University of Arkansas, Fayetteville
ScholarWorks@UARK

Graduate Theses and Dissertations

5-2021

Climate-driven Impacts on Himalayan Aquatic Biodiversity: A Case Study Involving Snowtrout (Cyprinidae: Schizothorax)

Riri Wiyanti Retnaningtyas
University of Arkansas, Fayetteville

Follow this and additional works at: https://scholarworks.uark.edu/etd

Part of the Animal Experimentation and Research Commons, Aquaculture and Fisheries Commons, Biodiversity Commons, Integrative Biology Commons, Natural Resources and Conservation Commons, Terrestrial and Aquatic Ecology Commons, and the Zoology Commons

Citation

Retnaningtyas, R. W. (2021). Climate-driven Impacts on Himalayan Aquatic Biodiversity: A Case Study Involving Snowtrout (Cyprinidae: Schizothorax). *Graduate Theses and Dissertations* Retrieved from https://scholarworks.uark.edu/etd/4096

This Thesis is brought to you for free and open access by ScholarWorks@UARK. It has been accepted for inclusion in Graduate Theses and Dissertations by an authorized administrator of ScholarWorks@UARK. For more information, please contact scholar@uark.edu.

Climate-driven Impacts on Himalayan Aquatic Biodiversity: A Case Study Involving Snowtrout (Cyprinidae: *Schizothorax)*

A thesis submitted in partial fulfillment
of the requirements for the degree of
Master of Science in Biology

by

Riri Wiyanti Retnaningtyas
Universitas Negeri Malang
Bachelor of Science in Biology, 2016

May 2021
University of Arkansas

This thesis is approved for recommendation to the Graduate Council.

____
Michael E. Douglas, Ph.D
Thesis Director

____
Marlis R. Douglas, Ph.D
Committee Member

____
W. Fred Limp Jr., Ph.D
Committee Member

ABSTRACT

Monitoring biodiversity, to include its relative dispersal and contraction, has become a conservation task of great importance, particularly given the catastrophic and ongoing loss of habitat due to climate change. However, the timing, direction, and magnitude of these rates vary across taxa and ecosystems. Predicting specific impacts of climate change can thus be difficult and this, in turn, hampers management action. Metrics are needed to not only quantify contemporary requirements of species, but also predict potential distributions that fluctuate in lockstep with climate.

Montane ecosystems in the Himalayas are highly impacted by climate change, yet remain largely understudied due to the harsh nature of their terrain. Riverine ecosystems are particularly vulnerable in this regard, as annual reductions in snow cover and rainfall will impair hydrologic discharge. This, in turn, places Himalayan aquatic biodiversity at the forefront of climate change.

In response, I developed Ecological Niche Models (ENMs) for two Himalayan fishes (Snowtrout: Family Cyprindae, *Schizothorax richardsonii*, *S. prograstus*) distributed broadly across the Himalaya. Each ENM evaluates species occurrence data, as derived from in-depth literature surveys and field sampling. These data, together with 19 bioclimatic, physiographic, and hydrologic variables, were then evaluated using Generalized Linear Modelling (GLM). Results, as gauged by relative Area Under Curve (AUC) values, indicate both study species are currently resident within western and eastern components of the Himalaya. Future predictions, based on bioclimatic variables, indicate potential expansion into higher elevations of the central Himalaya as the regional climate elevates substantially.

ACKNOWLEDGEMENTS

Support for my thesis was provided by academic advisors, friends, and family. I would like to thank Dr. Michael Douglas for his enormous support and rigorous guidance during this challenging time. I also thank my Thesis Committee: Dr. Marlis Douglas for her thorough and constructive advice, and Dr. W. Fred Limp Jr. for support and input regarding analytical issues.

Douglas Lab members (i.e., Sonam Wangmo, Whitney Murchison-Kastner, Katelyn McDaniels, Griffin McDaniels, Zachery Zbinden, Karma Wangchuk, and Tim Goodhart) accepted me and provided a friendly environment to learn and do research. They made graduate school a memorable experience. Thanks also to my Indonesian friends in Fayetteville, particularly Harumi, Yheni, Meutia, Putu, Audrey, and Rian for being such a wonderful support system, and for listening when no English words could express my thoughts. In so doing, they successfully provided a fragment of Indonesia and an echo of home.

I also thank my parents for nurturing my curiosity and interest in science and the natural world, without foregoing our traditional ways. I thank my best friends in Indonesia for being there, despite the thousands of miles and differences in time zones. Also, I owe deep gratitude to my fiancé, Dustin Faust, for his love, enormous support, and relentless care throughout this difficult time, and for always reminding me that my education does not end with a degree. Lastly, I acknowledge the multiple funding sources that made my degree possible. These includes generous University endowments: 21st Century Chair in Global Change Biology (Michael E. Douglas) and Bruker Professorship in Life Sciences (Marlis R. Douglas). I was also fortunate to receive a Fulbright Master's Degree Scholarship administered by Institute of International Education, and generous endowments from Sponsored Students and Special Programs at University of Arkansas.

TABLE OF CONTENTS

INTRODUCTION

Monitoring biodiversity, and gauging its relative dispersal and contraction, has become a conservation task of great importance (Lepetz et al., 2009), particularly given the catastrophic and ongoing loss of habitat due to climate change (Mantyka-pringle et al., 2012). The latter is a complex amalgamation of disturbances and stressors, including temperature alterations, increase in atmospheric CO_2, as well as frequent droughts and extreme flow events (Barnett et al., 2005; Milly et al., 2005). Species rapidly shift their geographic ranges, distributions, and phenology in response to a changing environment (Lawing & Polly, 2011), yet the direction, timing and magnitude of these alterations are highly variable across both species and ecosystems. Hence predicting specific impacts is quite difficult, and this, in turn, hampers proactive management (Staudinger et al., 2013). Thus, metrics are needed not only to quantify contemporary ecological requirements of species, but also combine them analytically so as to accurately predict the location of species-specific conditions within a contemporary matrix in flux due to climate change.

Montane and high-altitude environments are global ecosystems within which biodiversity and its capacity for dispersal are seriously impacted by climate change (Hannah et al., 2002). For example, the complexities of topography and structure within these habitats serve to retain microclimates that act as refugia, with rates of change markedly slower (Loarie et al., 2009). In addition, as climate change advances, species migrate upward in elevation towards cooler areas so as to maintain favorable habitat conditions (Parmesan, 2006). Given this, additional stressors are exerted in montane or high-altitude communities as increased competition occurs over limited resources and diminishing space (Chen et al., 2011). Therefore, major conservation concerns for these communities have focused on the manner by which they respond to potential

range expansions, contractions, and the declining population numbers and local extinction these conditions elicit (La Sorte & Jetz, 2010).

High-altitude freshwater biodiversity is particularly vulnerable in this regard, due to several factors: 1) They occupy relatively fragmented habitats that incorporate specific environmental conditions, such as reduced water temperature; 2) Their dispersal is limited and often unidirectional (i.e., upstream towards cooler waters), with more predictable downstream dispersal being environmentally constrained; and 3) Their susceptibility to anthropogenic stressors such as impoundments and overfishing is amplified (Woodward et al., 2010). Numerous studies to quantify the occurrence of climate-induced range shifts in mountainous ecosystems have involved salmonids, given the wide distribution these species display (Comte & Grenouillet, 2013). However, many such species have been translocated globally to regions far beyond their endemic range. Two in particular [i.e., brown trout, *Salmo trutta*; rainbow trout, *Oncorhynchus mykiss*) rank 5th and 6th (among eight fishes) in a list of the world's 100-worst invasive species (Lowe et al. 2000).

This, in turn, leaves open similar questions regarding high-altitude aquatic biodiversity that is: (1) taxonomically quite disjunct from salmonids, and (2) has much greater endemicity and thus, conservation merit. This is particularly so when globally more remote and least-explored areas are evaluated, those in which aquatic biodiversity are not only less well studied, but also less capable of fitting within an ENM developed for a more plastic and invasive salmonid. The Himalaya is one such region that not only contains introduced salmonids (Sharma et al., 2021b), but also a variety of endemic and little-studied fishes, many of which have yet to be identified to species.

The Himalaya spans nearly 3.4 million km^2 and falls under the sovereignty of numerous countries: Afghanistan, Pakistan, India, Nepal, China (Tibetan Autonomous Region), Bhutan, and Myanmar (Pandit et al., 2014). It represents the largest and highest mountain range on the planet, averaging >4,000 m in elevation, accentuated by 18 peaks >8,000 m (Pant et al., 2018). It stores the largest mid-altitude alpine glaciers, high-altitude permafrost, as well as overall snow cover (Kang et al., 2019). It is thus referred as the "Third Pole," in that it represents one of the globally most important cryospheric regions outside of the Arctic/ Antarctic (Qiu, 2008). The Himalaya has experienced drastic changes in climate, similar to those observed at the poles (Qiu, 2008). These include glacial retreats (Kang et al., 2019; Yao, 2004; Yao et al., 2012) and permafrost degradation (Yao et al., 2012). In addition, it represents "… the water tower of the world" (Xu et al., 2009), in that it contains the headwaters of 10 major Asian rivers that collaboratively support the livelihood of approximately 1.3 billion people (approximately 15% of the global population; Srivastava et al., 2017; Pant et al., 2018).

Survey efforts in the Himalaya are often constrained, due to inaccessibility and the harsh nature of its high-altitude terrain (Dimri et al., 2018), such that important parts of resident riverscapes remain uncharted, with extant freshwater species unrecorded. Hence, there is a lack of information regarding the effects of climate change on Himalayan riverine ecosystems and their biodiversity (Shah et al., 2015). Preserving these systems thus becomes imperative within the context of global climate change, and the monitoring of resident fishes is an excellent mechanism to ascertain if, and how rapidly, environmental conditions are deteriorating within these high-altitude riverscapes (Woodward et al., 2010).

In this study, I focus on two Himalayan snowtrout species that are broadly distributed across the Himalaya. They comprise one component of the largest and most diverse of global

freshwater fish families (i.e., Cyprinidae: 1,700+ valid species, with 10 recognized subfamilies) (Fricke et al. 2020). These taxa can potentially serve as bioindicators for climate change impacts (Sharma et al., 2021a), in that many are adapted to high-elevation, cold-water streams and thus are particularly vulnerable to climate change (Regmi et al., 2021). However, their potential responses remain unclear, due mostly to the limitations with regard to monitoring biodiversity within the region (Regmi et al., 2021).

One widely distributed study species, *S. richardsonii*, is important for the livelihood of communities in the region, and has thus been extensively studied (Sharma et al., 2021a). A previously derived comprehensive species distribution model suggests a potential range shift upwards in elevation due to climate change. Other snowtrout species, such as *S. progastus*, are also important in this regard, but are less broadly distributed and, again, remain relatively understudied (Regmi et al., 2021).

