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REVIEW ARTICLE

Climate Change Impacts on Himalayan Biodiversity: Evidence-Based Perception and Current Approaches to Evaluate Threats Under Climate Change

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Abstract | Predicting the response of biota to climate change is an active field of research. Advancements in the field of genomics has revolutionized climate change research. Genomic approaches used together with other ecological tools have the potential to identify the population and/or species at higher risk of extinction due to climate change. Himalayan biodiversity has faced drastic impacts of climate change in the past and is predicted to be vulnerable to future climate change. In this review, we provide a scientific evidence-based understanding about the impacts of climate change on Himalayan biodiversity. We summarize reported patterns of climate change in the Himalayas across time scales, their impacts on biodiversity and summarize hypotheses laid out by others to be tested in the future. We restrict our choice of study species to mammals, birds, reptiles and amphibians and discuss the application of an integrated approach using genomics and ecological tools to better understand the consequences of climate change on Himalayan biodiversity.

1 Introduction

Will a species survive a predicted accelerated rate of climate change in the future? The question has intrigued researchers for years and more so now with reports like that stating one of six species are threatened by climate change[1]. Substantial research is focused on identifying the roles of various life-history properties (e.g., dispersal ability, genetic diversity, population responses, phenotypic plasticity, etc.) on adaptation to changing climate. Impact of global climatic fluctuations is not uniform across the globe. High elevation mountains, including the uppermost vegetation limit with permanent glaciers and permafrost, are likely to experience these drastic climatic fluctuations in the past and are also predicted to be vulnerable to future climate change[2,3]. The Himalayas, in particular, are identified as vulnerable as the rate of warming there is estimated to be higher than the global average[4]. The fate of Himalayan biodiversity is expected to be grim based on generalities regarding climate change impacts on the mountains[5]. However, the impacts of climate change on Himalayan biodiversity have not been well-founded. The hypothesis of elevation-dependent warming[3]; hypothesized area loss in montane system, assuming conical shape of mountains, caused by upslope range shift[5]; and assumed temperature constraints of montane species[6] are the bases of such generalized prediction. In this review, we aim to collate scientific evidences on climate change-related studies in the Himalayas to provide a scientific-evidence based perception on the impacts of climate change on the Himalayan biodiversity. Based on evidence from multidisciplinary studies, we review reported patterns of climate change in the Himalayan mountain across timescales, their impacts on biodiversity and summarize hypotheses laid out by other studies to be tested in the future.

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The study of impacts of climate change is incomplete without the knowledge of the evolutionary history of the species or an ecosystem that is experiencing the associated climate. Biodiversity is a result of over 3.5 billion years of evolutionary history on earth. The current knowledge of a species or an ecosystem is often used to predict their persistence through future climate change, but a lot of clues can be drawn from their response to past climate change[7]. The Himalayan mountains are recognized as the most glaciated areas outside of the polar region[8] and during the LGM (Last glacial maxima) the glaciers had advanced several kilometers[9]. Indisputably, the Himalayas are a climatically unstable mountain range with enormous biodiversity[10]. The Himalayan mountains span from low-latitude tropical regions in the southeast to higher latitude temperate northwestern region with differences in climatic history. Furthermore, the inherent climatic heterogeneity of the Himalayan mountains influences the broad assessment of the impacts of climate change on its biodiversity. Most of the phylogenetic studies associate diversification (a key source of biodiversity) in the Himalaya with tectonic uplift and climate[11–14]. A few metanalyses tested the role of past climate on the species richness pattern of the Himalaya[15]. However, a perception of the role of past climatic history on the responses of Himalayan biota to future climate change is absent. To summarize our knowledge on spatial and temporal climatic heterogeneity, we (1) review the current knowledge on the paleoclimatic scenarios for the Himalaya to promote hypothesis-based research and (2) collate studies of future climate change to identify regions of predicted high climatic instability and associated organismal response within regions of the Himalaya. Finally, we recommend integrated approach (using ecological and modern genomic tools) to identify underlying signatures of three well-established fingerprints of climate change. We restrict our choice of study species to mammals, birds, reptiles and amphibians, with a special focus on genetic/genomic consequences of climate change. However, we have also drawn comparison from studies on plants, specifically to compare degree of range shift (a climate change fingerprint discussed in detail for Himalayan mountain).

