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Prediction of faunal distribution: Comparative evaluation of common spatial models using Himalayan bumblebee

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ABSTRACT

Species distribution models (SDMs) are computational tools utilized to predict the geographical range of species by analyzing occurrence data and environmental conditions. While multiple algorithms are available for implementing SDMs, studies focusing on pollinators like bumblebees (genus *Bombus*) in the Himalayas remain scarce, despite their ecological importance in forest and agroecosystems. We performed this work to identify the most effective SDM algorithms for modeling the distribution of genus *Bombus* in the Himalayas, thereby improving conservation strategies. We compared eight SDM algorithms, including Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF), along with an ensemble method. Evaluations were based on metrics such as the area under the curve (AUC) for receiver operating characteristic (ROC), true skill statistic (TSS), and statistical properties like skewness and kurtosis. Among single models, RF stood out for its strong ROC, TSS, and statistical properties. The ensemble approach, however, was overall the best option across these metrics. Researchers are encouraged to select SDM algorithms after careful evaluation of study-specific factors such as geographic area, sample size, species diversity, and spatial variables. The scientific community should develop and authenticate optimal standards that integrate biodiversity concepts, ecological traits, environmental factors, ecosystem-based approaches, and field data to ensure effective model assessment, informed decision-making, and policy formulation for conserving biodiversity and advancing sustainable development goals in the Himalayas.

1. Introduction

Over the past few decades, ecologists have focused on understanding the mechanisms that drive biodiversity patterns at different spatial scales (Dey et al., 2024). Species Distribution Models (SDMs) are such techniques that integrate environmental variables and occurrence of species to forecast the distribution of species across landscapes. When paired with geographic information systems (GIS), SDMs provide spatial predictions of species presence in areas lacking prior distribution data. Despite variations in algorithms, the underlying principles of SDMs are similar. First, the area of interest is divided into grid cells at a defined resolution. Next, species presence (or abundance) data are used as the dependent variable, while environmental factors such as elevation, temperature, and precipitation serve as predictor variables. The model then calculates the suitability of each grid cell for species occurrence based on these environmental inputs. The final goal of conservation, which is to protect maximum species and habitats with limited resources, depends on identifying distribution patterns and extinction

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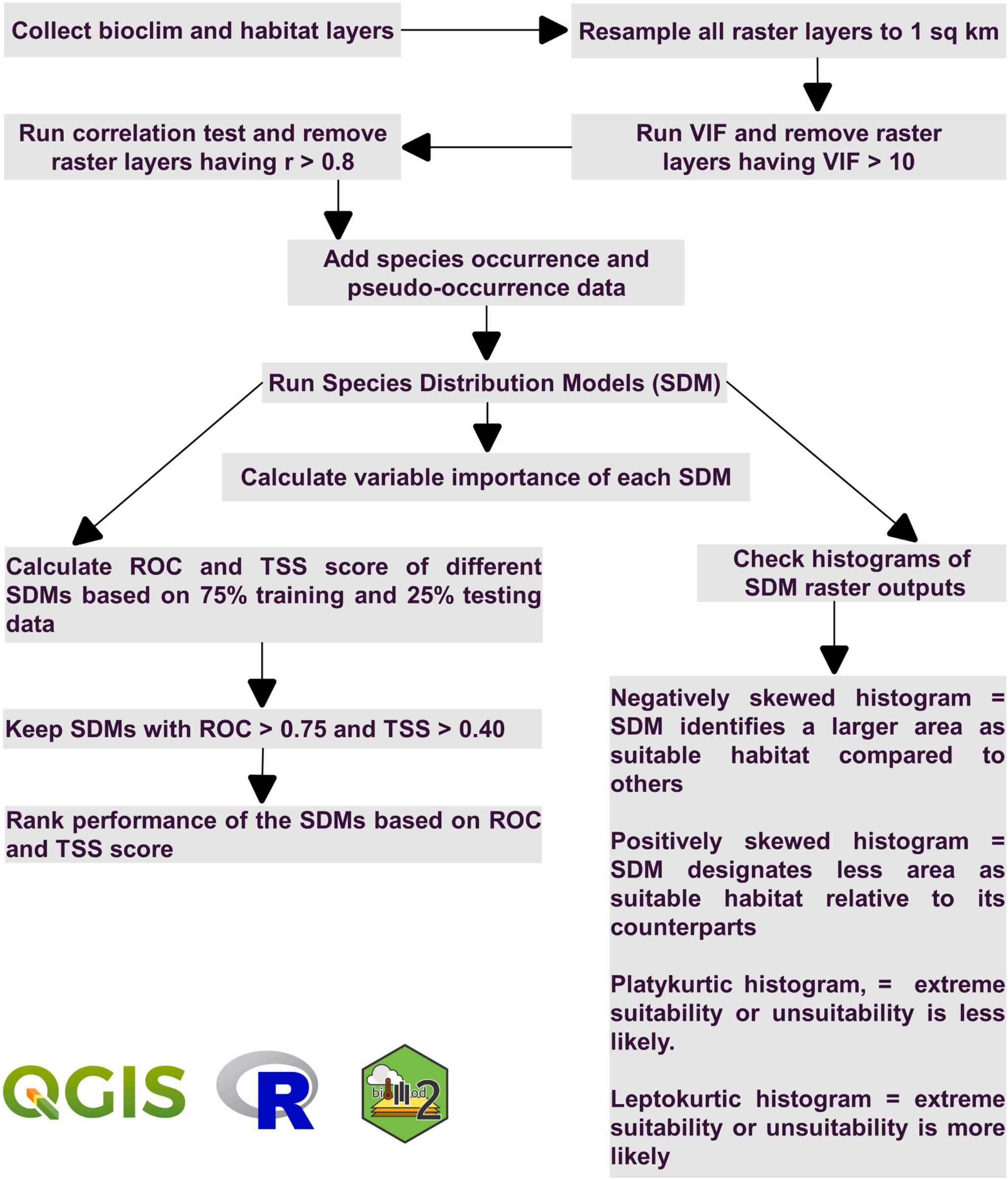