Given that climate responses will vary amongst species (Travis et al., 2013), an important management consideration is a more comprehensive perspective that can consider freshwater fish communities as a whole. This can be accomplished by deriving ecological niche models (ENMs), a valuable tool by which to derive spatially explicit predictions for species-specific habitat suitability. It does so by quantifying the statistical relationships between species locations and environmental predictors (Guisan et al., 2013). ENMs are effective tools not only for predicting how climate change affects current species distributions, but also how these may vary with regards to future environmental scenarios that are markedly different than those extant (Elith et al., 2010).

OBJECTIVES

In this study, I develop an ENM for Himalayan snowtrout (*S. richardsonii*, *S. prograstus*) which are distributed broadly in the foothills of western and central Himalaya. In doing so, I address the following objectives: 1) What are the current distributions of *S. richardsonii and S. progastus?* 2) What data are most relevant with regard to the definition of current distributions? and 3) How will the habitats of these study species be distributed in the future?

To address these questions, I have: 1) Constructed an ENM for *S.richardsonii* and *S. progastus*; 2) Described the breadth and extent of their ENMs, as interpreted from conditions inherent to the current distribution; and 3) Predicted the responses of each species to future climate scenarios.

METHODS AND MATERIALS

I developed an ENM for two Himalayan snowtrout species (*S. richardsonii* and *S. progastus*), then applied separate ENMs for each to predict their distributions. To construct the ENMs, I followed Zurell et al. (2020) by applying ODMAP (i.e., Overview, Data, Model, Assessment and Prediction) using R (R Core Teams, 2020) and ArcGIS Pro 2.6 (ESRI Inc., 2020). The ODMAP protocol details key steps in model building, as well as in analyses and assessment. This is done as a mechanism to ensure the reproducibility and transparency of the process. The methodology is divided into four separate components: Data Preparation; Species Distribution Models; Model Assessment; and Future Predictions. These are detailed below and subdivided into appropriate sub-categories.

Data preparation

Study area—The Himalaya spans approximately 2400 km long arc. I focused on the core Himalaya which extend from 73° to 97° E and 24° to 35.5° N. My study region includes the western part of the range which lies under the administration of India and Pakistan, as well as the central part which includes Nepal and Bhutan, with particular focus on the rivers and their tributaries within these ecoregions.

I derived the maps and boundaries of the Himalaya from ESRI ArcGIS Living Atlas (ESRI Inc., 2020). I created the boundaries of the Himalayan through application of a raster package in R (R Core Teams, 2020), which dissolved the polygons of administrative areas that extended (west-to-east) from Jammu-Kashmir, Himachal Pradesh, Uttarakhand (India), Nepal, Bhutan, Sikkim, Assam, and Arunachal Pradesh (India). This Himalaya boundary was then used to crop the environmental variables that were applied in this study.

Environmental variables—Bioclimatic variables are commonly used to develop climate envelope models (Austin & Niel, 2011; Zurell et al., 2020) and I employed them herein as a mechanism to model the potential distributions of *S. progastus* and *S. richardsonii*. In doing so, I extracted 19 bioclimatic variables (Appendix 1) from WorldClim Climate Database ver. 2.1 (http://www.worldclim.org/) (Fick & Hijmans, 2017): Monthly temperature and precipitation values represent annual trends, seasonality, and extreme or limiting environmental factors that fall within the temporal span of 1970-2000. The present study was based on 5 minute resolution on the Himalayan scale.

Data on stream topography and morphology were extracted from HydroSHEDS, hosted by WWF (World Wildlife Fund) and the USGS (United States Geological Survey; http://hydrosheds.cr.usgs.gov) (Lehner et al., 2006). I derived hydro-morphological and hydrological data from the RiverAtlas, which is part of HydroSHEDS database, and extracted several raster layers from the river shapefiles (Appendix 2), using ArcGIS Pro 2.6 (ESRI Inc, 2020). Data represent: Natural Discharge Minimum and Maximum, Stream Gradient (1 layer), River Area (1 layer), River Volume (1 layer), Land Surface Runoff (1 layer), Elevation (1 layer), and Slope (1 layer). Flow accumulation raster layers were also downloaded from HydroSHEDS and fitted to the study area.

Occurrences and pseudo-absences of study species—The occurrence records for the two study species were collected from 2 main sources: 1) Global Biodiversity Information Facility (GBIF; http://www.gbif.org/); 2) Literature survey; and 3) Douglas Lab field sampling dataset. Occurrence data were then compiled into a single data frame containing geographic coordinates in decimal degrees. A total of 84 presence points were recorded for *S. progastus* and 189 for *S.*

richardsonii (Figure 1), which were further reduced to 22 (*S. progastus*) and 23 (*S. richardsonii*) locations for modelling. This were done by retaining one occurrence point per 5-minute cell to minimize autocorrelation.

Since my compiled data represent only presence data, I derived background data (i.e., pseudo-absence data) to contrast against presence data (Barbet-Massin et al., 2012), following previously-published protocols (Zurell et al., 2020). Here, pseudo-absences provide a comparative data set from which to enable the conditions under which a species occurs, as contrasted against those in which it is absent. I restricted the random-point samples to those within a specific area by placed a 50 km buffer around species-records, then sampling the background points at random within the buffer zone around presence points. The presence location was excluded so as to eliminate bias and minimize the potential for spatial autocorrelation (Barbet-Massin et al., 2012).

I then combined occurrence, pseudo-absence, and bioclimatic data into a single dataset. Bioclimatic variables had a 5-minute resolution whereas species-data (i.e., occurrence and pseudo-absence data) represented a much finer resolution. Given this, I fitted the species-data to the spatial resolution of the bioclimatic variables, then removed duplications within 5-minute cells.

Species Distribution Models

Selection of variables—Generalized Linear Models (GLMs) often have multicollinearity issues when parameters are fitted, particularly when two or more predictors are highly correlated (Dormann et al., 2013). To avoid these issues, I tested for multicollinearity by using the

Spearman correlation coefficient to gauge highly intercorrelated variables, then selected an initial set of predictor variables prior to fitting the GLM (Guisan et al., 2017).

The relative importance of univariate variables can be determined by employing either the AIC (Akaike Information Criterion) or the explained deviance (Dormann et al., 2013). To do so, I fitted a GLM separately for each predictor, assessed the variable importance, then ranked the variables according to their univariate importance (Zurell et al., 2020). I also examined pairwise correlations among predictors. In general, r-values < 0.7 are considered potentially problematic. To evaluate, I identified all pairs of variables with $r > 0.7$ and removed those less important (i.e., $r < 0.7$) (Dormann et al., 2013).Uncorrelated variables differed for each study species.

Schizothorax progastus—The important variables for *S. progastus* are: Natural Discharge Minimum (NDMIN), Mean Diurnal Range (MDR), Mean Temperature of Coldest Quarter (MTCQ), Precipitation Seasonality (PS), Precipitation of Warmest Quarter (PptWQ), Temperature Annual Range (TAR), Stream Gradient (StrG), Isothermality (ISO), and Flow Accumulation (FLAcc) (Table 1). From these, I selected the four most important and meaningful for further analysis, in accordance with the niche of snowtrout. Guisan et al. (2017) suggested 10 presence points per parameter must be fitted in the model. However, in this study, only 22 presence points were available. Therefore, I fitted the four most important variables in terms of univariate AIC scores. These included: Natural Discharge Minimum (NDMin), Mean Diurnal Range (MRD), mean Temperature of Coldest Quarter (MTCQ), and Precipitation Seasonality (PS).

Schizothorax richardsonii—The variable selection process for *S. richardsonii* resulted in 12 predictor***s*** being selected. These are: River Area (RivA), Mean Temperature of Driest Quarter (MTDQ); Flow Accumulation (FLAcc), Annual Precipitation (AP), Slope (SLP), Isothermality (ISO), Land Surface Runoff (LSR), Precipitation Seasonality (PS), Mean Diurnal Range (MDR), Temperature Annual Range (YAR), and Precipitation of Driest Month (PptDM) (Table 2). I again selected the four most important variables in terms of AIC scores, meaningful in accordance with the niche of *S. richardsonii*. These differed from *S. progastus* and were as follows: River Area (RivA), Mean Temperature of Driest Quarter (MTDQ), Flow Accumulation (FLAcc), and Annual Precipitation (AP).

Ecological Niche Modeling

After selecting weakly correlated variables, I then fitted the full model and simplified it. The models included a GLM with polynomial terms, and a stepwise procedure then selected the most important variables based on AIC.

Study species—The stepwise procedure in the final model for *S. progastus* explained the linear term for Natural Discharge Minimum (NDMin), Mean Diurnal Range (MDR), Mean Temperature of Coldest Quarter (MTCQ), and Precipitation Seasonality (PS). These explained approximately 44% of the deviance.

For *S. richardsonii*, the stepwise procedure explained the linear term for the following: River Area (RivA), Mean Temperature of Driest Quarter (MTDQ), Flow Accumulation (FLAcc), and Annual Precipitation (AP). This model effectively explained approximately 27 % of the deviance.

Model Assessment

A grid containing all combinations of the variables must first be defined to predict the model response along two environmental gradients, I visualize this response in the form of partial data structure that provides the mean predictive values of a model, given an environmental situation.

The modeling algorithms were evaluated based on (a) Receiver Operator Characteristic (ROC) or AUC (Area Under Curve of ROC), a threshold-independent model evaluation indicator, and (b) True Skill Statistics (a threshold-dependent measure for model accuracy that ranges from -1 to +1 (Dormann et al., 2013). An AUC value > 0.7 indicates a fair prediction, meaning that the observed and projected distribution are fairly consistent, while TSS >0.5 reflects a good prediction (Araújo et al., 2005).

Future Predictions

The physiographic and hydrologic variables were considered as temporally consistent for the future modelling process (Filipe et al., 2013; Ruaro et al., 2019). Therefore, the future predictions were based on climatic variables downloaded from WorldClim. I used the phase 5 of Coupled Model Intercomparison Project (CMIP5) to predict the model to climate layers based future climate scenario, and historical bioclimatic data (1970-2000) as the current climate scenario. The datasets were at different resolutions in geographic coordinates (latitude/longitude) projection with the occurrence data, and at the appropriate spatial resolution of 5-min.

To produce a model with appropriate resolution, I re-projected the species and climate data into 5-min resolution, then matched it with the spatial resolution of the Himalaya. I used the Himalaya background mask to clip the data and re-project the climate data accordingly. Binary

consensus habitat suitability prediction maps were then developed for the extant versus future projected time period (i.e., 2021 versus 2050).

Study species—To predict the future distribution of *S. progastus*, I eliminated the physiographic and hydrological variables and used only the following bioclimatic variables: Mean Diurnal Range (MDR), Mean Temperature of Coldest Quarter (MTCQ) and Precipitation Seasonality (PS). I repeated the same procedure as above for *S. richardsonii*. Here, I instead employed the following to predict the future distribution: Mean Temperature of Driest Quarter (MTDQ), Annual Precipitation (AP) and Isothermality (ISO).

