shortwing	LC	16
Passeriformes	Muscicapidae	<i>Cinclidium frontale</i>	Blue-fronted Robin	LC	8
Passeriformes	Muscicapidae	<i>Copsychus malabaricus</i>	White-rumped Shama	LC	13
Passeriformes	Muscicapidae	<i>Copsychus saularis</i>	Oriental Magpie-Robin	LC	5
Passeriformes	Muscicapidae	<i>Cyornis banyumas</i>	Hill Blue Flycatcher	LC	4
Passeriformes	Muscicapidae	<i>Cyornis concretus</i>	White-tailed Flycatcher	LC	1

Passeriformes	Muscicapidae	<i>Cyornis magnirostris</i>	Large Blue Flycatcher	LC	11
Passeriformes	Muscicapidae	<i>Cyornis poliogenys</i>	Pale-chinned Blue Flycatcher	LC	5
Passeriformes	Muscicapidae	<i>Cyornis rubeculoides</i>	Blue-throated Blue Flycatcher	LC	12
Passeriformes	Muscicapidae	<i>Cyornis unicolor</i>	Pale Blue Flycatcher	LC	31
Passeriformes	Muscicapidae	<i>Enicurus immaculatus</i>	Black-backed Forktail	LC	1
Passeriformes	Muscicapidae	<i>Enicurus maculatus</i>	Spotted Forktail	LC	1
Passeriformes	Muscicapidae	<i>Enicurus schistaceus</i>	Slaty-backed Forktail	LC	1
Passeriformes	Muscicapidae	<i>Eumyias thalassinus</i>	Verditer Flycatcher	LC	54
Passeriformes	Muscicapidae	<i>Ficedula hyperythra</i>	Snowy-browed Flycatcher	LC	1
Passeriformes	Muscicapidae	<i>Ficedula sapphira</i>	Sapphire Flycatcher	LC	4
Passeriformes	Muscicapidae	<i>Ficedula strophciata</i>	Rufous-gorgeted Flycatcher	LC	5
Passeriformes	Muscicapidae	<i>Ficedula superciliaris</i>	Ultramarine Flycatcher	LC	3
Passeriformes	Muscicapidae	<i>Ficedula tricolor</i>	Slaty-blue Flycatcher	LC	7
Passeriformes	Muscicapidae	<i>Ficedula westermanni</i>	Little Pied Flycatcher	LC	5
Passeriformes	Muscicapidae	<i>Heteroxenicus stellatus</i>	Gould's Shortwing	LC	2
Passeriformes	Muscicapidae	<i>Larvivora brunnea</i>	Indian Blue Robin	LC	1
Passeriformes	Muscicapidae	<i>Monticola cinclorhynchus</i>	Blue-capped Rock Thrush	LC	4
Passeriformes	Muscicapidae	<i>Monticola rufiventris</i>	Chestnut-bellied Rock Thrush	LC	6
Passeriformes	Muscicapidae	<i>Muscicapa ferruginea</i>	Ferruginous Flycatcher	LC	4
Passeriformes	Muscicapidae	<i>Muscicapa muttui</i>	Brown-breasted Flycatcher	LC	1
Passeriformes	Muscicapidae	<i>Muscicapa sibirica</i>	Dark-sided Flycatcher	LC	14
Passeriformes	Muscicapidae	<i>Muscicapella hodgsoni</i>	Pygmy Flycatcher	LC	2
Passeriformes	Muscicapidae	<i>Myiomela leucura</i>	White-tailed Robin	LC	16
Passeriformes	Muscicapidae	<i>Niltava grandis</i>	Large Niltava	LC	25
Passeriformes	Muscicapidae	<i>Niltava macgrigoriae</i>	Small Niltava	LC	38
Passeriformes	Muscicapidae	<i>Niltava sundara</i>	Rufous-bellied Niltava	LC	12
Passeriformes	Muscicapidae	<i>Phoenicurus frontalis</i>	Blue-fronted Redstart	LC	9
Passeriformes	Muscicapidae	<i>Phoenicurus fuliginosus</i>	Plumbeous Water Redstart	LC	3