2 Methods

We used Google Scholar to review published papers on climate change in the Himalaya. Each section had different keyword; for Sect. 3 we used key words like Paleoclimatic history, Himalaya, LGM, Pleistocene, past climate, Himalaya + uplift, etc. Among the search results, we chose to either include reviews/studies that have included both eastern and western. We got many hits for regional studies on climatic history, but they were excluded for the current review as we were interested in the overall pattern. For Sect. 4, we used the following key words: Himalaya, climate change, genetics and/or genomics, range shift, community assembly and phenology (the keywords for three fingerprints of climate change), etc. We did not apply time line filter for our search results for review articles, but for research articles we chose to include studies since the year 2000. For the rest of the sections, we focused mostly on review articles, perspectives and opinions.

One of the objectives of the review was to recommend integrated methods to study climate change; therefore, we did a thorough review of the methods used so far to study climate change impacts. We found species distribution models to be the most popular methods and hence range shift as the most reported signature of climate change. This method was used to model shift in plant invasion, Indian biome, treelines, mammalian and amphibians (refer to Table 1). Only two studies on birds have used long-term empirical data to quantify range shift. Studies on phenology shifts and community composition changes in the Himalaya are still at an early stage of pattern description and mostly focussed on plants.

3 Paleoclimatic History of the Himalaya—A Biological Perspective to Explore Past Climate Change

Climatic fluctuation in the past have shaped the current distribution pattern and intraspecies genetic diversity[16]. Therefore, information on response of a population to past climate change will be of paramount significance for assessment of future climate change responses. The Himalaya is a young mountain fold formed by the collision of the Indian and Eurasian plates, about 50–60 million years ago (mya)[17,18]. This massive landmass had a strong impact on atmospheric circulation, creating complex climatic and biological patterns[19], which also led to the formation of the high-altitude desert, the Tibetan Plateau. After the formation of the Himalayan mountains, repeated climatic fluctuation (glacial-interglacial periods) resulted in the advancement and retreat of glaciers[9].

The reconstruction of quaternary glaciation events in the Himalaya relies on an accurate interpretation of landforms and sediments[20] and has led to many misinterpretations in the past[21].

Table 1 Examples of evolution (range shift, population expansion and divergence) facilitated by past climate in the Himalaya

Species	Elevation range of species	Events of expansion and speciation
Woolly flying squirrel[115]	2400–3400 m, trans Himalayan species	Divergence of east and west trans Himalayan population estimated as 10.8myr
Five bird species[13]	Elevation ranges spanning 1000–5000 m	➢Three species restricted to Tibetan plateau platform showed signatures of expansion around 0.5–0.175 myr ➢Two species with range restricted at the eastern edge of Tibetan plateau showed stable population
Blood pheasant[26]	2500–4500 m, alpine species	➢ Diverged from SE population 1.20 myr ➢ Eastern edge of TP as refugia for quaternary glaciation
Seven passerine families[24]	Subalpine, broad-leafed forest and subtropical Himalaya	Only true boreal species were impacted by Pleistocene
Arunachal macaque[28]	2000–3500 m, alpine forest	➢ Hypothesized to have diverged from high altitude ancestor 1.61 myr ➢ Signatures of population expansion early to mid-Pleistocene
Hot- spring snake[25]	3650–4890 m, trans Himalayan species	➢ Divergence of two lineages hypothesized to be over glacial climate oscillations ➢ Expansion of two lineages around 30 ka, before LGM
Greenish Warbler[23]	Upper elevation limit - 4500 m, breeding range in the treelines of the Himalaya	➢ East and West populations are diverged but has not attained reproductive isolation ➢ The Central Himalayan represents the transitional form
Sikkim pika14	2600–3500 m, alpine species	Diverged from sister species located in NE Himalaya (China) ~ 1.7–0.8 myr
Assamese macaque[27]	200–2750 m, sub-tropical habitat specialists	Predicted post-Pleistocene (10kbp) expansion of habitat and population

Climatic reconstruction studies overall suggest that the pattern and extent of the Himalayan glaciation were limited to ice caps and expanded valley glaciers and were perhaps driven by monsoon patterns, unlike the glaciation event in Europe and North America where the entire landmasses were covered with ice sheets[21,22]. The glaciation was monsoon-influenced and thus the timing, in general, was synchronous in monsoon-fed regions, but the semi-arid regions of the Himalaya were probably in synchrony with the Northern hemisphere ice sheets[23]. In the Himalaya the eastern and southern slopes of the Himalaya receive maximum precipitation during the summer and the north-western Himalaya receive moisture in the form of heavy snow fall during winter. Thus, the glaciation history in these two regions were probably asynchronous.