RESULTS

Environmental variables and model performance

The partial response plots (Figure 2) indicate the probable presence of *S. progastus* is greater at higher values of natural discharge (NDMin), lower mean diurnal temperatures (MDR), and greater variability in seasonal precipitation (PS). Furthermore, the AUC (ROC) and TSS score of the GLM were calculated from different cross-validation runs. The model displayed AUC values of 0.806, while TSS was 0.51. The sensitivity and specificity of the model were 0.727 and 0.79 respectively, indicating a relatively good prediction (Araújo et al., 2005).

The partial response plots of *S. richardsonii* (Figure 3) indicated the occurrence probability of this species increased at greater values of River Area (RivA), lower values of Flow Accumulation (FLAcc), and somewhat higher values for Annual Precipitation (AP). The Mean temperature of Driest Quarter (MTDQ), although trending positively, was scarcely diagnostic. The AUC (ROC) and TSS scores of GLM based on those parameters are 0.789 and 0.282 respectively. Based on the AUC score, the GLM for *S. richardsonii* indicated a good prediction, but is much reduced according to the TSS score. The sensitivity and specificity of the model were 0.695 and 0.753, respectively.

Habitat Suitability and Potential Range Shifts

Schizothorax progastus—The present ENM indicated that the most favorable current habitat for *S. progastus* reflects a low-to-moderate distribution towards the eastern Himalaya, with the strongest epicenter in Northern India/ Bhutan (Figure 4, left). Future (2050) predictions in terms of potential occurrence [as generated from bioclimatic variables: Mean Diurnal Range (MDR), Mean Temperature of Coldest Quarter (MTCQ) and Precipitation Seasonality (PS)], indicated an

increased occurrence in some areas of Nepal and an elevated probability of potential occurrence in the eastern Himalaya (predominantly Northeastern India), with and a diminutive epicenter in the upper elevations of far Eastern Himalaya (Figure 4, right).

The current distributional prediction for *S. progastus* (Figure 5, left) were translated into a binary prediction that suggests a strong presence along the entire southern Himalaya border, extending from Nepal to Northeastern India. The Central, Southeastern (lower elevation). In addition, the far Eastern (higher elevation) Himalaya is also clearly represented (Figure 5, right).

The predicted 2050 distribution, based upon climatic variables, was also translated into a binary prediction. Here, the distribution to the Northeast and Central Himalaya remains similar to that found in Figure 5 (right), save for a much more enhanced distribution in the Southeastern (lower elevation) and Northeastern (higher elevation) regions (Figure 6, right).

Schizothorax richardsonii—The predictions of potential occurrence based on bioclimatic variables [Mean Temperature of Driest Quarter (MTDQ), Annual Precipitation (AP) and Isothermality (ISO)] in 2021 supports an extant distribution broadly arrayed along the southern border of the Himalaya, predominately to the Northwest, but with a continuous accumulation extending through to the East-Central region, then extending again in the far Eastern section (Figure 7, left). Future occurrences (Figure 7, right), dwindle somewhat however, and become much more fragmented in the Northwest Himalaya and Nepal, whereas the strong East-Central and Eastern concentrations are clearly sustained (but far Eastern diminished somewhat).

The binary prediction of potential occurrence of *S. richardsonii* based on the 2021 climate scenario (Figure 8, left) indicated high potential for a broad occurrence in the eastern and central Himalaya (Figure 8, right), extending into higher elevations as well. Northern India/

Bhutan and far Eastern Himalaya are greatly enhanced as well (seemingly more so than Eastern/ Northeastern). However, by 2050, the Northeastern/ Eastern/ Central distribution is sustained, whereas a much broader distribution occurs in Bhutan/ Eastern/ Far Eastern regions, particularly extending into much higher elevations (Figure 9, right).

DISCUSSION

Himalayan rivers are characterized as fast-flowing, given their increased elevation, highly heterogeneous substrates and dissolved oxygen levels (Rajput et al., 2013). Two riverine snowtrout species, *S. progastus* and S. *richardsonii*, are widely distributed in Central Himalayan drainages (Dimmick & Edds, 2002; Regmi et al., 2021), and this study attempted to interpret not only the climatic potential for currently recognized distributions, but also how these might change as climate continues to impact the Himalaya.

ENMs of Study Species

The ENMs in this study incorporated different sets of environmental variables respective to each species. The extant occurrence of *S. progastus* was predicted based on four environmental variables: Natural Discharge Minimum (NDMin), Mean Diurnal Range (MDR), Mean Temperature of Coldest Quarter (MTCQ), and Precipitation Seasonality (PS).

Schizothorax progastus—The ENM for *S. progastus* suggests it is widely distributed but at moderate densities and at moderate elevations, with a greater probability of occurrence in the central Himalaya (Northeastern Nepal/ Northern India/ Bhutan). A smaller focal point occurs in the lowlands of Northeastern India. According to the models, the distribution is predicted to increase in 2050, and to include locations at higher elevation (Northwest Nepal, Far Eastern Himalaya). Importantly, I judged the NDMin graph (Figure 2A) as conveying little information, in that it seemingly depicts either presence or absence of natural discharge (i.e., values start at zero, quickly peaking at <50, followed by a sustained plateau >175. In short, this variable contains scant information, and is not further considered.

The binary predictors of current occurrence supported the fact that *S. progastus* is largely distributed in spring-fed streams found in outer Himalaya. It can be found in such locations where monthly temperature and precipitation are elevated, yielding moderate-to-high natural discharge (Bookhagen & Burbank, 2010). The habitat preference of *S. progastus* spans pool, riffle and rapid habitat-types (Singh & Agarwal, 2013), commonly found in the foothills of the Himalaya.

Schizothorax richardsonii—The occurrence probability for *S. richardsonii* was also identified using four predictors, but different from the above, given its different ecology. These were: River Area (RivA), Mean Temperature of Driest Quarter (MTDQ), Flow Accumulation (FlAcc), and Annual Precipitation (AP). All have previously been employed in species distribution models (SDMs) (Molloy et al., 2014).

The ENM for *S. richardsonii* indicated a wide distribution across the Himalaya, much more than that found for *S. progastus*. This included higher elevations in the east, as well as the foothills in the west, again supporting its generalist life history. Given this, *S. richardsonii* was predicted to reduce its density in the Northwestern/ Northern Himalaya and this was sustained in the higher elevations of the Central and Eastern Himalaya (Northwest Nepal/ Northern India/ Bhutan), where rivers are larger. These areas also receive greater annual precipitation with a reduced flow accumulation, given the higher elevations.

The binary predictors of climate-induced extant distribution indicated considerable habitat currently available throughout the Himalaya, again indicative of the generalist ecology found in *S. richardsonii*. It is widely distributed in habitats that span from snow-fed glacial streams of the Greater Himalaya to spring-fed streams in the outer Himalaya. This result is

congruent with studies that have reported *S. richardsonii* as being distributed in headwaters of Himalayan rivers, with a preference for streams that possess gravel and/or rocky substrates (Wagle et al., 2015).

According to the binary model, predictors for a climate-induced 2050 distribution were sustained to the Northwest/ North and Central Himalaya, but broadly supportive of an extended distribution into higher altitudes of Northeast Nepal/ Northern India/ Bhutan, as well as Eastern and Far Eastern India. Furthermore, the models suggest that *S. richardsonii* is present in a more widespread area across the Himalayas, thus supporting the notion that it can survive a wide range of environmental gradients. In this sense, it can be considered a habitat generalist capable of tolerating a wide range of environmental conditions (Wagle et al., 2015).

Overview—Predictions for both *S. progastus* and *S. richardsonii* stand in contrast to our current knowledge about snowtrout habitat, as the genus is known to inhabit areas below 1600 msl (meters above sea level), with air temperature 5-10°C, with a mean during the wettest quarter of the year between 15 and 20°C (Sharma et al., 2021a). The ENMs of both species are influenced by precipitation. This suggests each requires habitat that receive greater amounts of either annual or seasonal precipitation. With a warming climate, precipitation will certainly increase in some regions of the Himalaya, which explain the potential future expansion of *S. richardsonii* towards larger rivers with greater natural discharge (Rajput et al., 2013).

Moreover, the binary prediction of future occurrence suggested an expansion towards areas at higher elevation. Both study species seemingly avoid near-freezing temperatures in the coldest winter months and tend to migrate downstream towards warmer water temperatures or to spring-fed tributaries to spawn (Sehgal, 1999). Snowtrout are also sensitive to thermal change,

and, it reflects the lowest maximum critical thermal limit (34.6°C) found among cold-water Himalaya fishes (Kamalam et al., 2019). A potential expansion to higher elevations, as suggested in this study, implies that elevating temperatures in their extant distribution will potentially force *S. progastus* and *S. richardsonii* towards higher elevations where temperatures are still favorable (Kamalam et al., 2019; Sharma et al., 2021a). The results of this study are thus comparable with previous results indicating a potential range shift in snowtrout towards higher elevation areas, as a means of compensating for the loss of thermal optima (Sharma et al., 2021a).

In this regard, the model reveals that high-altitude tributaries such as Satluj (northern India/ Pakistan), Beas (norther India). and upper Ganges basin (Nepal/ northwest India) would potentially provide future refugia. However, an expansion of distribution in the study species will also depend on the availability of environmental corridors that can facilitate dispersal (Robillard et al., 2015). As an example, the current network of dams across the Himalaya poses a deterrent for snowtrout to colonize potential refugia at higher altitude (Grumbine & Pandit, 2013; Sharma et al., 2021a). Moreover, another serious concern is that many higher-altitude cold-water regions in the Himalaya are dominated by introduced species such as brown trout (*Salmo trutta*) which will compete for trophic and spatial resources with adult snowtrout, while also predating upon young-of-year and juveniles (Sharma et al., 2021b; Thapliyal et al., 2013).

Study Limitations

The ENMs in this study displayed predictions that were judges as fair-to-poor, based on the TSS and/or AUC scores. Moreover, future predictions were also in line with those from a previous study (Sharma et al., 2021a), which indicated a range shift towards higher elevation and into areas where the precipitation regime is seasonally greater. However, model projections cannot

ignore the uncertainties that encompass the complex interplay of bioclimatic variables, species-responses, anthropogenic stressors, and temporal impacts upon demography that can drive more accurate and realistic predictions. For this to occur, additional occurrence data are needed.

In this sense, current predictions are based on but a limited set of bioclimatic variables (i.e., monthly mean temperature, mean temperature of driest month, annual precipitation and its seasonality, as well as a minimum rate of natural discharge for Himalayan streams). To produce more compelling results, more accurate information regarding the response of *S. progastus* to seasonal temperatures would be important (Isaak et al., 2016; Rajput et al., 2013). Furthermore, and with regard to future development of snowtrout ENMs, more accurate niche predictions and subsequent responses to ongoing climate change would be required, as would land cover and water velocity parameters.