Fig. 1. The flow-chart of the preparation of species distribution models (SDMs) and their evaluation processes.

risks of biodiversity at regional and local scales, a process dependent on information about the spatial variation of species composition (De et al., 2023a). Thus, the SDMs allow for a better understanding of species distributions, even in regions with limited biological data, offering valuable insights for conservation and land-use planning.

Bumblebees (Hymenoptera: Apidae: Bombini: *Bombus*) are insect pollinators adapted to thrive in cold environments due to their thermoregulatory abilities, which allow them to remain active even at low temperatures. This adaptation is particularly crucial in high-altitude regions, where harsh conditions such as cold temperatures and reduced oxygen levels limit the activity of other pollinators (Dillon and Dudley, 2014). Bumblebees play an indispensable role in pollinating both wild and agricultural plants in these extreme environments, sustaining the health of mountain ecosystems and temperate zones. Easily recognized by their large, fuzzy bodies adorned with black-and-yellow stripes, bumblebees consist of approximately 265 species worldwide, with 62 species found in the Himalayas, nine of which are endemic to the region (Williams, 2022; https://bumblebeespecialistgroup.org/). However, recent studies have raised alarms about a significant decline in insect populations, especially among flying insects like bumblebees, in temperate regions (Eggleton, 2020). In America, Europe and Asia this decline is driven by several detrimental factors like climate change, competition with invasive species, attack of pathogen, loss of habitat and use of pesticides (Cameron and Sadd, 2020). In Asia, they are facing threats in the highlands of Japan, China, the Tibetan Plateau and the Himalayas (Nagamitsu, 2023; Singh et al., 2022a; Singh et al., 2024; Naeem et al., 2024). The loss of bumblebee species threatens to disrupt crucial pollination services, potentially triggering an extinction vortex where both pollinators and the plants they support face mutual extinction (Goulson et al., 2008). Furthermore, climate change is forcing bumblebees to shift their ranges to higher elevations, creating spatial mismatches between the bees and their plant pollinators (Egawa and Itino, 2019). The introduction of bumblebees for agricultural pollination has led some species to become invasive (López-Aguilar et al., 2024). Monitoring changes in bumblebee distribution and abundance is essential for effective conservation efforts in mountain regions to mitigate these risks.

The SDMs of pollinators are transformative tools for sustainable development in fragile ecosystems like the Himalayas. The SDMs serve as essential tools for pollinator conservation, aiding in various

Table 1
Comparative account of the receiver operating characteristic (ROC) and true skill statistic (TSS) values of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), Random Forest (RF) and Ensemble model.

Models	Evaluation methods	Mean	SD
ANN	TSS	0.507	0.075
	ROC	0.804	0.035
CTA	TSS	0.568	0.038
	ROC	0.827	0.024
FDA	TSS	0.512	0.028
	ROC	0.83	0.013
GAM	TSS	0.563	0.022
	ROC	0.842	0.014
GBM	TSS	0.589	0.025
	ROC	0.864	0.012
GLM	TSS	0.388	0.036
	ROC	0.745	0.018
MAXENT	TSS	0.507	0.034
	ROC	0.822	0.021
RF	TSS	0.69	0.02
	ROC	0.925	0.008
Ensemble	TSS	0.71	-
	ROC	0.945	-

sustainable development goals (SDGs). Firstly, they can identify critical habitats crucial for pollinators' survival, facilitating targeted conservation strategies that support terrestrial biodiversity (SDG 15). Secondly, SDMs forecast regions where pollination services are vulnerable to habitat degradation or climatic changes, enabling sustainable agriculture and enhancing food security (SDG 2). Thirdly, by examining climate change impacts on pollinator distributions, SDMs contribute to adaptive approaches for ecological resilience (SDG 13). Beyond ecological applications, SDMs can integrate citizen science contributions, encouraging community engagement and enhancing knowledge dissemination. This promotes educational development (SDG 4) and strengthens collaborative global efforts (SDG 17). By preserving essential services like pollination, SDMs reinforce sustainable natural resource use and boost long-term agricultural productivity (SDG 12). In addition, effective pollinator management contributes to poverty alleviation by improving agricultural yields and farmer incomes (SDG 1). It also promotes healthier environments by minimizing pesticide reliance and maintaining natural areas that benefit human well-being (SDG 3). Incorporating climate adaptation into pollinator strategies safeguards ecological services while creating employment opportunities in rural landscapes (SDG 8). By connecting biodiversity conservation with economic and social growth, SDM supports multiple SDGs and promotes resilience in Himalayan communities.