Passeriformes	Muscicapidae	<i>Phoenicurus leucocephalus</i>	White-capped Redstart	LC	7
Passeriformes	Muscicapidae	<i>Saxicola ferreus</i>	Grey Bush Chat	LC	19
Passeriformes	Muscicapidae	<i>Tarsiger chrysaeus</i>	Golden Bush Robin	LC	5
Passeriformes	Muscicapidae	<i>Tarsiger hyperythrus</i>	Rufous-breasted Bush Robin	LC	2
Passeriformes	Muscicapidae	<i>Tarsiger rufilatus</i>	Himalayan Bluetail	LC	2
Passeriformes	Nectariniidae	<i>Aethopyga gouldiae</i>	Mrs. Gould's Sunbird	LC	15
Passeriformes	Nectariniidae	<i>Aethopyga ignicauda</i>	Fire-tailed Sunbird	LC	17
Passeriformes	Nectariniidae	<i>Aethopyga nipalensis</i>	Green-tailed Sunbird	LC	56
Passeriformes	Nectariniidae	<i>Aethopyga saturata</i>	Black-throated Sunbird	LC	44
Passeriformes	Nectariniidae	<i>Aethopyga siparaja</i>	Crimson Sunbird	LC	5
Passeriformes	Nectariniidae	<i>Arachnothera longirostra</i>	Little Spiderhunter	LC	7
Passeriformes	Nectariniidae	<i>Arachnothera magna</i>	Streaked Spiderhunter	LC	51
Passeriformes	Nectariniidae	<i>Chalcoparia singalensis</i>	Ruby-cheeked Sunbird	LC	1
Passeriformes	Oriolidae	<i>Oriolus traillii</i>	Maroon Oriole	LC	33
Passeriformes	Oriolidae	<i>Oriolus xanthornus</i>	Black-hooded Oriole	LC	6
Passeriformes	Paridae	<i>Lophophanes dichrous</i>	Grey Crested Tit	LC	1
Passeriformes	Paridae	<i>Machlolophus spilonotus</i>	Yellow-cheeked Tit	LC	25
Passeriformes	Paridae	<i>Melanochlora sultanea</i>	Sultan Tit	LC	9
Passeriformes	Paridae	<i>Parus cinereus</i>	Cinereous Tit	LC	1
Passeriformes	Paridae	<i>Parus monticolus</i>	Green-backed Tit	LC	21
Passeriformes	Paridae	<i>Periparus ater</i>	Coal Tit	LC	5
Passeriformes	Paridae	<i>Periparus rubidiventris</i>	Rufous-vented Tit	LC	3
Passeriformes	Paridae	<i>Sylviparus modestus</i>	Yellow-browed Tit	LC	12
Passeriformes	Passeridae	<i>Passer domesticus</i>	House Sparrow	LC	3
Passeriformes	Passeridae	<i>Passer montanus</i>	Eurasian Tree Sparrow	LC	8
Passeriformes	Passeridae	<i>Passer rutilans</i>	Russet Sparrow	LC	7
Passeriformes	Pellorneidae	<i>Alcippe castaneiceps</i>	Rufous-winged Fulvetta	LC	11
Passeriformes	Pellorneidae	<i>Alcippe cinerea</i>	Yellow-throated Fulvetta	LC	23