CONCLUSIONS

The ENMs for Himalayan snowtrout study species (*S. richardsonii*, *S. prograstus*) were based on eight environmental variables (four each for both study species). Those results suggest that *S. progastus* is widely distributed in rivers that receive higher precipitation (and hence higher natural discharge) during periods with elevated mean monthly temperature. This differs somewhat from that of *S. richardsonii*, which is more widely distributed across Himalayan rivers. Its preferred habitat includes high-altitude rivers that exhibit low flow accumulation, despite the fact that the region still receives higher rates of precipitation. The ENMs of both species predict their expansion towards the eastern part of Himalaya by 2050.

LITERATURE CITED

Araújo, M. B., Pearson, R. G., Thuiller, W., & Erhard, M. (2005). Validation of species–climate impact models under climate change. *Global Change Biology*, *11*(9), 1504–1513. https://doi.org/10.1111/j.1365-2486.2005.01000.x

Austin, M. P., & Niel, K. P. V. (2011). Improving species distribution models for climate change studies: Variable selection and scale. *Journal of Biogeography*, *38*(1), 1–8. https://doi.org/10.1111/j.1365-2699.2010.02416.x

Barbet-Massin, M., Jiguet, F., Albert, C. H., & Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: How, where and how many? *Methods in Ecology and Evolution*, *3*(2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x

Barnett, T. P., Adam, J. C., & Lettenmaier, D. P. (2005). Potential impacts of a warming climate on water availability in snow-dominated regions. *Nature*, *438*(7066), 303–309. https://doi.org/10.1038/nature04141

Bookhagen, B., & Burbank, D. W. (2010). Toward a complete Himalayan hydrological budget: Spatiotemporal distribution of snowmelt and rainfall and their impact on river discharge. *Journal of Geophysical Research: Earth Surface*, *115*(F3). https://doi.org/10.1029/2009JF001426

Chen, I.-C., Hill, J. K., Ohlemuller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, *333*(6045), 1024–1026. https://doi.org/10.1126/science.1206432

Comte, L., & Grenouillet, G. (2013). Do stream fish track climate change? Assessing distribution shifts in recent decades. *Ecography*, *36*(11), 1236–1246. https://doi.org/10.1111/j.1600-0587.2013.00282.x

Dimmick, W. W., & Edds, D. R. (2002). Evolutionary genetics of the endemic Schizorathicine (Cypriniformes: Cyprinidae) fishes of Lake Rara, Nepal. *Biochemical Systematics and Ecology*, *30*(10), 919–929. https://doi.org/10.1016/S0305-1978(02)00030-3

Dimri, A. P., Kumar, D., Choudhary, A., & Maharana, P. (2018). Future changes over the Himalayas: Maximum and minimum temperature. *Global and Planetary Change*, *162*, 212–234. https://doi.org/10.1016/j.gloplacha.2018.01.015

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D., & Lautenbach, S. (2013). Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, *36*(1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x

Elith, J., Kearney, M., & Phillips, S. (2010). The art of modelling range-shifting species. *Methods in Ecology and Evolution*, *1*(4), 330–342. https://doi.org/10.1111/j.2041-210X.2010.00036.x

Esri Inc. (2020). ArcGIS Pro (Version 2.6). Esri Inc. https://www.esri.com/en-us/arcgis/products/arcgis-pro/overview.

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Filipe, A. F., Markovic, D., Pletterbauer, F., Tisseuil, C., Wever, A. D., Schmutz, S., Bonada, N., & Freyhof, J. (2013). Forecasting fish distribution along stream networks: Brown trout (Salmo trutta) in Europe. *Diversity and Distributions*, *19*(8), 1059–1071. https://doi.org/10.1111/ddi.12086

Fricke R., Eschmeyer W. N., & van der Laan R. (eds) (2020). Eschmeyer's Catalog of Fishes: Genera, Species, References. http://researcharchive.calacademy.org/research/ichthyology/catalog/fishcatmain.asp

Grumbine, R. E., & Pandit, M. K. (2013). Threats from India's Himalaya Dams. *Science*, *339*(6115), 36–37. https://doi.org/10.1126/science.1227211

Guisan, A., Thuiller, W., & Zimmermann, N. E. (2017). *Habitat Suitability and Distribution Models: With Applications in R*. Cambridge University Press. https://doi.org/10.1017/9781139028271

Guisan, A., Tingley, R., Baumgartner, J. B., Naujokaitis-Lewis, I., Sutcliffe, P. R., Tulloch, A. I. T., Regan, T. J., Brotons, L., McDonald-Madden, E., Mantyka-Pringle, C., Martin, T. G., Rhodes, J. R., Maggini, R., Setterfield, S. A., Elith, J., Schwartz, M. W., Wintle, B. A., Broennimann, O., Austin, M., … Buckley, Y. M. (2013). Predicting species distributions for conservation decisions. *Ecology Letters*, *16*(12), 1424–1435. https://doi.org/10.1111/ele.12189

Hannah, L., Midgley, G. F., & Millar, D. (2002). Climate change-integrated conservation strategies. *Global Ecology and Biogeography*, *11*(6), 485–495. https://doi.org/10.1046/j.1466-822X.2002.00306.x

Isaak, D. J., Young, M. K., Luce, C. H., Hostetler, S. W., Wenger, S. J., Peterson, E. E., Ver Hoef, J. M., Groce, M. C., Horan, D. L., & Nagel, D. E. (2016). Slow climate velocities of mountain streams portend their role as refugia for cold-water biodiversity. *Proceedings of the National Academy of Sciences*, *113*(16), 4374–4379. https://doi.org/10.1073/pnas.1522429113

Kamalam, B. S., Mahija, J., Baral, P., Pandey, A., Akhtar, M. S., Ciji, A., & Rajesh, M. (2019). Temperature and oxygen related ecophysiological traits of snow trout (*Schizothorax richardsonii)* are sensitive to seasonal changes in a Himalayan stream environment. *Journal of Thermal Biology*, *83*, 22–29. https://doi.org/10.1016/j.jtherbio.2019.04.014

Kang, S., Zhang, Q., Qian, Y., Ji, Z., Li, C., Cong, Z., Zhang, Y., Guo, J., Du, W., Huang, J., You, Q., Panday, A. K., Rupakheti, M., Chen, D., Gustafsson, Ö., Thiemens, M. H., & Qin, D. (2019). Linking atmospheric pollution to cryospheric change in the Third Pole region: Current progress and future prospects. *National Science Review*, *6*(4), 796–809. https://doi.org/10.1093/nsr/nwz031

La Sorte, F. A., & Jetz, W. (2010). Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1699), 3401–3410. https://doi.org/10.1098/rspb.2010.0612

Lawing, A. M., & Polly, P. D. (2011). Pleistocene climate, phylogeny, and climate envelope models: an integrative approach to better understand species' response to climate change. *PLoS ONE 6*(12), e28554. https://doi.org/10.1371/journal.pone.0028554

Lehner, B., Verdin, K., & Jarvis, A. (2006). HydroSHEDS Technical Documentation. Washington, DC. *World Wildlife Fund US, Available at Http://Hydrosheds. Cr. Usgs. Gov*.

Lepetz, V., Massot, M., Schmeller, D. S., & Clobert, J. (2009). Biodiversity monitoring: Some proposals to adequately study species' responses to climate change. *Biodiversity and Conservation*, *18*(12), 3185. https://doi.org/10.1007/s10531-009-9636-0

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055. https://doi.org/10.1038/nature08649

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, *18*(4), 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Milly, P. C. D., Dunne, K. A., & Vecchia, A. V. (2005). Global pattern of trends in streamflow and water availability in a changing climate. *Nature*, *438*(7066), 347–350. https://doi.org/10.1038/nature04312

Molloy, S., Davis, R., & Van Etten, E. (2014). Species distribution modelling using bioclimatic variables to determine the impacts of a changing climate on the western ringtail possum (*Pseudocheirus occidentals*; Pseudocheiridae). *Environmental Conservation*, *41*, 176–186. https://doi.org/10.1017/S0376892913000337

Pandit, M. K., Manish, K., & Koh, L. P. (2014). Dancing on the roof of the world: ecological transformation of the Himalayan landscape. *BioScience*, *64*(11), 980–992. https://doi.org/10.1093/biosci/biu152

Pant, N. C., Ravindra, R., Srivastava, D., & Thompson, L. (2018). The Himalayan cryosphere: Past and present variability of the 'third pole.' *Geological Society, London, Special Publications*, *462*(1), 1–6. https://doi.org/10.1144/SP462.13

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*(1), 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Qiu, J. (2008). China: The third pole. *Nature*, *454*(7203), 393–396. https://doi.org/10.1038/454393a

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rajput, V., Johnson, J., & Kuppusamy, S. (2013). Environmental effects on the morphology of the snow trout *Schizothorax richardsonii* (Gray, 1832). *TAPROBANICA: The Journal of Asian Biodiversity*, *5*. https://doi.org/10.4038/tapro.v5i2.6283

Regmi, B., Douglas, M., Edds, D., & Douglas, M. (2021). Geometric morphometric analyses define riverine and lacustrine species flocks of Himalayan snowtrout (Cyprinidae: *Schizothorax)* in Nepal. *Aquatic Biology*, *30*, 19–31. https://doi.org/10.3354/ab00737

Robillard, C. M., Coristine, L. E., Soares, R. N., & Kerr, J. T. (2015). Facilitating climate-change-induced range shifts across continental land-use barriers. *Conservation Biology*, *29*(6), 1586–1595. https://doi.org/10.1111/cobi.12556

Ruaro, R., Link to external site, this link will open in a new window, Conceição, E. O., Silva, J. C., Cafofo, E. G., Angulo-Valencia, M. A., Mantovano, T., Pineda, A., Paula, A. C. M. de, Zanco, B. F., Capparros, E. M., Moresco, G. A., de Oliveira, I. J., Antiqueira, J. L., Ernandes-Silva, J., Silva, J. V. F. da, Adelino, J. R. P., dos Santos, J. A., Ganassin, M. J. M., … Bailly, D. (2019). Climate change will decrease the range of a keystone fish species in La Plata River Basin, South America. *Hydrobiologia*, *836*(1), 1–19. http://dx.doi.org/10.1007/s10750-019-3904-0

Sehgal, K. L. (1999). Coldwater fish and fisheries in the Indian Himalayas: Rivers and streams. In: Fish and Fisheries at Higher Altitudes: Asia (Ed.: T. Petr). FAO Fisheries Technical Paper No. 385. Rome, Italy. http://www.fao.org/3/x2614e/x2614e00.htm#TopOfPage

Shah, R. D. T., Sharma, S., Haase, P., Jähnig, S. C., & Pauls, S. U. (2015). The climate sensitive zone along an altitudinal gradient in central Himalayan rivers: A useful concept to monitor climate change impacts in mountain regions. *Climatic Change*, *132*(2), 265–278. https://doi.org/10.1007/s10584-015-1417-z