Recent works on SDMs for various animals and plants, including bumblebees, have increasingly adopted an ensemble approach, which combines multiple models rather than relying on a single one. However, research suggests that single-algorithm models can produce distribution maps with accuracy comparable to those generated by ensemble methods (Kaky et al., 2020). This raises questions about the supposed superiority of ensemble models, indicating that they may not offer a distinct advantage. The challenge, however, lies in determining which model is best suited for a particular species and habitat, as no single algorithm consistently outperforms others. Different algorithms can produce varying results depending on the species and environmental conditions studied. Despite the growing use of SDMs in biodiversity assessments, there are no universally accepted standards or best practices for building these models or evaluating their effectiveness. Given the importance of species distribution studies in shaping conservation policies, especially in the face of global climate changes standardized process for developing SDMs tailored to specific taxa and regions is needed to ensure accurate and actionable insights for conservation efforts.

The Himalayas, with rich biodiversity shaped by diverse landscapes and microclimatic conditions, provide a unique opportunity for genetic, evolutionary, and ecological studies, while the recent decline in species highlights the urgent need to understand the relationship between ecological factors and biodiversity for effective conservation and management (Singh et al., 2022b; De and Dwivedi, 2023; Parab et al., 2023). The Himalayas is the most extensively studied region among all Indian biogeographical zones for understanding the potential current and future distribution of species using SDMs. In the Himalayan ecosystem, bumblebees play a crucial ecological role, yet studies focusing on their distribution models are sparse and rely mainly on single-algorithm methods (Singh et al., 2022a; Singh et al., 2024). The present study aims to determine which algorithm performs better for modeling the distribution of bumblebees in the Himalayan mountain environment, providing insights that could lead to more accurate and effective conservation strategies for this important species.

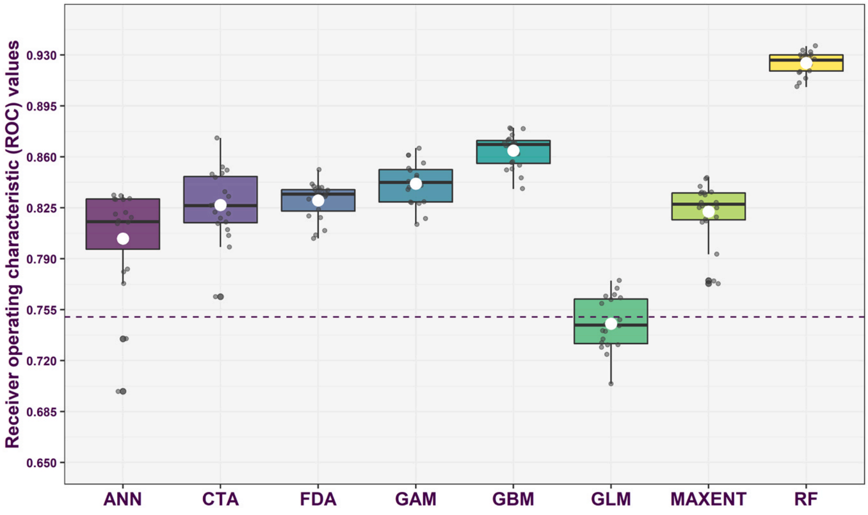

Fig. 2. Comparative account of the receiver operating characteristic (ROC) values of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF).

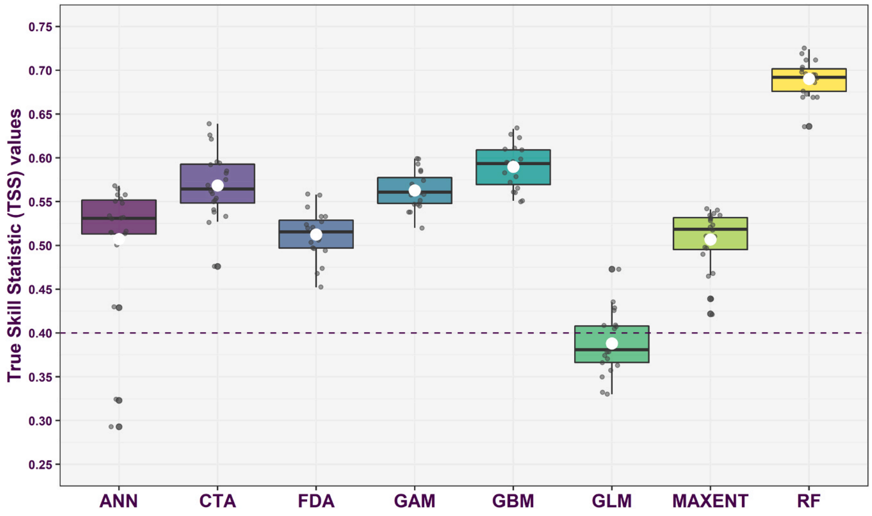

Fig. 3. Comparative account of the true skill statistic (TSS) values of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF).