Studies from the Himalayan region have implicated the role of climatic history on the diversification, distributional limits and species richness patterns of Himalayan biodiversity, but a comprehensive summarization of the patterns driven by past climatic fluctuation is absent for Himalayan biodiversity. Based on some of the phylogeographic studies listed in Table 1, many species have their range restricted to the eastern Himalaya and some wide-ranging species demonstrate genetic and/or morphological divergence between populations in the east and west of the Himalayan arc. Range shifts during climate fluctuations and population size changes are likely to cause fragmentation or connectivity of isolated ranges leading to[24] intraspecific differentiation in species. In the Himalaya, the date of the split between east and west populations has not been investigated but a few studies confirm recent hybridisation at the contact zone located in the Central Himalayan region in Nepal[25]. Similar patterns of hybridisation dating to the late glaciation is suggested for several families of Passerines[26]. [27]Natural hybridization between species from different ecotones (perhaps between east and west Himalaya—a potential contact zone as exemplified by past climate change studies from the region) may be common avenue to increase the evolutionary resilience and rapid adaptation as climate changes in the Himalaya. [28]Hybridization started new adaptation to previously unused food resource in Galapagos by changing beaks in hybrids (cross-island migrant bred with a native species). In a similar way, hybridization can create new adaptive traits in high altitude to cope with climate change.

The estimated timing of historic demographic expansion is often correlated with the climatic events in the past. For some Himalayan fauna, demographic history suggests a pattern perhaps driven by the biogeographic origin of the species. For example, population expansion of the trans-Himalayan snake and blood pheasant, an alpine species, is estimated before the Pliestocene[29,30], whereas for Assamese macaque, a sub-tropical species, demographic expansion is estimated post Pliestocene[31]. The sister species of Assamese macaque, found in higher elevation alpine forest, is estimated to show signatures of population expansion dating early to middle Pleistocene[32]. Thus, based on the correlation of population expansion and the timing of glaciation events, it might be reasonable to hypothesize that the high-altitude fauna experienced Pleistocene glaciation much early compared to their low altitude neighbours as predicted by climatic reconstruction studies[9]. Pleistocene glacial refugia—regions, where organisms took refuge during the glacial advance and retreat during the Pleistocene[33], also appear to have shaped the current species richness pattern. The Himalaya spans lower latitude east to higher latitude in the west with approximately 5° latitudinal increase[34], but the rate of species decline between east to west is much higher than expected by latitude alone[35]. Metanalyses of murids and babblers[15] identified a progressively nested species richness pattern from east to west Himalaya and explained this pattern to be driven by past climate change. However, the authors[15] warn against the simplistic explanation of the single refugia hypothesis as repeated glaciation cycles and multiple refugial expansion might also influence the diversification and hence the species richness pattern.

Overall, the past climatic fluctuations, specifically the Pleistocene, impacted Himalayan biodiversity by facilitating divergence and emergence of Himalayan endemics, (refer to examples in Table 1) and perhaps led to east–west population divergence. The demographic expansion studies suggest older expansion for the high-altitude specialists indicating the timing of Pleistocene glaciation in the Himalaya to be earlier (~30 kbp) than North America and Europe (~20 kbp)[36]. The absence of fossil records from the Pleistocene period of the Himalayas limits our knowledge of species diversity and extinctions during the glacial cycles. Nevertheless, older fossils from the Tibetan plateau suggest the 'out of Tibet' hypothesis for the high-altitude cold-adapted mammals, and the Tibetan plateau is suggested as a training ground for the high-altitude fauna in the neighbouring regions, including the Himalaya[37].

4 Impacts of Contemporary and Predicted Future Climate Change on Himalayan Biodiversity

Direct detection of climate change through glacier melts[38], permafrost temperature regime[39] and trends of surface temperature records[40] are key in detecting the rate of warming in the mountains. Direct assessments of climate change in the Himalayas have implicated the rate of climate change to be region-specific and highly variable, but many reviews have implicated extreme overall impacts on the Himalayan biodiversity[41,42]. These extreme impacts predicted by such models need to be examined in the light of empirical data, which can be challenging to collect and complicated by non-climatic, local or short-term changes. Here, we will summarize scientific evidence of climate change impacts on the Himalayan fauna by examining effects related to climate change (collectively termed as global fingerprints of climate change[43,44]). We will explore three widely accepted global fingerprints of climate change: (a) distributional range shift, (b) community studies related to community shifts and abundances and (c) phenological shifts. Some studies have attempted to characterize evolutionary responses of climate change[45,46] , but the generalisation of the evolutionary pattern associated with climate change still remains unknown. Therefore, for this review, we will discuss potential patterns of evolutionary responses of climate change in the Himalayan fauna based on evidence from the three widely accepted fingerprints of climate change.