Sharma, A., Dubey, V. K., Johnson, J. A., Rawal, Y. K., & Sivakumar, K. (2021a). Is there always space at the top? Ensemble modeling reveals climate-driven high-altitude squeeze for the vulnerable snow trout *Schizothorax richardsonii* in Himalaya. *Ecological Indicators*, *120*, 106900. https://doi.org/10.1016/j.ecolind.2020.106900

Sharma, A., Dubey, V. K., Johnson, J. A., Rawal, Y. K., & Sivakumar, K. (2021b). Introduced, invaded and forgotten: Allopatric and sympatric native snow trout life-histories indicate brown trout invasion effects in the Himalayan hinterlands. *Biological Invasions 23(4), 1-19*. https://doi.org/10.1007/s10530-020-02454-8

Shrestha, U. B., Gautam, S., & Bawa, K. S. (2012). Widespread climate change in the Himalayas and associated changes in local ecosystems. *PLoS ONE*, *7*(5), e36741. https://doi.org/10.1371/journal.pone.0036741

Singh, G., & Agarwal, N. K. (2013). Fish diversity of Laster stream, a major tributary of river Mandakini in Central Himalaya (India) with regard to altitude and habitat specificity of fishes. *Journal of Applied and Natural Science*, *5*(2), 369–374. https://doi.org/10.31018/jans.v5i2.334

Srivastava, P., Agnihotri, R., Sharma, D., Meena, N., Sundriyal, Y. P., Saxena, A., Bhushan, R., Sawlani, R., Banerji, U. S., Sharma, C., Bisht, P., Rana, N., & Jayangondaperumal, R. (2017). 8000-year monsoonal record from Himalaya revealing reinforcement of tropical and global climate systems since mid-Holocene. *Scientific Reports*, *7*(1), 14515. https://doi.org/10.1038/s41598-017-15143-9

Staudinger, M. D., Carter, S. L., Cross, M. S., Dubois, N. S., Duffy, J. E., Enquist, C., Griffis, R., Hellmann, J. J., Lawler, J. J., O'Leary, J., Morrison, S. A., Sneddon, L., Stein, B. A., Thompson, L. M., & Turner, W. (2013). Biodiversity in a changing climate: A synthesis of current and projected trends in the US. *Frontiers in Ecology and the Environment*, *11*(9), 465–473. https://doi.org/10.1890/120272

Thapliyal, M., Barthwal, M., Chandra, T., Bahuguna, S., Bhatt, J., & Thapliyal, A. (2013). Establishment of population of introduced brown trout (*Salmo trutta*) corelated to their feeding habits in river Asiganga, district Uttarkashi, Uttarakhand. *Environment Conservation Journal*, *13*, 15–21.

Travis, J. M. J., Delgado, M., Bocedi, G., Baguette, M., Bartoń, K., Bonte, D., Boulangeat, I., Hodgson, J. A., Kubisch, A., Penteriani, V., Saastamoinen, M., Stevens, V. M., & Bullock, J. M. (2013). Dispersal and species' responses to climate change. *Oikos*, *122*(11), 1532–1540. https://doi.org/10.1111/j.1600-0706.2013.00399.x

Wagle, S. K., Pradhan, N., & Shrestha, M. K. (2015). Morphological divergence of snow trout (*Schizothorax richardsonii*, Gray 1932) from rivers of nepal with insights from a morphometric analysis. *International Journal of Applied Sciences and Biotechnology*, *3*(3), 464–473. https://doi.org/10.3126/ijasbt.v3i3.13123

Woodward, G., Perkins, D. M., & Brown, L. E. (2010). Climate change and freshwater ecosystems: Impacts across multiple levels of organization. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1549), 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Xu, J., Grumbine, R. E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., & Wilkes, A. (2009). The Melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology*, *23*(3), 520–530. https://doi.org/10.1111/j.1523-1739.2009.01237.x

Yao, T. (2004). Recent glacial retreat in High Asia in China and its impact on water resource in Northwest China. *Science in China Series D*, *47*(12), 1065. https://doi.org/10.1360/03yd0256

Yao, T., Thompson, L. G., Mosbrugger, V., Zhang, F., Ma, Y., Luo, T., Xu, B., Yang, X., Joswiak, D. R., Wang, W., Joswiak, M. E., Devkota, L. P., Tayal, S., Jilani, R., & Fayziev, R. (2012). Third Pole Environment (TPE). *Environmental Development*, *3*, 52–64. https://doi.org/10.1016/j.envdev.2012.04.002

Zurell, D., Franklin, J., König, C., Bouchet, P. J., Dormann, C. F., Elith, J., Fandos, G., Feng, X., Guillera-Arroita, G., & Guisan, A. (2020). A standard protocol for reporting species distribution models. *Ecography*, *43*(9), 1261–1277. https://doi.org/10.1111/ecog.04960

TABLES

Table 1. Climatic variables used in the General Linear Model (GLM) to predict distribution of *Shizothorax progastus* in the Himalayas.

Predictor	Description	Spatial resolution
NDMIN	Natural Discharge Minimum	15 arc-second
MDR	Mean Diurnal Range	5 minute
MTCQ	Mean Temperature of Coldest Quarter	5 minute
PptS	Precipitation Seasonality	5 minute
PptWQ	Precipitation of Warmest Quarter	5 minute
TAR	Temperature Annual Range	5 minute
StrG	Stream Gradient	5 minute
PptDM	Precipitation of Driest Month	5 minute
ISO	Isothermality	
FLAcc	Flow Accumulation	30 arc-second

Table 2. Climatic variables used in the General Linear Model (GLM) to predict distribution of *Shizothorax richardsonii* in the Himalayas.

Predictor	Description	Spatial resolution
RIVA	River Area	15 arc-second
MTDQ	Mean Temperature of Driest Quarter	5 minute
FLAcc	Flow Accumulation	30 arc-second
AP	Annual Precipitation	5 minute
SLP	Slope	3 arc-second
ISO	Isothermality	5 minute
LSR	Land Surface Runoff	15 arc-minute
SPPT	Precipitation Seasonality	5 minute
MDR	Mean Diurnal Range	5 minute
TAR	Temperature Annual Range	5 minute
PptDM	Precipitation of Driest Month	5 minute

FIGURES

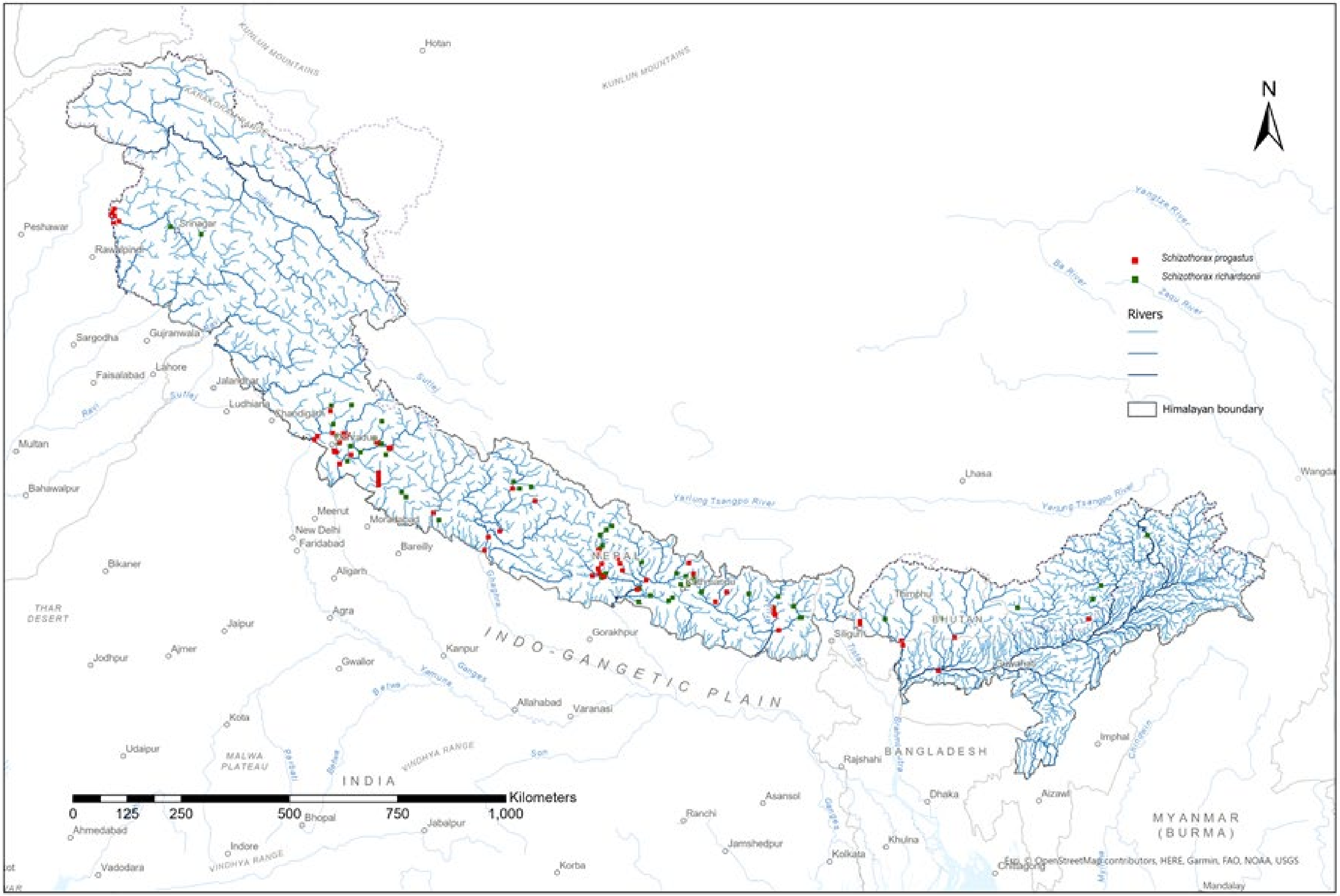

Figure 1. Occurrence points of study species (Snowtrout, *Schizothorax spp.*) in the core Himalaya region.