Passeriformes	Pellorneidae	<i>Alcippe nipalensis</i>	Nepal Fulvetta	LC	47
Passeriformes	Pellorneidae	<i>Alcippe rufogularis</i>	Rufous-throated Fulvetta	LC	4
Passeriformes	Pellorneidae	<i>Gampsorhynchus rufulus</i>	White-hooded Babbler	LC	1
Passeriformes	Pellorneidae	<i>Laticilla cinerascens</i>	Swamp Prinia	NT	3
Passeriformes	Pellorneidae	<i>Napothera epilepidota</i>	Eyebrowed Wren-Babbler	LC	4
Passeriformes	Pellorneidae	<i>Pellorneum albiventre</i>	Spot-throated Babbler	LC	5
Passeriformes	Pellorneidae	<i>Pellorneum palustre</i>	Marsh Babbler	VU	4
Passeriformes	Pellorneidae	<i>Pellorneum ruficeps</i>	Puff-throated Babbler	LC	9
Passeriformes	Pellorneidae	<i>Pellorneum tickelli</i>	Buff-breasted Babbler	LC	9
Passeriformes	Pellorneidae	<i>Rimator malacoptilus</i>	Long-billed Wren-Babbler	LC	7
Passeriformes	Phylloscopidae	<i>Phylloscopus affinis</i>	Tickell's Leaf Warbler	LC	1
Passeriformes	Phylloscopidae	<i>Phylloscopus cantator</i>	Yellow-vented Warbler	LC	5
Passeriformes	Phylloscopidae	<i>Phylloscopus chloronotus</i>	Lemon-rumped Warbler	LC	4
Passeriformes	Phylloscopidae	<i>Phylloscopus maculipennis</i>	Ashy-throated Warbler	LC	13
Passeriformes	Phylloscopidae	<i>Phylloscopus magnirostris</i>	Large-billed Leaf Warbler	LC	20
Passeriformes	Phylloscopidae	<i>Phylloscopus pulcher</i>	Buff-barred Warbler	LC	7
Passeriformes	Phylloscopidae	<i>Phylloscopus reguloides</i>	Blyth's Leaf Warbler	LC	62
Passeriformes	Phylloscopidae	<i>Phylloscopus trochiloides</i>	Greenish Warbler	LC	10
Passeriformes	Phylloscopidae	<i>Phylloscopus xanthoschistos</i>	Grey-hooded Warbler	LC	33
Passeriformes	Phylloscopidae	<i>Seicercus affinis</i>	White-spectacled Warbler	LC	7
Passeriformes	Phylloscopidae	<i>Seicercus castaniceps</i>	Chestnut-crowned Warbler	LC	25
Passeriformes	Phylloscopidae	<i>Seicercus poliogenys</i>	Grey-cheeked Warbler	LC	36
Passeriformes	Phylloscopidae	<i>Seicercus tephrocephalus</i>	Grey-crowned Warbler	LC	7
Passeriformes	Phylloscopidae	<i>Seicercus whistleri</i>	Whistler's Warbler	LC	37
Passeriformes	Pittidae	<i>Hydrornis nipalensis</i>	Blue-naped Pitta	LC	5
Passeriformes	Pittidae	<i>Pitta sordida</i>	Hooded Pitta	LC	2
Passeriformes	Ploceidae	<i>Ploceus manyar</i>	Streaked Weaver	LC	3
Passeriformes	Pnoepygidae	<i>Pnoepyga albiventer</i>	Scaly-breasted Wren-babbler	LC	2