4.1 Range Shift

A species range along an altitudinal gradient of a mountain is controlled by multiple biotic and abiotic factors. Climatic change is expected to disrupt both the biotic and abiotic conditions, resulting in a shift of species range. Climate-induced range shift is the most commonly documented fingerprints of climate change and is shown typically through model projections.

Limited studies (outside Himalaya) have followed a stepwise approach of first determining the climatic niche space of the species followed by quantification of niche tracking[47]. Studies describing the importance of biotic factors in climate change-induced shifts are limited[48].

Empirical data on direct evidence of range shift of Himalayan fauna are mostly known from birds in the Eastern Himalaya. For example, two studies from the eastern Himalaya have utilized the occurrence data from 13[49] to 8[50] years for such comparisons. One of the studies[49] found evidence of upslope shift, but the result appeared to depend on the location of birdwatching hotspot. Therefore, the range shift reported here could not be compared with other studies with consistent sampling efforts. Temporally longest comparisons of elevation range (approximately 160 years, between 1849 and 2010) were made of a Himalayan endemic alpine plant[51]. Both the studies with consistent sampling effort across the study area highlighted the range shift to be higher for the group with comparatively lower elevation range ([51] studied elevation range spanning 4000–5500 m and[50] birds within 1000–2000 m elevation range). The authors[50] quantified the impact in terms of survival rate—documenting increased survival at the cold range-edge (at the upper elevation) for the low-elevation range group. Expansion of the range by lower elevation groups at their upper elevation but stability of the range of higher elevation groups identified in both of these studies perhaps needs to be confirmed from other taxa spanning wider elevational ranges. A metanalysis[52] of range shift from 987 montane species across the world also suggests movement of lower elevation species compared to the higher elevation species. Nevertheless, based on circumstantial evidence from these two studies from the Himalaya, lower elevation range groups are in peril compared to higher elevation range, contrary to general expectations.

Studies aimed at predicting range shift of Indian biomes[53,54] indicate the dynamic nature of Himalayan forest ranges. Such shift in forest ranges probably have already started the processes of range shift among birds and large mammals associated with these forest types[50,55–57]. These studies have highlighted the need for maintenance of continuous forests across elevation gradients in the future to aid range shift of forest-dwelling species that are facing the stress of human-induced land-use change in addition to the challenges imposed by climate change. Treeline is reported to have moved 388 ± 80 m upslope in the Indian Himalayas between 1970 and 2006[58]. Although such a significant upslope shift is expected in the Anthropocene, the consequence of “treeline shifts” into the “treeless ecosystems” will certainly modify the ecosystem functions and services and may also lead to the reductions in alpine diversity[59]. Therefore, change in climate and land-use patterns together should be jointly considered while studying the response of forest-dwelling biota to climate change. The interaction between land use change and climate change is ascertained by many studies[60,61] and experts have suggested effective study designs to incorporate these interactions. Additionally, other drivers (eg. species invasion) may also interact and facilitate generalist species, impeding habitat specialists[62]. Cold-adapted species in mountain ecosystems, with an established strong correlation between temperature and elevation, are expected to move upslope or poleward in latitude as climate warms. Contemplating the expectations, niche model-based studies from the Himalaya predicted up slope range shift of alpine specialists, for, e.g., Pikas[63], Snow Leopard and Blue Sheep[64,65]. All the high-altitude species were predicted to contract their range in the future. These studies have perhaps underestimated the rate of range contraction as they have not accounted for dispersal which could drastically reduce the amount of accessible habitat for these species as shown in Frogs[66].

4.2 Species Assemblage

The response of species to climate change is not isolated and is connected through interactions with other members of the community[67]. The impact of past climate change on altering biotic interactions and driving species to extinction or the emergence of new species have been demonstrated with fossil records[68]. A majority of studies on climate change focus on individual species responses like range shift, phenology, physiology, etc. of an organism and typically ignore the impact on the linkages within the ecological network. This failure to include interactions among community members while addressing climate change impacts has been argued to have stemmed from a lack of a strong foundation (both empirical and theoretical)[69]. Attempts to integrate interaction networks are now being made in predicting species distribution models[70].

In the Himalayan scenario, faunal interactions and community response to climate change are yet to receive evidence from empirical data.

Several single system studies from the Himalayas (listed in Table 2) have predicted different rates of altitudinal and latitudinal range shifts indicating that a species does not always respond in synchrony with space and time. A meta-analyses approach, including entire community member and their interactions (like predation, competition, mutualism, etc.) probably can provide insights into the observed asynchrony.