2. Study area

For this study we chose the Himalayan and Trans-Himalayan territories of India, Nepal, and Bhutan, spanning a geographic extent from to 26.395343°N to 37.088362°N and to 97.412895°E to 72.513077°E. The Himalayas, formed approximately 55 million years ago through the convergence of the Indian and Eurasian Plates, is a tectonically active and young mountain system. Known for its complex topography and ecological richness, this region exhibits significant biodiversity, diverse landscapes, and distinct climatic conditions. The Himalayan range is divided into four biogeographic provinces namely North-West Himalaya, West Himalaya, Central Himalaya, and Eastern Himalaya (Rodgers et al., 2000). The Trans-Himalayan region, recognized as a high-altitude cold desert, is subdivided into the Ladakh Mountains, the Tibetan Plateau, and the Sikkim Plateau (Rawat et al., 2023). The Ladakh Mountains include areas such as Kargil, Nubra, and Zanskar in Ladakh and parts of Himachal Pradesh like Lahaul-Spiti and Kinnaur, while the Tibetan Plateau encompasses the Changthang region of Ladakh and northern Uttarakhand. Besides being climatically sensitive, the region also faces ongoing geological instability, which increases its risk of earthquakes and other natural disasters.

3. Data

We collected occurrence records of bumblebees through a combination of fieldwork and literature surveys. We performed fieldwork between May 2018 and February 2020 in the western Himalaya, specifically in the Great Himalayan National Park Conservation Area (GHNPCA), and the Trans-Himalayan regions of Lahaul-Spiti and Leh-Ladakh. In GHNPCA, we sampled bumblebees from the Parvati, Tirthan, Sainj, and Jiwa Nala valleys. In Ladakh, we gathered samples from the Shyok, Nubra, and Indus valleys, while in Lahaul, our sampling sites were the Bhaga, Chandra, Miyar, and Chenab valleys. At each site, we made a single visit and recorded species occurrences by direct observation along roadsides, forest trails, and hilly treks during the day. We collected specimens using the sweep netting method, with sampling locations purposefully chosen near streams due to the higher abundance of flowering plants, which are important for bumblebee foraging. Our methodology relied on opportunistic sampling, which offers insights into ecological changes, especially on a large scale (van Strien et al., 2013). We identified 13 species from the field using identification keys for Indian bumblebees (Saini et al., 2015), and submitted voucher specimens to the museum. For further details on the sampling methods, please refer to Singh et al., 2022 and Singh et al., 2024. Through an extensive literature survey, we gathered secondary data on bumblebee occurrences across the Trans-Himalaya and Western Himalaya regions (Williams, 1991; Williams, 2004; Williams et al., 2010; Saini et al., 2011; Streinzer et al., 2019). Although these references lacked GPS coordinates for most species, they provided the names of specific localities and their elevational ranges. Given the narrow foraging range of bumblebees (Gómez-Martínez et al., 2020), we used Google Earth Pro to carefully extract GPS coordinates for each species at each location (Singh et al., 2024). To standardize the data, we constructed a 1 km^2 grid covering the entire study area. As the home range of bumblebees is typically 250–350 m from the nest (Dramstad, 1996), this grid size maximized the encounter rate for individual species. We eliminated duplicate species records within the same grid to ensure data accuracy. This led us to make occurrence data on a total of 32 species of the genus *Bombus* (*B. abnormis*, *B. agrorum*, *B. asiaticus*, *B. avinoviellus*, *B. breviceps*, *B. eximius*, *B. ferganicus*, *B. festivus*, *B. flavescens*, *B. funerarius*, *B. genalis*, *B. grahami*, *B. haemorrhoidalis*, *B. hypnorum*, *B. lapidarius*, *B. lemniscatus*, *B. lepidus*, *B. lucorum*, *B. luteipes*, *B. melanurus*, *B. miniatus*, *B. mirus*, *B. parthenius*, *B. pressus*, *B. pyrosoma*, *B. rufofasciatus*, *B. semenovianus*, *B. simillimus*, *B. subtypicus*, *B. trifasciatus*, *B. tunicatus* and *B. waltoni*) from 1177 locations.

For analysis we collected bioclimatic layers (WorldClim version 2) from worldclim gridded climate data (Fick and Hijmans, 2017) (https://www.worldclim.org/data/index.html), land use land cover (LULC) data (Buchhorn et al., 2020) from https://land.copernicus.eu/global/products/lc and human footprint (Venter et al., 2018) from NASA Socioeconomic Data and Applications Center (SEDAC) (https://sedac.ciesin.columbia.edu/data/set/wildareas-v3-2009-human-footprint).

4. Methods

We resampled all the spatial layers to 1 km^2 resolution by nearest neighbour method, as this method is appropriate for both continuous and categorical layers (Johnson and Clarke, 2021). To avoid multicollinearity, we tested both the variance inflation factor (VIF), removing variables with $\text{VIF} > 10$, and Pearson's correlation coefficient (r), excluding variables with $r > 0.80$. For modeling we used LULC, human footprint and six bioclimatic layers namely Bio 2 (mean diurnal range), Bio 7 (temperature annual range), Bio 10 (mean temperature of warmest quarter), Bio 12 (annual precipitation), Bio 15 (precipitation seasonality), and Bio 19 (precipitation of coldest quarter). We performed all