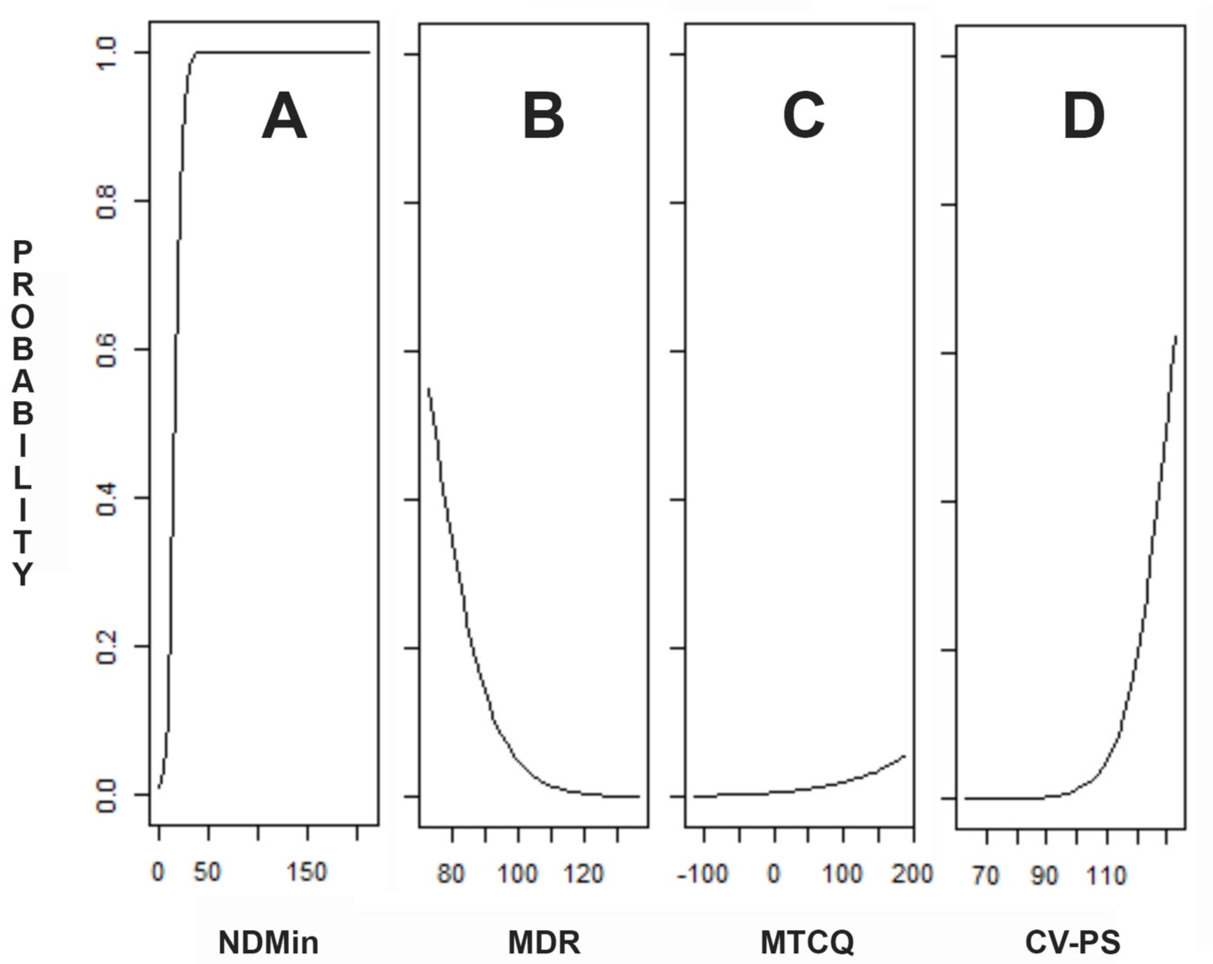

Figure 2. The partial response plots of the Generalized Linear Model (GLM) indicating a higher probability of occurrence for *Schizothorax progastus* given: (A) Natural Discharge Minimum (NDMin); (B) Lower Mean Diurnal Range (MDR); (C) Mean Temperature of Coldest Quarter (MTCQ); and (D) Precipitation Seasonality (PS).

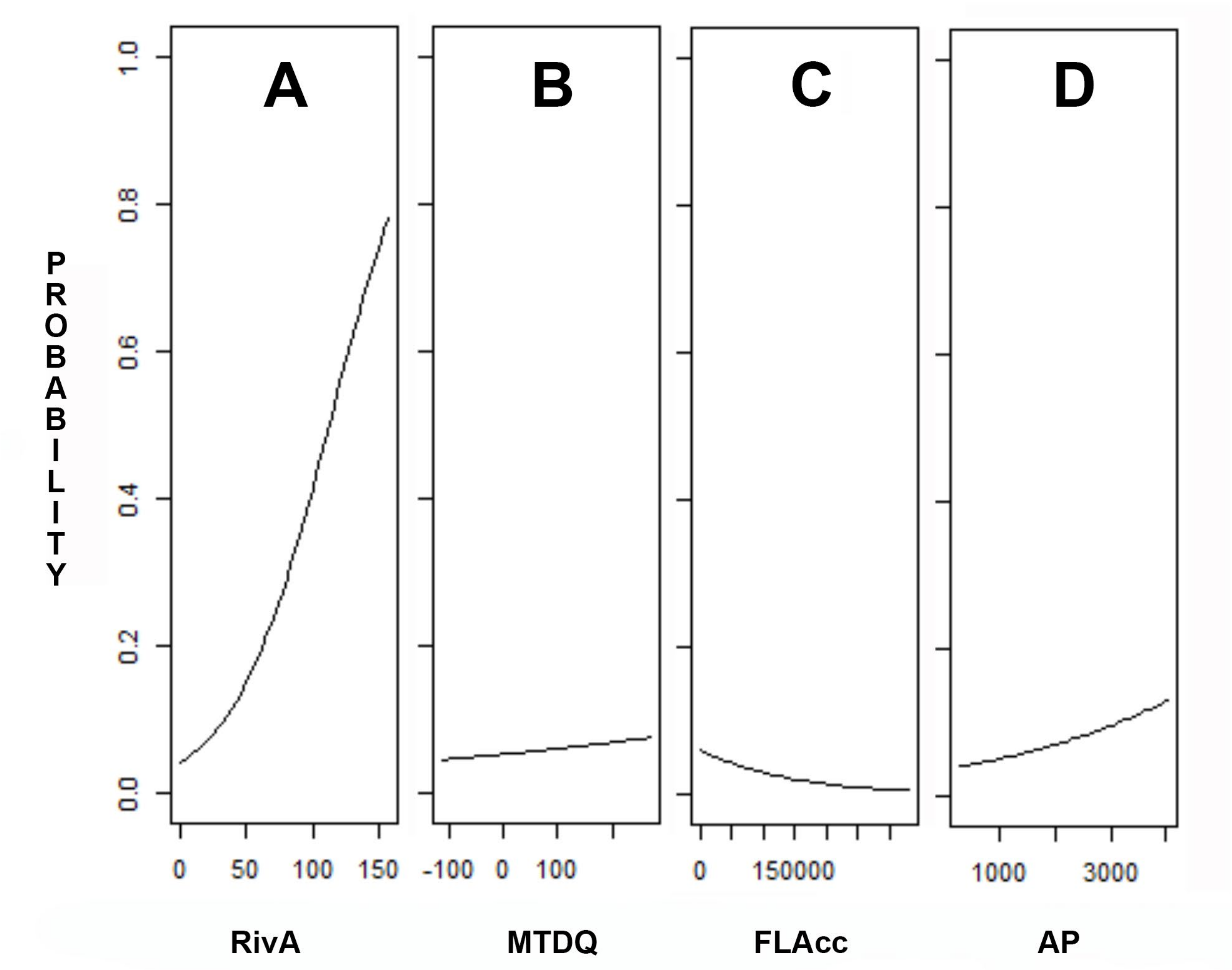

Figure 3. The partial response plots of the Generalized Linear Model indicate higher probability of occurrence of *Schizothorax richardsonii* given (A) River Area (in ha) (RivA); (B) Mean Temperature of Driest Quarter (MTDQ); (C) Flow Accumulation (FLAcc); and (D) Annual Precipitation (AP).

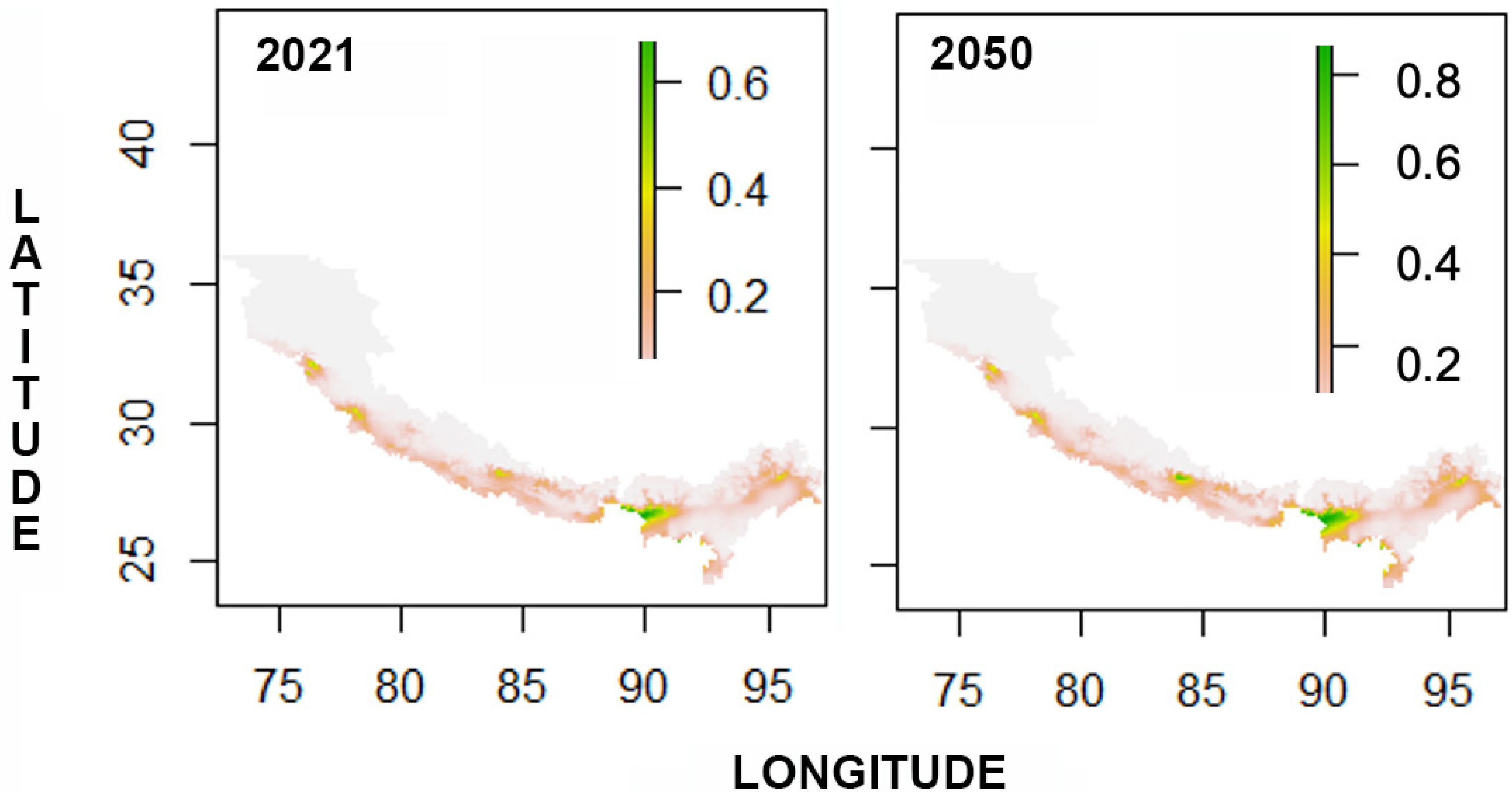

Figure 4. Potential occurrence of Himalayan *Schizothorax progastus* in 2012 (left) and 2050 (right).