Spatial range shift nevertheless will force species to interact with a new neighbour, perhaps changing the type of interactions—for example, dominant species might no longer be dominant in the new community (as shown[71] through species addition experiments in grassland ecosystem). The dominance of weedy plant species is expected to reorganize the plant community composition in the Himalaya[72]. Certain new members might also have an inhibitory effect (for example, an increase in the predation risks of boreal keystone species[73]) or may lead to competition[74]. Community alteration may disrupt biotic interaction altering the prey–predator spatial congruency as predicted for endangered flagship predator of the Himalayan high altitude, Snow leopards[64]. Species in the same a guild, having similar resource requirements might strongly oppose an invasion of the new members (competitive exclusion). Homogenization of habitat may promote range expansion of generalists which may ultimately reduce competition for them[75]. Nordberg and Schwarzkopf[76D], using an enclosure experiment in western North America, described an interconnected nature of declining snowfall on plant, herbivory and bird community and their interactions. Warming experiments in the trans-Himalayan region have indicated a warming of just 1 °C could impact the pastoralists and persistence of wildlife across Asian montane rangelands[77]. Similar warming experiments in the Arctic show shrubs will be favoured[78]. Thus, highlighting that these changes in the vegetation can have a direct and visible impact on the communities. Recent studies have also begun to investigate the role of community composition change on the trait variation, identifying traits that are plastic and aplastic in response to community change[79]. Changing climate can reshape community composition but our ability to detect these mismatches often go undetected due to lack of theory and baseline to set our expectations. Bonachela et al.[80] provide a null model to detect community—climate mismatches, through shape of species' climate response curve.

Climate change impacts biotic response but given the complexity of factors that determine community composition, individual species distribution models are unlikely to address this complexly and predict future ecological changes. The foundation for studies monitoring the response of the ecological community to change in the montane landscape is to understand how ecological communities are structured along the altitudinal gradient at present. Examining spatial and temporal patterns of species co-occurrences is suggested to understand the response of community composition[81]. Such baseline data are important to be able to identify community change in future climate change scenarios. Plant community structure along Himalayan altitudinal gradient is studied to a certain extent[82,83] but very limited studies have addressed faunal community structure change (amphibian[84]; birds[85]; mammal[86]). We are not aware of studies addressing the response of faunal composition to future climate change in the Himalayas, but past climate appears to have caused displacement creating the current diversity patterns of birds in the eastern Himalaya[87].

4.3 Phenological Changes

Range shift and phenology (timing of life-history events) both provide opportunities for tracking suitable habitat and resources, but the role of phenological shift is often overlooked while studying climate change responses. Climate change alters phenological events disrupting the timing of ecological interactions, temporal coordination and long-established partnerships between community members, thereby threatening ecosystem functions. The field has progressed from reporting the degree of phenological shifts to identifying patterns of shift and reporting explanatory factors like trophic level, latitudinal position, etc. correlating with the pattern[88]. This has led to hypothesis-based research for exploring phenological patterns, which heavily relies on exploring correlative patterns rather than causative mechanisms[89]. Further, there are very few studies that have gone further to explore costs associated with phenological shifts and constraints on phenological plasticity[90,91]. Seasonal changes may further complicate climate change-induced phenological changes by altering the length of the optimal time of life-history events like development, reproduction, hibernation (dormancy) and migration. A met-analyses study has indicated that phenological

Table 2: Examples of studies on ongoing and future climate change from Himalayan region

Species	Data type	Implication on climate change in the Himalaya
Alpine plants (124 endemics)[47]	Temperature and endemic plant species elevation range compared across time	➢ Upslope shift of elevation range documented for ~116 species ➢ Median shift of ~240 m per 160 years ➢ 52% of the plant shifted in both - rear and leading elevational margin, 20% shifted only in the upper margin ➢ Species richness peak shifted towards higher elevation ➢ More warming was recorded for the higher elevation, more shift recorded for lower elevation group (~300m on average) Rate of warming higher in high altitudes during winter
Modelled major biomes of Indian subcontinent[48]	~ 9km sq. resolution raster data, time period 1950–2000, temperature, precipitation and elevation	➢ Temperate broadleaf and mixed forest of Himalaya are predicted to lose as much as third of their potential area ➢ Temperate coniferous forests are predicted to expand in the high-elevation montane grassland and shrublands
Modelled major biomes of India[49]	~ 4km resolution data	➢ Montane grasslands and shrublands are predicted to expand to temperate broad-leaved and mixed forest ➢ Western part of the Himalaya predicted to be highly vulnerable ➢ Higher elevation region predicted to be highly vulnerable in future
Alpine musk deer[51]	Occurrence data (*n*=80), 11 predictor variables	➢ The study predicts longitudinal shift of habitat rather than elevational shift ➢ Predicts expansion of climatic habitat between 2600 and 4600 m
Kashmir musk deer[52]	Occurrence data (*n* =136)	➢ Habitat shift predicted northwards ➢ Limited protected area to support specialist species predicted to be vulnerable ➢ Identified 22–24% of current range as refugia for future climate change
Snow Leopard and Blue sheep[57]	Occurrence data (*n*= 364 for snow leopard; *n* = 201 for blue sheep)	➢ Sharp decline predicted (14–21% of current range) when the model included prey occurrence (Blue sheep), as oppose to 2–3% decline predicted in climate only model ➢ Predicted mismatch of predator-prey spatial overlap
Four high elevation frogs (*Scutiger* spp)[59]	Occurrence data (14–100 for different species)	➢ Highlights the need of including migration in species distribution models ➢ Even under unlimited migration scenarios frogs might not be able to track the majority of areas predicted as suitable