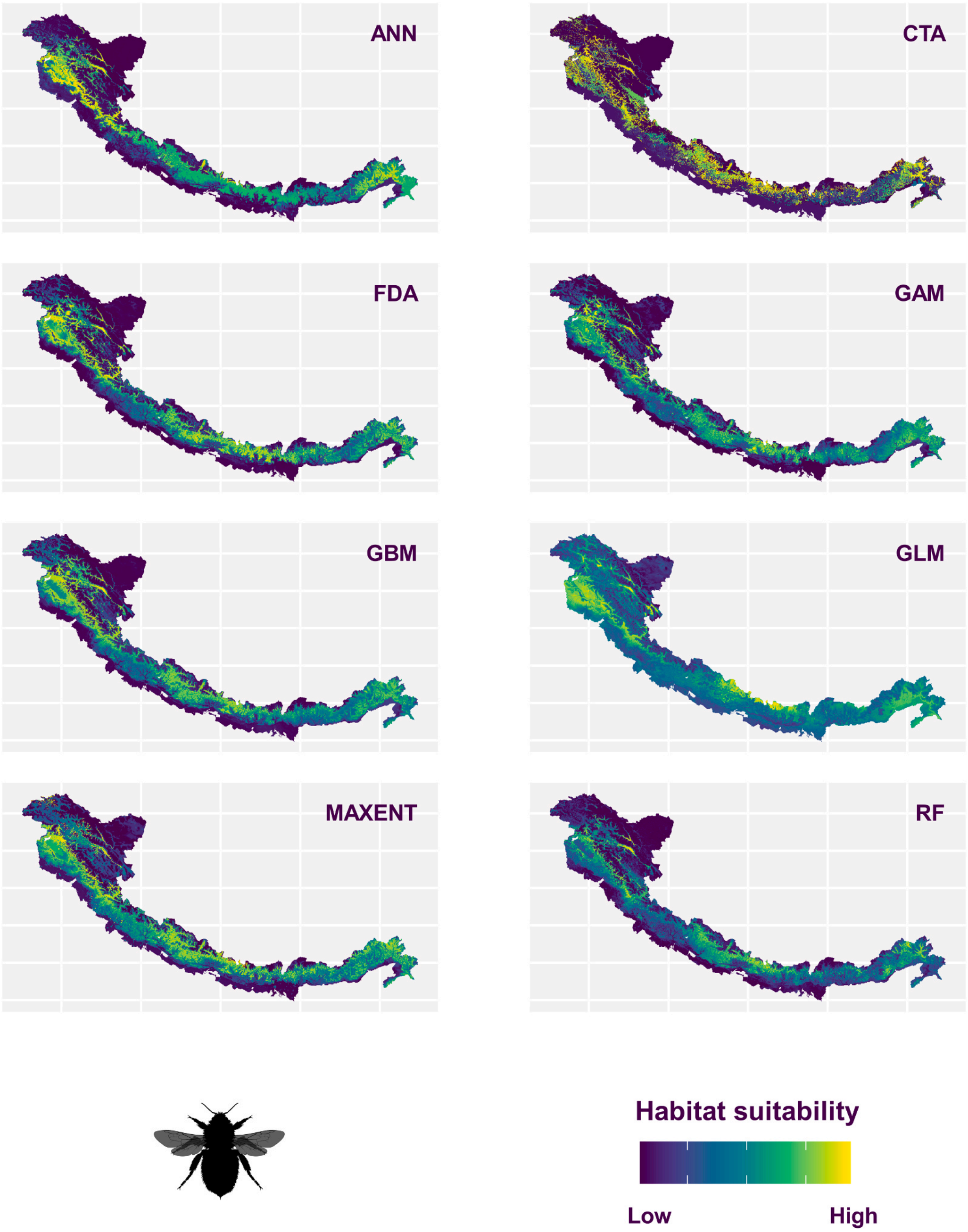

Fig. 4. Comparative account of habitat suitability of bumblebees for eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF).

the raster processing work in open source QGIS software version 3.28.11 (https://www.qgis.org/en/site/forusers/download.html), R package ‘usdm’ (Naimi et al., 2013) and ‘raster’ (Hijmans, 2022).

Species within the same genus often occupy distinct environmental niches, making it preferable to model taxa at the finest possible taxonomic resolution (Benkendorf et al., 2023). However, traditional SDMs generally assume that species within a genus exist independently, a scenario rarely observed in natural ecosystems. Genus-level models help overcome this limitation by incorporating ecological relationships among species. These models, when combined with co-occurrence data and environmental factors, improve predictive accuracy, making them a valuable resource for understanding distributions (Stas et al., 2020). They can inform conservation strategies by highlighting areas that may support multiple species within a genus, thus enhancing ecological resilience (Clarke-Crespo et al., 2020; Moradmand and Yousefi, 2022). Moreover, genus-level data is typically sufficient in distribution modeling for assessment of biodiversity as well as conservation planning (Benkendorf et al., 2023). This approach has been shown to be effective across various taxa, offering practical insights into species distribution patterns (Stas et al., 2020; Greenspan et al., 2021; Ross et al., 2021; Fan et al., 2022; Claerhout et al., 2023; Wan et al., 2023). In this work, we considered all species of bumblebees under the genus *Bombus* as a single taxonomic unit for distribution modeling because all of them are high-elevation specialist pollinators having similar habitat requirements.