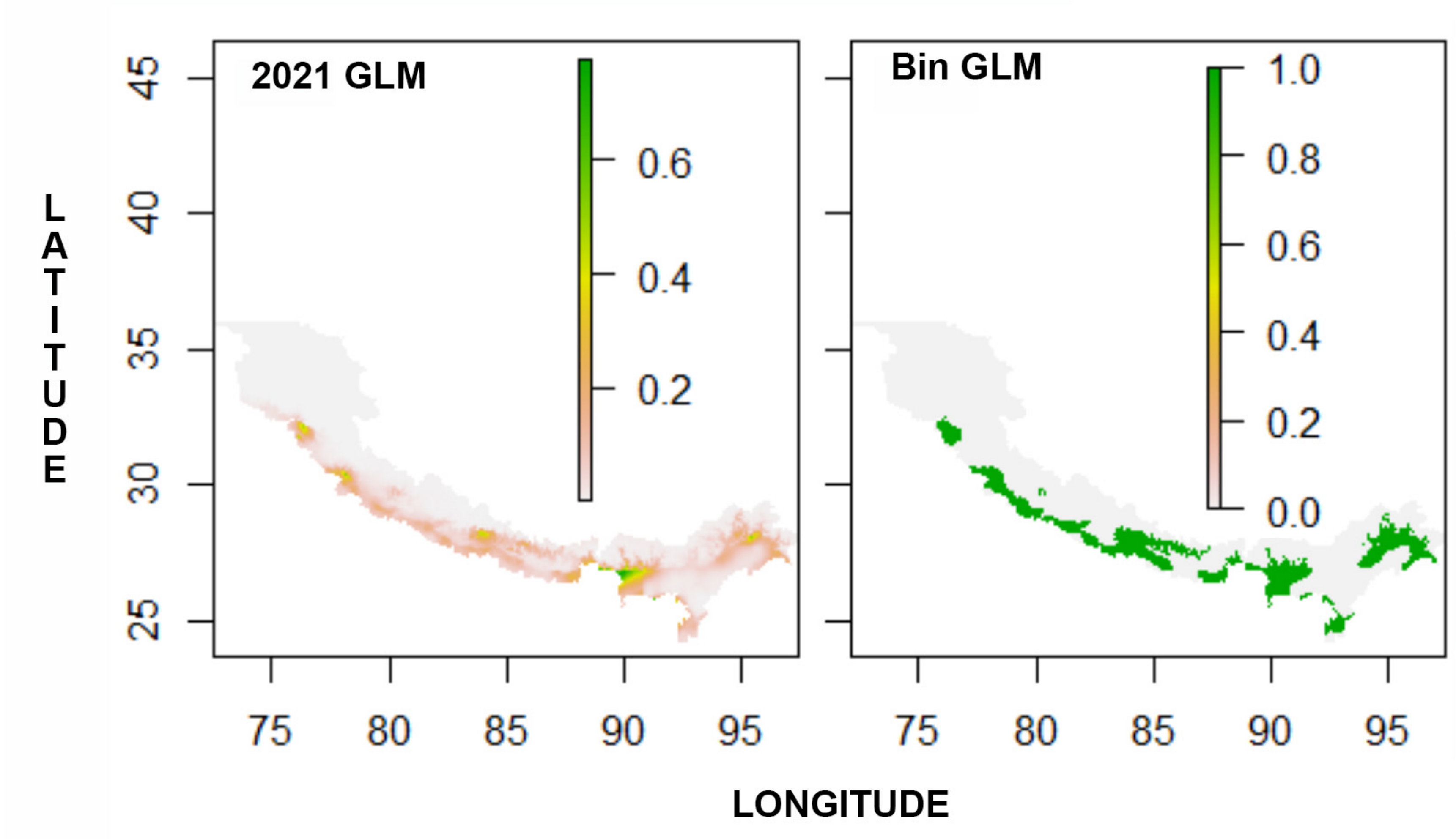

Figure 5. Binary prediction of occurrence for Himalayan *Schizothorax progastus* (right) based on current climate scenario (left).

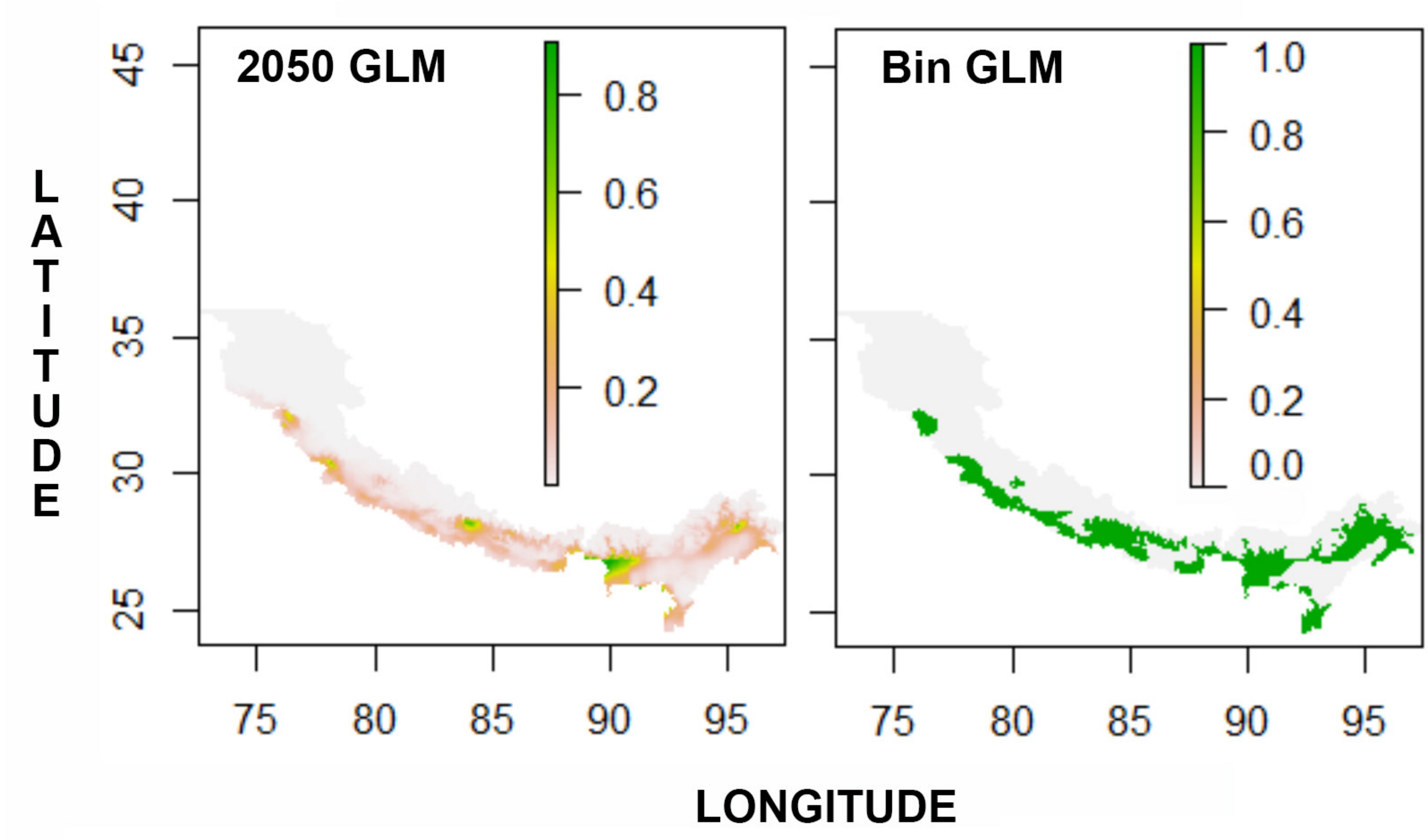

Figure 6. Binary prediction of occurrence for Himalayan *Schizothorax progastus* (right), based on a 2050 climate scenario (left).

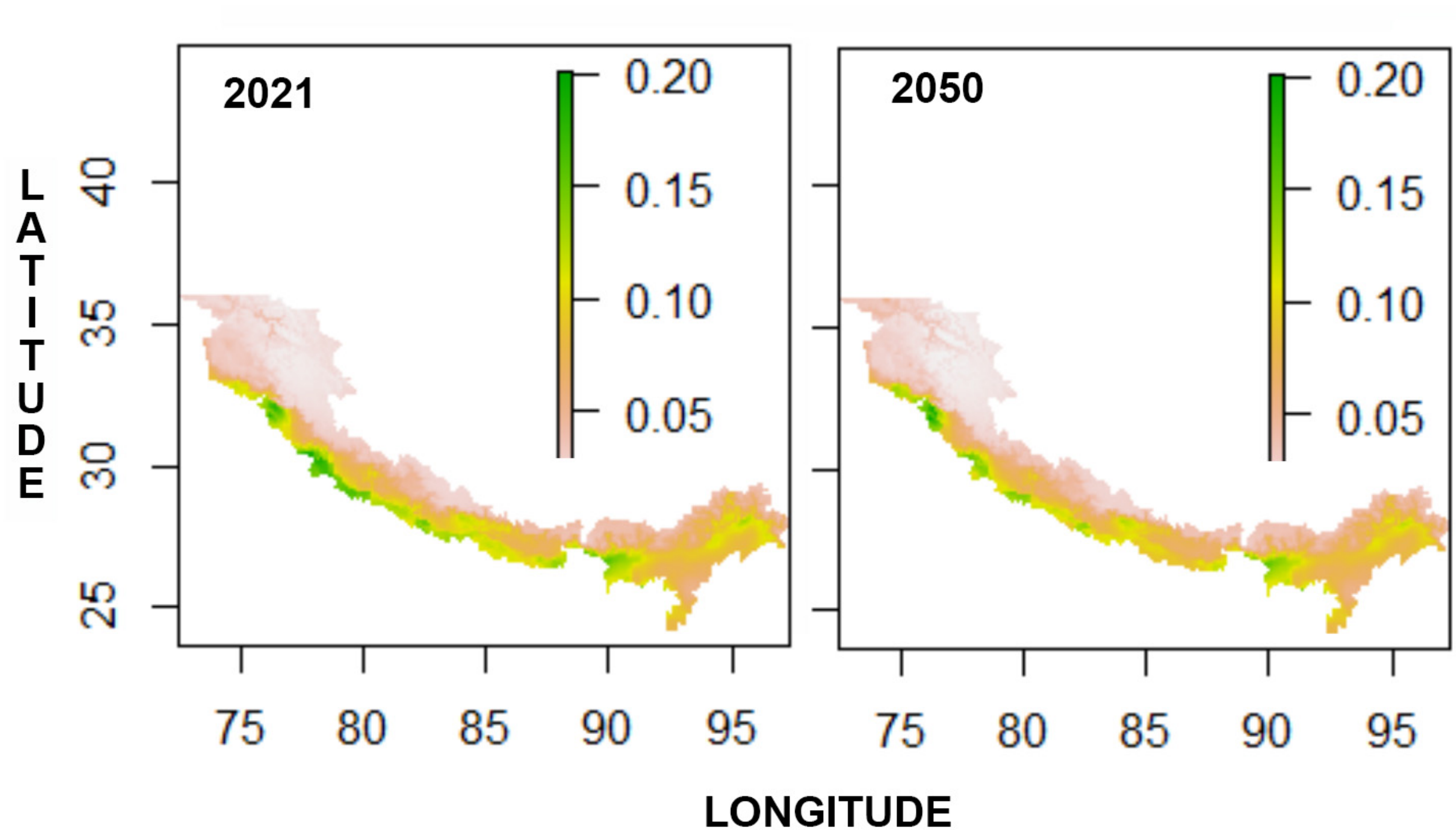

Figure 7. The occurrence probability of Himalayan *Schizothorax richardsonii* in 2021 (left) and 2050 (right).