Table 2: (continued)

Species	Data type	Implication on climate change in the Himalaya
15 Birds[46]	8-years data, 4027 captures, 15 species, logged and primary forest	➢ Species close to their warm edge range suffered more population decline, close to their cold edge range showed increased survival ➢ Adaptation to the thermal environment - rather than other species traits influence the response to anthropogenic habitat change ➢ Temperature difference between logged and primary forest influence the fitness rather than physiology (thermal tolerance) ➢ As temperature rise thermal condition should be more favourable to pop closer to the cold-range edge, leading to higher survivorship and/or persistence ➢ 6 out of 15 lower elevation sp. showed consistent increase in survival in logged forest - these sp could cope with warm climate in future by moving upslope ➢ For high elevation species, elevation above 2000 m (not sampled in the study) would be the leading edge (with increased survival) ➢ Reduction in body mass in logged and primary forest - smaller body size can dissipate heat better or lower food available in the logged forest could select individuals with lower body weight ➢ Moving upslope in logged could be worst, recommends conservation of forest in the high altitude
Various taxa (birds, reptiles, amphibians, butterflies of Sikkim Himalaya)[74]	Compared historical record with current (descriptive)	➢ Upward shift of elevation range of 25 bird species, 21 species of butterflies, 5 snakes and two toads ➢ Breeding shifted to latter half of the earlier reported breeding time (for 6 species) ➢ Shortening of breeding season of Tailorbird by 2–3 months ➢ Reduction in clutch size reported for 3 species ➢ Range overlap of *Ptyas mucosus* and *P. korros* ➢ Turtle disappearance from Sikkim ➢ Advancement of breeding in three species of frogs ➢ Fungal disease reported in mid-range of amphibians of Sikkim

shifts under climate change may have the highest impact on the soil fauna[94], which may result in cascading impact on the ecosystem. Such phenological changes may be more in soil experiencing the freeze–thaw cycle.

Phenological studies in the Himalaya have typically focussed on short-term studies highlighting the sensitivity of plant phenology to temperature[95–97] and plant–animal interactions along altitudinal gradient[97,98]. Though thermal tolerance is often shown to determine the resilience of species to climate change, few authors have discussed photoperiodism[99] as a key cue to program seasonal activities across different taxa. Photoperiodism might be especially important for temperate and polar species and cited several examples of genetic changes due to climate warming.

We are not aware of any study on Himalayan faunal phenology, except for a few descriptive report[100]. But studies have shown that climate change can have direct impacts on the timing of faunal life history events like hibernation, a key life-history strategy adopted by many taxa living in extreme environments to winter survival through metabolic plasticity. Climate change caused changes in litter size can have a direct impact on the demography of the hibernating small mammal. The demographic trends, however, may be difficult to predict as the link between climate and litter size of hibernating small mammals is complex, indicated by opposing trends of two closely related hibernating marmot species[101,102]. Events of migration in birds and butterflies is another important phenological trait that has been studied in the light of climate change[103]. A study on Himalayan birds examined the role of altitudinal migration (a key life-history strategy in montane birds) in coping with hypoxia and found an association between the physiological parameters of blood-oxygen transport as a function of the migratory status of a species[104].