A model can yield useful results if it is generated with random pseudo-absences (PA) for an adequate set of presence locations. To achieve optimal results in SDMs, it is recommended to run a minimum of

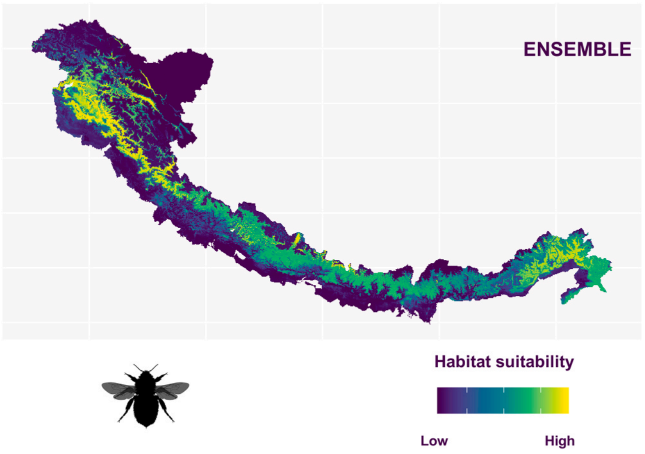

Fig. 5. Habitat suitability of bumblebees for as per ensemble species distribution model.

10 iterations for each model using at least 1000 pseudo-absences with equal prevalence between presences and absences (Barbet-Massin et al., 2012). For this study we randomly generated 1117 pseudo-absences locations across the study area, matching the number of observed bumblebee presence locations. We generated the same number of pseudo-absences as presences to avoid problems associated with unbalanced prevalence (Titeux, 2006; Mateo et al., 2012). We independently ran eight modeling algorithms namely Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy (MAXENT), and Random Forest (RF). During modeling, we kept Prevalence = 0.5 to ensure equal weighting of presences and absences, as this approach yields the best results (Barbet-Massin et al., 2012; Thuiller et al., 2020). To evaluate model performance, we used the area under the curve (AUC) of the receiver operating characteristic (ROC) and true skill statistic (TSS) based on 20 model runs with a randomly sampled training and testing data set of 75 % and 25 % of the presence records, respectively. We compared each model based on mean values (of 20 model runs) of ROC and TSS score. Apart from individual modeling, we also used an ensemble approach where we took the mean and variance of all the models. We included a model in ensembling if it had AUC > 0.75 and true skill statistics (TSS) > 0.4; as these values are considered minimum evaluation scores for a useful model (Engler et al., 2011). In order to compare values among models, we normalized variable importance per model to 100 (Sherpa et al., 2021). We performed all the modeling and evaluation procedure using the R package ‘biomod2’ (Thuiller et al., 2020).

To evaluate the performance of different SDMs, we compared the histograms of their raster outputs. A raster histogram is a bar chart depicting the distribution of pixel values in a raster image, with the x-axis representing pixel values and the y-axis indicating pixel counts. In the context of SDMs, the x-axis shows habitat suitability, ranging from 0 (not suitable) to 1 (most suitable), while the y-axis represents the number of pixels corresponding to each suitability score. A negatively skewed histogram suggests that more pixels are assigned higher suitability scores, indicating that the SDM identifies a larger area as suitable habitat compared to others. Conversely, a positively skewed histogram implies fewer pixels are deemed highly suitable, meaning this SDM designates less area as suitable habitat relative to its counterparts. This comparison helps in assessing how different SDMs categorize habitat suitability. A platykurtic histogram, with a kurtosis value less than 0, indicates a flatter distribution with fewer outliers, meaning the pixel values are more evenly spread, and extreme suitability or unsuitability is less likely. Conversely, a leptokurtic histogram, with a kurtosis value greater than 0, suggests a sharper peak and a higher likelihood of outliers. In SDMs, this implies that certain areas may be unusually marked as highly suitable or unsuitable for a species. We calculated the histogram of each SDM raster in R package raster (Hijmans, 2022), then calculated skewness and kurtosis of each histogram as described by Joanes and Gill (1998) in R package ‘e1071’ (Meyer et al., 2022). A complete workflow is given in the Fig. 1.

We performed statistical and spatial analysis in R (version 4.2.1) language and environment for statistical computing (R Core Team, 2022).

5. Results

In this study, we evaluated model performance using both ROC and TSS metrics. The ROC values above 0.8 are generally considered reasonable and informative, but it can be biased (Swets, 1988). To mitigate this, we also used TSS, which is prevalence-independent, with values over 0.4 being deemed acceptable (Araújo et al., 2005). The evaluation of eight SDMs based on TSS and ROC values revealed significant differences in performance. The Ensemble model stood out with the highest TSS of 0.710 and ROC of 0.945, closely followed by RF with a TSS of 0.690 and ROC of 0.925, indicating their superior predictive accuracy and discrimination capabilities. Moderate performers included GBM at TSS 0.589 and ROC 0.864, GAM at TSS 0.563 and ROC 0.842, CTA at TSS 0.568 and ROC 0.827, and FDA at TSS 0.512 and ROC 0.830. In contrast, ANN and MAXENT both scored a TSS of 0.507 with ROC values of 0.804 and 0.822, respectively, while the GLM performed the poorest with a TSS of 0.388 and ROC of 0.745. Table 1, Figs. 2 and 3 provide a comparative account of the ROC and TSS values of eight SDMs, while Fig. 9 A presents the ROC and TSS values for the ensemble SDM.