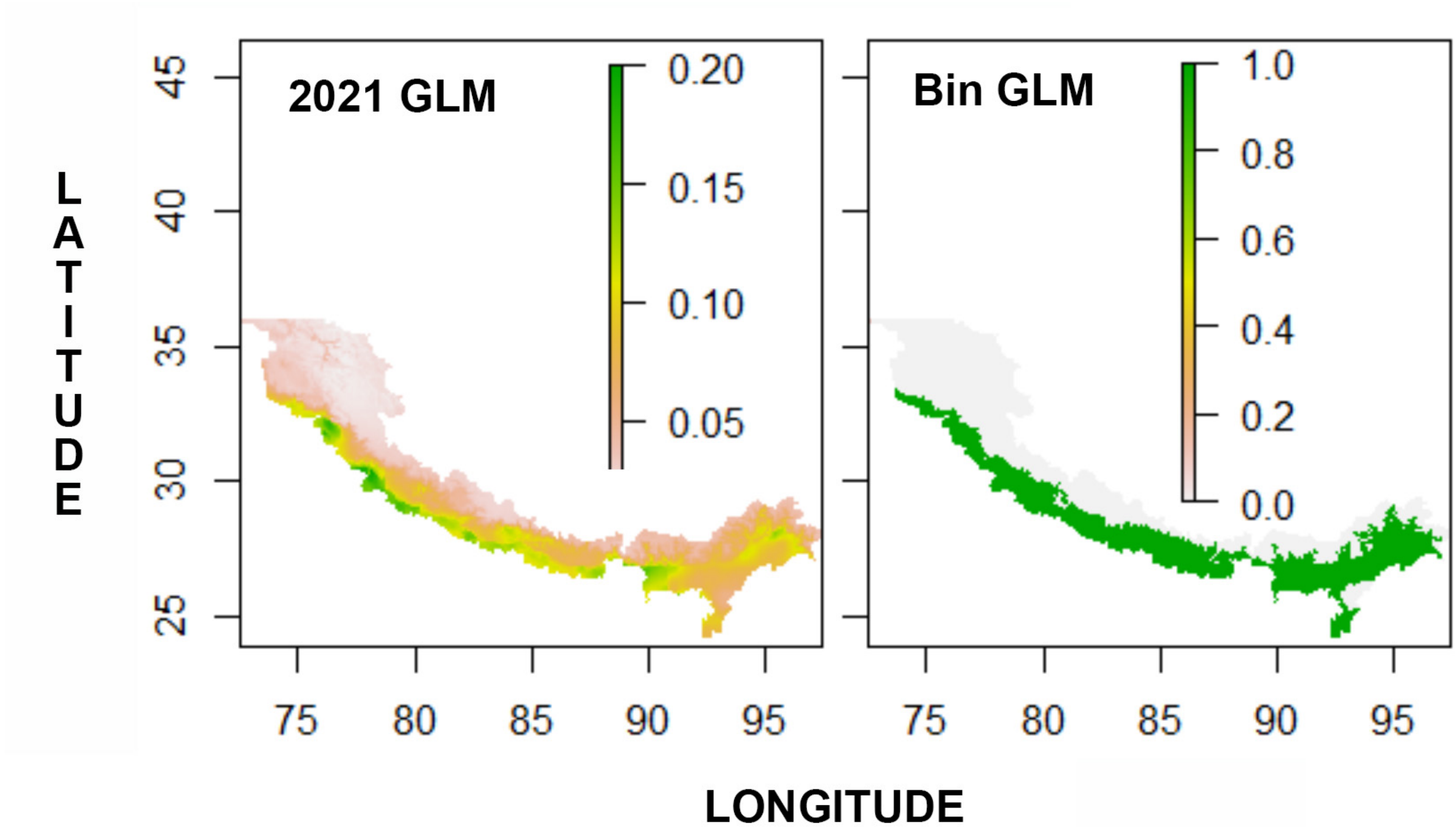

Figure 8. Binary prediction of occurrence for Himalayan *S. richardsonii* (right) based on current climate scenario (left).

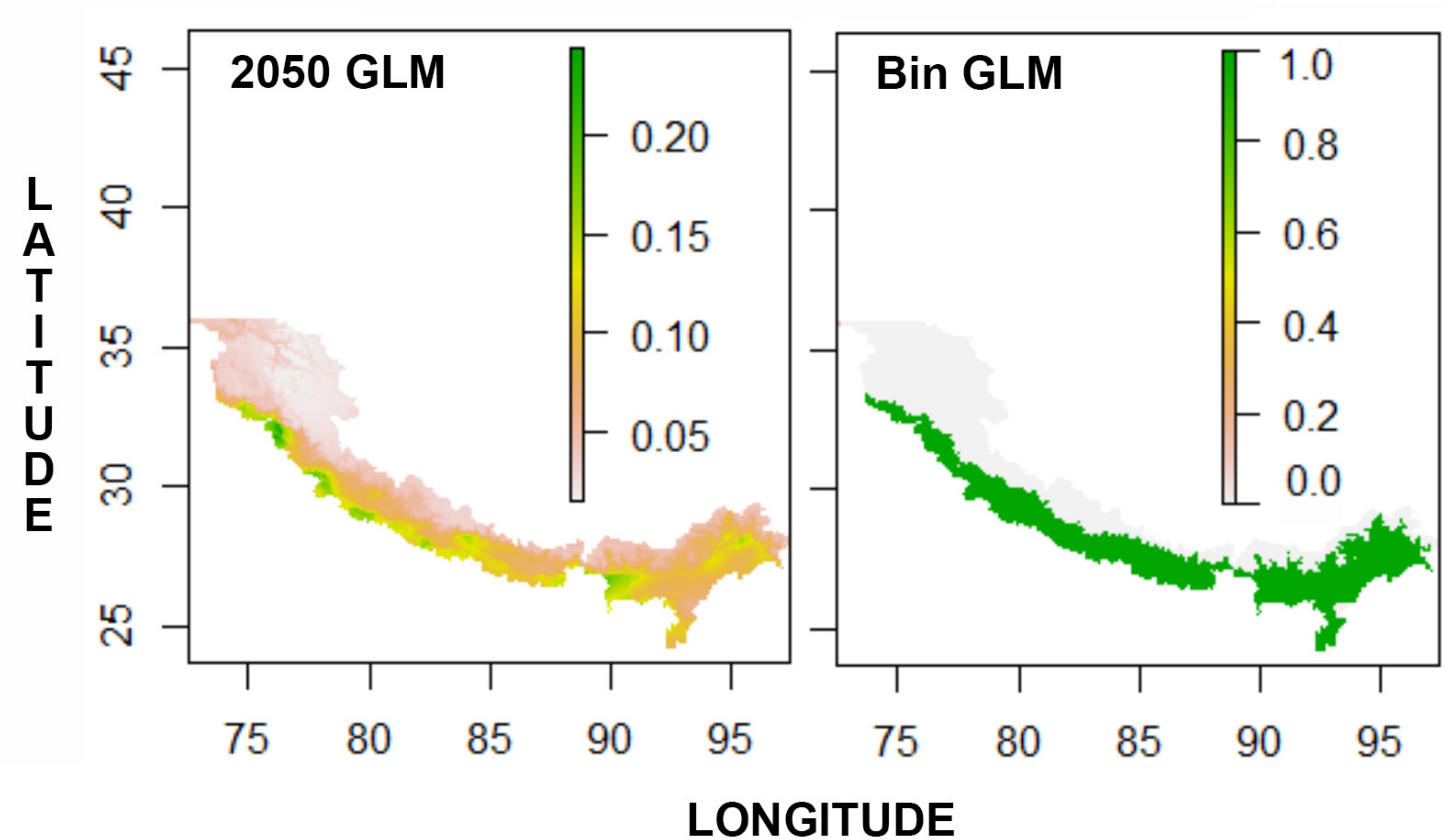

Figure 9. Binary prediction of occurrence for Himalayan *Schizothorax richardsonii* (right) based on 2050 climate scenario (left).

APPENDICES

Appendix 1. Bioclimatic variables derived from WorldClim database (http://www.worldclim.org).

Bioclimatic Variable	**Description**
AMT	Annual Mean Temperature
MDR	Mean Diurnal Range
ISO	Isothermality
TS	Temperature Seasonality (standard deviation x 100)
MTWQ	Maximum Temperature of Wettest Quarter
MTCM	Minimum Temperature of Coldest Month
TAR	Temperature Annual Range
MTWQ	Mean Temperature of Wettest Quarter
MTDQ	Mean Temperature of Driest Quarter
MTWQ	Mean Temperature of Warmest Quarter
MTCQ	Mean Temperature of Coldest Quarter
AP	Annual Precipitation
PptWM	Precipitation of Wettest Month
PptDM	Precipitation of Driest Month
PS	Precipitation Seasonality
PptWQ	Precipitation of Wettest Quarter
PptDQ	Precipitation of Driest Quarter
PptWQ	Precipitation of Warmest Quarter
PptCQ	Precipitation of Coldest Quarter

Appendix 2. Physiographic and hydrologic variables used in this study were derived from RiverATLAS shapefile datasets (http: //https://www.hydrosheds.org/page/hydroatlas).

Variables	Description	Spatial Resolution
Hydrology		
AND	Average Natural Discharge	15 arc-second
NDMin	Natural Discharge Minimum	15 arc-second
NDMax	Natural Discharge Maximum	15 arc-second
LSR	Land Surface Runoff	15 arc-second
RivA	River Area	15 arc-second
RiVOL	River Volume	15 arc-second
Physiography		
ELV	Elevation	3 arc-second
SLP	Slope	3 arc-second
STRG	Stream Gradient	3 arc-second