5 Underlying Genetic Patterns of Climate Change Using Integrative Approach

From the review of literature, we have seen that climate change impacts in the Himalayas are mostly assessed through species distribution models (SDM) without considering the ability of a species to adapt to an altered condition through genetic adaptation and/or phenotypic plasticity (sensitivity of a species) and ability of a species to track their habitat. Species when faced with challenges of climate change respond by shifting to a new habitat to maintain their existing physiological association, or persist in their habitat enduring the altered climate through phenotypic plasticity or genetic adaptation. Species that fail to persist or shift range undergo demographic bottleneck and may finally go extinct. The entire process of range shift leaves characteristic signatures on the demography history of a population, especially at their range edge which faces the[105] climatic fluctuation (refer to Fig. 1). To increase the predictive ability of SDMs and improve the forecast under climate change, it is important to include these biological processes that determine the sensitivity of a species to climate change along with exposure. Urban et al.[106], have identified the biological mechanisms important to be included in such predictive models to increase the accuracy of future climate change forecasts. Urban et al.[107] exposure to altered climate can lead to natural selection acting on standing genetic variation, but heritable epigenetic changes (inherited changes in the phenotype not directly related to genetic changes) can also serve as a rapid mode of evolution of organismal persistence to climate change[108]. Current advancements in genomics allow us to integrate genomic data and quantify sensitivity of a species across its range exposed to varying degrees of climate change. We recommend an integrated framework (adapted from Rozgour et al.[109]) in Fig. 1, for Himalayan species to be considered for improving predictive models.

Range-wise[110] genetic studies have now begun to correlate amount of exposure on the standing genetic variation. Standing genetic variation cannot be directly linked to traits useful for climate change adaptation. However, it will be useful to identify different haplotypes. Using global mammalian genetic diversity, a study showed that at least 30% of most genetically rich areas in montane regions will be exposed to an increase of mean annual temperature > 2 °C, but land use change and deforestation can put additional pressure apart from climate change. A study on a boreal mammal in North America used SDM to identify climatically suitable regions and showed that regions that maintained higher climatic stability also maintained higher genetic diversity[16], as expected from the central-marginal-model of species distribution which suggests population density decline gradually towards the boundaries[111]. For dispersal limited small mammals, however, the genetic structure can be much more complex, as they are primarily driven by their fragmented range[112]. With the advancement in genome sequencing technologies studies have begun to focus on detecting causative adaptive genetic variations rather than characterizing overall genetic diversity associated with organismal persistence to novel environment[112,113]. Adaptive genetic variations are often identified in the background of overall genetic variations by quantifying the magnitude of genetic divergence and comparing the genomes between current and altered environment[113]. It would be useful to link haplotypes by generating large-scale population genomic data and trait information to a more meaningful climate and land use change metrics. The majority of genome-scale studies are based on pairwise comparisons of population in extreme environments. Similar studies that will explore adaptive genetic variation along elevation range limits of a montane species can help us understand genetic variation driven by species range dynamics.

Transplantation studies are promising ways of understanding climate-driven range shift in the natural habitat of the species, using space for time approach (higher elevation—leading-edge, lower elevation—trailing edge). Transplantation followed by comparisons of gene expression

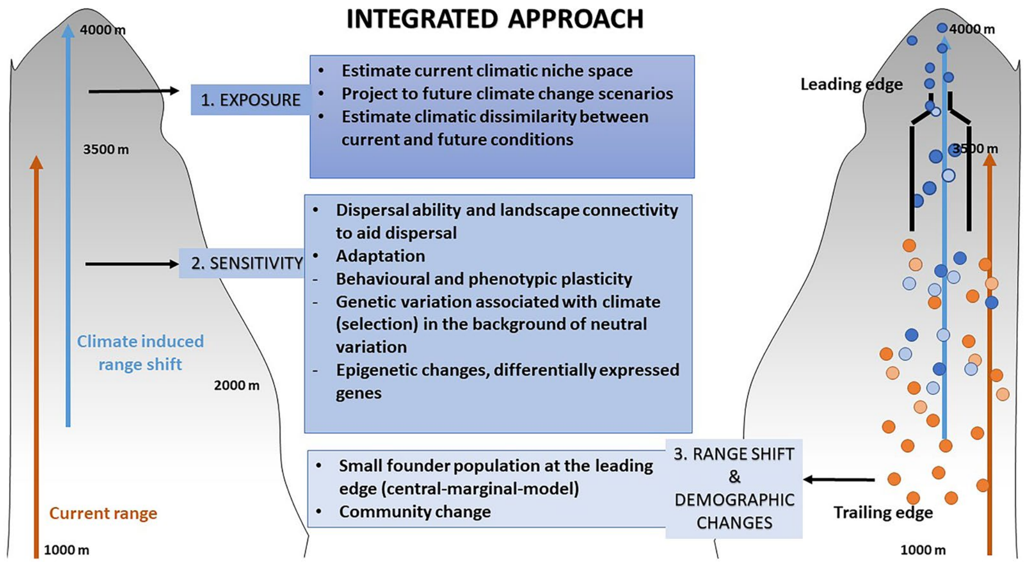

Figure 1: Integrated approach (adapted from Razgour et al.[109]) to assess range dynamics mediated by climate change in a montane landscape. (1) Exposure (degree of climatic variation), (2) sensitivity and adaptive potential and (3) range shift and demographic changes are the key to understanding climate change-mediated range dynamics. Range shift and demographic changes can be tracked using genetic variation across species range. The amount of genetic variation distributed across species' range are represented by coloured circles; trailing edge (orange circles), centre-edge (mixed coloured circles which shows highest genetic variation) and leading-edge (blue circles) under central-marginal-model