Passeriformes	Pnoepygidae	<i>Pnoepyga pusilla</i>	Pygmy Wren-babbler	LC	21
Passeriformes	Prunellidae	<i>Prunella collaris</i>	Alpine Accentor	LC	4
Passeriformes	Prunellidae	<i>Prunella strophciata</i>	Rufous-breasted Accentor	LC	2
Passeriformes	Pycnonotidae	<i>Alophoixus flaveolus</i>	White-throated Bulbul	LC	26
Passeriformes	Pycnonotidae	<i>Hemixos flava</i>	Ashy Bulbul	LC	9
Passeriformes	Pycnonotidae	<i>Hypsipetes leucocephalus</i>	Black Bulbul	LC	71
Passeriformes	Pycnonotidae	<i>Ixos mccllellandii</i>	Mountain Bulbul	LC	15
Passeriformes	Pycnonotidae	<i>Pycnonotus cafer</i>	Red-vented Bulbul	LC	42
Passeriformes	Pycnonotidae	<i>Pycnonotus flavescens</i>	Flavescent Bulbul	LC	4
Passeriformes	Pycnonotidae	<i>Pycnonotus flaviventris</i>	Black-crested Bulbul	LC	1
Passeriformes	Pycnonotidae	<i>Pycnonotus jocosus</i>	Red-whiskered Bulbul	LC	30
Passeriformes	Pycnonotidae	<i>Pycnonotus striatus</i>	Striated Bulbul	LC	30
Passeriformes	Rhipiduridae	<i>Rhipidura albicollis</i>	White-throated Fantail	LC	45
Passeriformes	Sittidae	<i>Sitta cinnamoventris</i>	Chestnut-bellied Nuthatch	LC	3
Passeriformes	Sittidae	<i>Sitta formosa</i>	Beautiful Nuthatch	VU	1
Passeriformes	Sittidae	<i>Sitta himalayensis</i>	White-tailed Nuthatch	LC	13
Passeriformes	Stenostiridae	<i>Chelidorphynx hypoxantha</i>	Yellow-bellied Fantail	LC	6
Passeriformes	Stenostiridae	<i>Culicicapa ceylonensis</i>	Grey-headed Canary-flycatcher	LC	53
Passeriformes	Sturnidae	<i>Acridotheres fuscus</i>	Jungle Myna	LC	5
Passeriformes	Sturnidae	<i>Acridotheres grandis</i>	Great Myna	LC	1
Passeriformes	Sturnidae	<i>Acridotheres tristis</i>	Common Myna	LC	6
Passeriformes	Sturnidae	<i>Gracupica contra</i>	Pied Myna	LC	1
Passeriformes	Sturnidae	<i>Saroglossa spiloptera</i>	Spot-winged Starling	LC	1
Passeriformes	Sturnidae	<i>Sturnia malabarica</i>	Chestnut-tailed Starling	LC	10
Passeriformes	Sylviidae	<i>Cholornis unicolor</i>	Brown Parrotbill	LC	2
Passeriformes	Sylviidae	<i>Chrysomma altirostre</i>	Jerdon's Babbler	VU	9
Passeriformes	Sylviidae	<i>Fulvetta ludlowi</i>	Brown-throated Fulvetta	LC	11
Passeriformes	Sylviidae	<i>Fulvetta manipurensis</i>	Manipur Fulvetta	LC	10

Passeriformes	Sylviidae	<i>Lioparus chrysotis</i>	Golden-breasted Fulvetta	LC	12
Passeriformes	Sylviidae	<i>Myzornis pyrrhoura</i>	Fire-tailed Myzornis	LC	1
Passeriformes	Sylviidae	<i>Paradoxornis flavirostris</i>	Black-breasted Parrotbill	VU	10
Passeriformes	Sylviidae	<i>Paradoxornis guttaticollis</i>	Spot-breasted Parrotbill	LC	2
Passeriformes	Sylviidae	<i>Psittiparus bakeri</i>	Rufous-headed Parrotbill	LC	4
Passeriformes	Sylviidae	<i>Psittiparus gularis</i>	Grey-headed Parrotbill	LC	1
Passeriformes	Sylviidae	<i>Psittiparus ruficeps</i>	White-breasted Parrotbill	LC	4
Passeriformes	Sylviidae	<i>Suthora nipalensis</i>	Black-throated Parrotbill	LC	12
Passeriformes	Tephrodornithidae	<i>Hemipus picatus</i>	Bar-winged Flycatcher-shrike	LC	4
Passeriformes	Tephrodornithidae	<i>Tephrodornis virgatus</i>	Large Woodshrike	LC	2
Passeriformes	Timaliidae	<i>Macronus gularis</i>	Pin-striped Tit-Babbler	LC	15
Passeriformes	Timaliidae	<i>Pomatorhinus ferruginosus</i>	Coral-billed Scimitar Babbler	LC	5
Passeriformes	Timaliidae	<i>Pomatorhinus ochraceiceps</i>	Red-billed Scimitar Babbler	LC	4
Passeriformes	Timaliidae	<i>Pomatorhinus ruficollis</i>	Streak-breasted Scimitar Babbler	LC	34
Passeriformes	Timaliidae	<i>Pomatorhinus schisticeps</i>	White-browed Scimitar Babbler	LC	4
Passeriformes	Timaliidae	<i>Pomatorhinus superciliaris</i>	Slender-billed Scimitar Babbler	LC	6
Passeriformes	Timaliidae	<i>Spelaeornis badeigularis</i>	Rusty-throated Wren-Babbler	VU	8
Passeriformes	Timaliidae	<i>Spelaeornis caudatus</i>	Rufous-throated Wren-Babbler	NT	7
Passeriformes	Timaliidae	<i>Spelaeornis troglodytoides</i>	Bar-winged Wren-Babbler	LC	2
Passeriformes	Timaliidae	<i>Sphenocichla humei</i>	Sikkim Wedge-billed Babbler	NT	1
Passeriformes	Timaliidae	<i>Sphenocichla roberti</i>	Cachar Wedge-billed Babbler	NT	9
Passeriformes	Timaliidae	<i>Stachyridopsis ambigua</i>	Buff-chested Babbler	LC	10
Passeriformes	Timaliidae	<i>Stachyridopsis chrysaea</i>	Golden Babbler	LC	51
Passeriformes	Timaliidae	<i>Stachyridopsis ruficeps</i>	Rufous-capped Babbler	LC	33
Passeriformes	Timaliidae	<i>Stachyris nigriceps</i>	Grey-throated Babbler	LC	29
Passeriformes	Timaliidae	<i>Timalia pileata</i>	Chestnut-capped Babbler	LC	9
Passeriformes	Troglodytidae	<i>Troglodytes troglodytes</i>	Eurasian Wren	LC	3
Passeriformes	Turdidae	<i>Cochoa purpurea</i>	Purple Cochoa	LC	4