All SDMs exhibit positive skewness, indicating right-skewed distributions where data is concentrated towards the lower values, with a few extreme higher values. The CTA has the highest skewness (1.186), implying the most pronounced asymmetry, while GLM has the lowest skewness (0.293), suggesting a distribution closer to symmetric. For kurtosis, all models are platykurtic, show negative values, signifying distributions with lighter tails and flatter peaks. The GBM (-1.206) and MAXENT (-1.189) have the most negative kurtosis, indicating very flat distributions with light tails. In contrast, CTA (-0.349) has the least negative kurtosis, meaning its distribution, while still flatter than normal, is closer to having normal-tailed behavior. Overall, these results suggest that all SDMs, while skewed to the right across all models, differ in their tail behavior and peak flatness. Fig. 4 presents a comparative account of habitat suitability for eight SDMs, and Fig. 5 shows the habitat suitability for the ensemble SDM. Fig. 6 provides a comparative account of the histograms for eight SDMs, while Fig. 7 presents the histogram for the ensemble SDM.

In this work, we found that among the bioclimatic variables, Bio 10 consistently emerged as the most influential factor across multiple models, with notable contributions in GBM at 53.259 %, Ensemble model at 38.777 %, MAXENT at 38.095 % and CTA at 33.168 %. Other significant bioclimatic variables included Bio 12 and Bio 2, which also showed substantial contributions across several models like CTA, Ensemble, FDA, GAM, GLM and MAXENT. Models such as ANN and RF demonstrated a relatively even distribution of importance among the environmental variables considered. In both of these models, the contribution of all the bioclimatic variables range between 10 % and 27 %. In contrast, anthropogenic factors such as Human Footprint and LULC exhibited lower contributions, across all models, with Human Footprint values dropping to 0.018 % in GLM and LULC values dropping to 0.095 % in GBM, indicating that while human impacts were present, they may not have been as immediate or influential as climatic factors in shaping bumblebee distribution. Table 2 and Fig. 8 provides a comparative account of variable contribution for eight SDMs, and Fig. 9b presents the variable contribution for the ensemble SDM.