patterns to understand the process of acclimatization suggested the important contribution of regulatory plasticity mediated by transcriptional plasticity[114]. Plasticity could induce biased adaptive evolution[116,117] in complex traits. Similarly, complex traits like thermogenic performance were studied integrating gene expression studies with metabolic enzyme activities[118]. Role of transcriptional or regulatory plasticity to range shift is studied in the high-altitude specialist, pikas and a plant species in the Himalaya with transplantation experiments[45,46]. While transplantation study on plants documented other fitness-related traits along with gene expression patterns in the transplanted individuals beyond species' natural elevational range limits[45], study on pika were limited to a comparison of gene expression pattern within species range limit[46]. These studies highlight the power of a multidisciplinary approach including gene expression plasticity in addressing the complex processes of range shift coupled with a good experimental design.

6 Integrative approach to identify climate change-induced patterns of community change and phenology

Climate change-induced alteration of community assemblages affect biotic interactions, possibly triggering adaption to compete, resistance to predators and diseases introduced by new community members. Species assemblage is determined by interactive factors like predation pressure, competitive interaction and habitat availability. Studies forecasting vulnerability to future climate change show that including potential to adapt reduces projected range loss, but increases the chances for competition between species. Competition can also lead to adaptive radiation by increasing the chances of interspecies introgressive hybridisation[119]. While the direct genetic effect of competition (for example genes associated to help compete) is not determined, competition can lead to alteration in genetic composition. Adaptive changes to compete for resources have been documented in Himalayan birds in the past[84].

An altered community can introduce a pathogen burden to the native species. Potential cross-species infection of Avian malaria is reported between native Himalayan high-altitude resident species and migratory birds[120]. Climate change is predicted to increase such incidences of pathogenic burden in native species as community assemblages get altered leading to an expansion of pathogens as documented recently in Saiga antelope of Kazakhstan[121]. The transmission of pathogens is associated with contact rate which is determined by space use, thereby putting social animals at a higher risk of disease transmission[122]. Limited evidence from wild populations has indicated an association of vulnerability to disease with inbreeding; however, it is unclear if this is applicable for all the pathogens[123]. The connection between host genetics and incidence of disease associated with climate change is an unexplored yet important topic to be explored. Sampling environmental samples using genomic approaches like metagenome sequencing have the potential to detect the early spread of disease. Metagenome sequencing is widely used to understand community change in soil due to warming[124].

Studies have revealed phylogenetic control of important plant traits like flowering phenology[94]. However, the evolutionary influence of disruption in breeding and migration and mismatched interaction between species is not well understood for most taxa. Disruption of the timing of interacting species resulting in mismatch can have evolutionary consequences (through selection) and demographic changes[89]. Adding a dimension of eco-evolutionary consequences to phenological studies can help in understanding the long-term consequences of such mismatches.

7 Conclusion

Uncovering the impacts of climate change has been the major focus of biodiversity research. In this review, we summarized studies on the Himalayan fauna that have witnessed the three fingerprints of climate change—range shift, phenological shift and community studies related to shifts and abundance. Species distribution models were found to be the most popular approach to assess impacts of climate change; thus, range shift was the most commonly reported patterns. However, range shift reported from the Himalaya does not take into account species ability to adapt and disperse. We recommend an integrated framework to be able to include sensitivity of the species while reporting range shifts. Studies on impacts of community composition and phenological changes are still at an early stage for the Himalayan fauna. We have reviewed recent studies that have identified patterns of climate mediated community shifts and phenological shifts. Community composition can be studied using modern metagenomic approaches. We have cited several examples on the importance of integrating genomics in climate change-based research. The field has progressed from studying range-wise genetic variation to identifying causative genetic traits.

Along with future climate change studies, we also reviewed patterns of past climatic fluctuation and their evolutionary impact on the current pattern of Himalayan faunal biodiversity. Few studies identify south eastern population to be climatic refugia during the most recent glaciation event in the Himalayas; however, this hypothesis warrants support from additional genetic data. Phylogeographic studies have identified genetic divergence of population in the east and western Himalaya. More phylogeographic studies will be useful to test this hypothesis.

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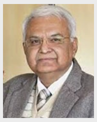

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