Passeriformes	Turdidae	<i>Cochoa viridis</i>	Green Cochoa	LC	8
Passeriformes	Turdidae	<i>Grandala coelicolor</i>	Grandala	LC	2
Passeriformes	Turdidae	<i>Myophonus caeruleus</i>	Blue Whistling Thrush	LC	14
Passeriformes	Turdidae	<i>Turdus albocinctus</i>	White-collared Blackbird	LC	10
Passeriformes	Turdidae	<i>Turdus atrogularis</i>	Black-throated Thrush	LC	1
Passeriformes	Turdidae	<i>Turdus boulboul</i>	Grey-winged Blackbird	LC	4
Passeriformes	Turdidae	<i>Turdus maximus</i>	Tibetan Blackbird	LC	1
Passeriformes	Turdidae	<i>Turdus unicolor</i>	Tickell's Thrush	LC	2
Passeriformes	Turdidae	<i>Zoothera mollissima</i>	Alpine Thrush	LC	2
Passeriformes	Vireonidae	<i>Erpornis zantholeuca</i>	White-bellied Erpornis	LC	4
Passeriformes	Vireonidae	<i>Pteruthius aeralatus</i>	Blyth's Shrike-babbler	LC	20
Passeriformes	Vireonidae	<i>Pteruthius melanotis</i>	Black-eared Shrike-babbler	LC	8
Passeriformes	Vireonidae	<i>Pteruthius rufiventer</i>	Black-headed Shrike-babbler	LC	1
Passeriformes	Vireonidae	<i>Pteruthius xanthochlorus</i>	Green Shrike-babbler	LC	1
Passeriformes	Zosteropidae	<i>Yuhina bakeri</i>	White-naped Yuhina	LC	24
Passeriformes	Zosteropidae	<i>Yuhina castaniceps</i>	Striated Yuhina	LC	25
Passeriformes	Zosteropidae	<i>Yuhina flavicollis</i>	Whiskered Yuhina	LC	44
Passeriformes	Zosteropidae	<i>Yuhina gularis</i>	Stripe-throated Yuhina	LC	35
Passeriformes	Zosteropidae	<i>Yuhina nigrimenta</i>	Black-chinned Yuhina	LC	17
Passeriformes	Zosteropidae	<i>Yuhina occipitalis</i>	Rufous-vented Yuhina	LC	17
Passeriformes	Zosteropidae	<i>Zosterops palpebrosus</i>	Oriental White-eye	LC	38
Pelecaniformes	Ardeidae	<i>Ardea alba</i>	Great Egret	LC	2
Pelecaniformes	Ardeidae	<i>Ardea purpurea</i>	Purple Heron	LC	3
Pelecaniformes	Ardeidae	<i>Bubulcus coromandus</i>	Eastern Cattle Egret	LC	9
Pelecaniformes	Ardeidae	<i>Egretta garzetta</i>	Little Egret	LC	3
Pelecaniformes	Ardeidae	<i>Egretta intermedia</i>	Intermediate Egret	LC	2
Pelecaniformes	Ardeidae	<i>Ixobrychus cinnamomeus</i>	Cinnamon Bittern	LC	2
Pelecaniformes	Ardeidae	<i>Nycticorax nycticorax</i>	Black-crowned Night Heron	LC	1

Pelecaniformes	Pelecanidae	<i>Pelecanus philippensis</i>	Spot-billed Pelican	NT	1
Pelecaniformes	Threskiornithidae	<i>Plegadis falcinellus</i>	Glossy Ibis	LC	1
Piciformes	Megalaimidae	<i>Psilopogon asiaticus</i>	Blue-throated Barbet	LC	54
Piciformes	Megalaimidae	<i>Psilopogon franklinii</i>	Golden-throated Barbet	LC	47
Piciformes	Megalaimidae	<i>Psilopogon virens</i>	Great Barbet	LC	93
Piciformes	Picidae	<i>Blythipicus pyrrhotis</i>	Bay Woodpecker	LC	26
Piciformes	Picidae	<i>Chrysocolaptes guttacristatus</i>	Greater Flameback	LC	1
Piciformes	Picidae	<i>Chrysophlegma flavinucha</i>	Greater Yellownape	LC	8
Piciformes	Picidae	<i>Dendrocopos canicapillus</i>	Grey-capped Pygmy Woodpecker	LC	2
Piciformes	Picidae	<i>Dendrocopos darjellensis</i>	Darjeeling Woodpecker	LC	10
Piciformes	Picidae	<i>Dendrocopos hyperythrus</i>	Rufous-bellied Woodpecker	LC	9
Piciformes	Picidae	<i>Dendrocopos macei</i>	Fulvous-breasted Woodpecker	LC	2
Piciformes	Picidae	<i>Micropternus brachyurus</i>	Rufous Woodpecker	LC	7
Piciformes	Picidae	<i>Picumnus innominatus</i>	Speckled Piculet	LC	1
Piciformes	Picidae	<i>Picus canus</i>	Grey-headed Woodpecker	LC	2
Piciformes	Picidae	<i>Picus chlorolophus</i>	Lesser Yellownape	LC	1
Piciformes	Picidae	<i>Sasia ochracea</i>	White-browed Piculet	LC	2
Psittaciformes	Psittaculidae	<i>Psittacula finschii</i>	Grey-headed Parakeet	NT	4
Strigiformes	Strigidae	<i>Glaucidium brodiei</i>	Collared Owlet	LC	16
Strigiformes	Strigidae	<i>Glaucidium cuculoides</i>	Asian Barred Owlet	LC	7
Suliformes	Phalacrocoracidae	<i>Microcarbo niger</i>	Little Cormorant	LC	5
Trogoniformes	Trogonidae	<i>Harpactes erythrocephalus</i>	Red-headed Trogon	LC	7
Trogoniformes	Trogonidae	<i>Harpactes wardi</i>	Ward's Trogon	NT	5

APPENDIX B: LIST OF CONGENERIC, SYMPATRIC SPECIES PAIRS

The following is the set of congeneric, sympatric sister species. Bold text indicates pairs where both species were detected at a minimum of five points, and hence were included in the analysis.

Species 1

Abroscopus albogularis

Accipiter virgatus

Acridotheres fuscus

Actinodura egertoni

Aegithalos concinnus

Aethopyga nipalensis

Aethopyga saturata

Alcedo hercules

Alcippe castaneiceps

Anthus hodgsoni

Apus leuconyx

Arachnothera longirostra

Arborophila rufogularis

Ardea purpurea

Brachypteryx leucophris

Cacomantis sonneratii

Carpodacus edwardsii

Centropus sinensis

Certhia nipalensis

Cettia brunnifrons

Chloropsis aurifrons

Cochoa viridis

Columba leuconota

Copsychus malabaricus

Coracina melaschistos

Corvus macrorhynchos

Cuculus canorus

Cyornis poliogenys

Delichon dasypus

Species 2

Abroscopus schisticeps

Accipiter badius

Acridotheres grandis

Actinodura waldeni

Aegithalos iouschistos

Aethopyga ignicauda

Aethopyga gouldiae

Alcedo atthis

Alcippe cinerea

Anthus roseatus

Apus nipalensis

Arachnothera magna

Arborophila torqueola

Ardea alba

Brachypteryx hyperythra

Cacomantis merulinus

Carpodacus thura

Centropus bengalensis

Certhia discolor

Cettia major

Chloropsis cochinchinensis

Cochoa purpurea

Columba livia

Copsychus saularis

Coracina macei

Corvus levaillantii

Cuculus saturatus

Cyornis banyumas

Delichon nipalense

Dendrocitta vagabunda
Dendrocopos macei
Dicaeum minullum
Dicrurus hottentottus
Dicrurus leucophaeus
Ducula badia
Egretta intermedia
Enicurus immaculatus
Falco subbuteo
Ficedula tricolor
Ficedula westermanni
Fulvetta ludlowi
Garrulax caerulatus
Garrulax rufogularis
Glaucidium cuculoides
Halcyon coromanda
Harpactes wardi
Heterophasia picaoides
Hierococcyx sparveroides
Horornis brunnescens
Lanius tephronotus
Leiothrix lutea
Liocichla bugunorum
Locustella luteoventris
Lonchura striata
Minla ignotincta
Monticola cinclorhynchus
Muscicapa ferruginea
Niltava macgrigoriae
Oriolus traillii
Paradoxornis flavirostris
Parus monticolus
Passer domesticus
Pellorneum albiventris
Pericrocotus brevirostris
Pericrocotus speciosus
Periparus ater
Phoenicurus fuliginosus
Phylloscopus pulcher
Phylloscopus trochiloides

Dendrocitta frontalis
Dendrocopos hyperythrus
Dicaeum ignipectus
Dicrurus paradiseus
Dicrurus macrocercus
Ducula aenea
Egretta garzetta
Enicurus maculatus
Falco tinnunculus
Ficedula hyperythra
Ficedula superciliaris
Fulvetta manipurensis
Garrulax pectoralis
Garrulax ocellatus
Glaucidium brodiei
Halcyon smyrnensis
Harpactes erythrocephalus
Heterophasia annectans
Hierococcyx nisicolor
Horornis fortipes
Lanius schach
Leiothrix argentea
Liocichla phoenicea
Locustella mandelli
Lonchura atricapilla
Minla strigula
Monticola rufiventris
Muscicapa sibirica
Niltava grandis
Oriolus xanthornus
Paradoxornis guttaticollis
Parus cinereus
Passer montanus
Pellorneum palustre
Pericrocotus ethologus
Pericrocotus roseus
Periparus rubidiventris
Phoenicurus leucocephalus
Phylloscopus maculipennis
Phylloscopus magnirostris

Phylloscopus xanthoschistos

Picus chlorolophus

Pnoepyga pusilla

Pomatorhinus ochraceiceps

Pomatorhinus schisticeps

Prinia crinigera

Prinia inornata

Prunella collaris

Psilopogon franklinii

Pteruthius rufiventer

Pteruthius xanthochlorus

Pycnonotus flavescens

Pycnonotus flaviventris

Pyrrhula nipalensis

Seicercus poliogenys

Sitta cinnamoventris

Stachyridopsis ambigua

Tarsiger rufilatus

Tesia cyaniventer

Tragopan blythii

Treron bicinctus

Trochalopteron erythrocephalum

Trochalopteron squamatum

Turdus albocinctus

Turdus boulboul

Vanellus duvaucelii

Yuhina bakeri**Yuhina occipitalis****Phylloscopus reguloides**

Picus canus

Pnoepyga albiventer

Pomatorhinus ferruginosus

Pomatorhinus ruficollis

Prinia atrogularis

Prinia hodgsonii

Prunella strophiatea

Psilopogon asiaticus

Pteruthius aeralatus

Pteruthius melanotis

Pycnonotus jocosus

Pycnonotus cafer

Pyrrhula erythrocephala

Seicercus affinis

Sitta formosa

Stachyridopsis ruficeps

Tarsiger hyperythrus

Tesia olivea

Tragopan temminckii

Treron apicauda

Trochalopteron affine

Trochalopteron subunicolor

Turdus atrogularis

Turdus unicolor

Vanellus indicus

Yuhina flavicollis**Yuhina gularis**

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Vita

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