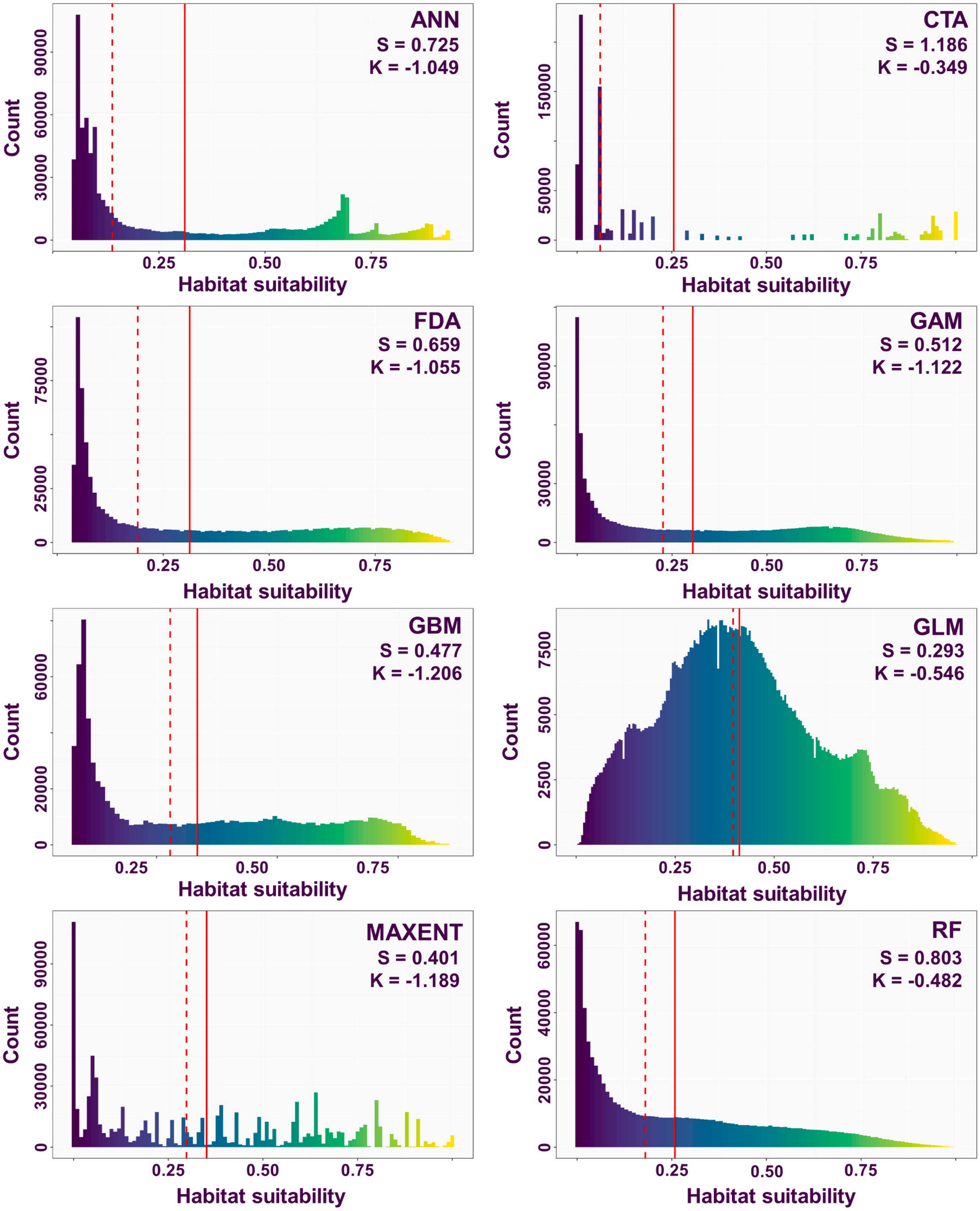

Fig. 6. Comparative account of the histograms of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF). The bins for each histogram were calculated by following Freedman and Diaconis (1981). The vertical straight line indicates mean value and vertical dotted line indicates median value. The x-axis shows habitat suitability (0 = not suitable, 1 = most suitable) and the y-axis represents the number of pixels corresponding to each suitability score. The S represents skewness and K represents kurtosis score for each histogram.

6. Discussion

There is a growing need for research on insect diversity in a changing world, with SDMs serving as the primary tool to assess the impacts of climate change, land use changes, and other environmental shifts on species distributions, while also supporting conservation planning and selection. Since mountain ecosystems consist of unique environments for living creatures due to their powerful climate gradients, they are crucial for studying the effects of climate change on biodiversity. In mountain variation in abiotic factors especially changes in temperature and precipitation can influence diversity and activity pattern of animals (Singh et al., 2021). Conservation biologists prioritize critical biodiversity areas to maximize conservation impact efficiently using limited resources (De et al., 2023a, De et al., 2023b). At present time, research on biodiversity has shifted from only documentation of biodiversity to finding the mechanisms that shape the biogeography, particularly in the

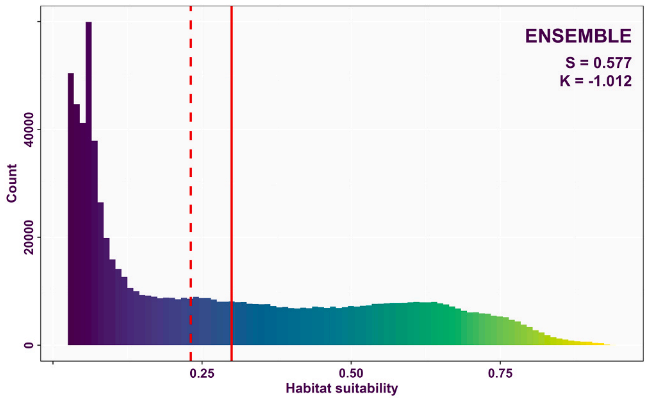

Fig. 7. Histogram of the ensemble species distribution model. The bin for the histogram was calculated by following Freedman and Diaconis (1981). The vertical straight line indicates mean value and vertical dotted line indicates median value. The x-axis shows habitat suitability (0 = not suitable, 1 = most suitable) and the y-axis represents the number of pixels corresponding to each suitability score. The S represents skewness and K represents kurtosis score.

light of climate and habitat change. Numerous ecological models have been developed for diverse purposes, such as biodiversity conservation, protecting rare species, and assessing habitat suitability. In many applications of SDMs, the predictive performance is important and most often, the users look for the algorithm that delivers most predictions (Hao et al., 2020). The predictive performance of SDM algorithms depends on situations and any single class of algorithms is not identified that can predict species distribution better than others consistently (Segurado and Araújo, 2004). It has been suggested that users may build an 'ensemble' prediction by combining predictions across different modeling methods to achieve better prediction, which is used in many recent SDM studies (Araujo and New, 2007; Hao et al., 2020). However, some study (Hao et al., 2020) found that there was no certain advantage to using ensembles over individual models.

In this work, the evaluation of eight SDMs for predicting Bumblebee habitats in high-altitude regions revealed important differences in model performance based on TSS and ROC values. The RF and Ensemble models performed the best, showing high agreement between predicted and observed distributions and strong discriminatory ability between presence and absence of species. In contrast, the GLM had poor results, making it unreliable for predicting Bumblebee distributions. The ANN also failed to deliver impressive outcomes, while the Generalized Boosted Model GBM offered a solid balance of accuracy and discrimination. Models such as the GAM and FDA performed moderately well, making them suitable for applications where a moderate level of accuracy was sufficient. Meanwhile, the MAXENT and CTA models showed intermediate results. Although they had decent ROC values, their lower TSS scores suggested they might not be as reliable in distinguishing between true positives and false positives.

The skewness and kurtosis values of the SDM raster data for Bumblebee distribution in high altitude provide critical insights into the behavior of each model's output. The asymmetry of distribution is measured by skewness and positive skewness values indicate right-skewed distribution. Higher skewness values indicate presence of outliers. In this work, we observed that the CTA had the highest skewness, indicating that its distribution was right-skewed, meaning it had a tendency to produce higher predicted values compared to other models. In contrast, GLM showed the lowest skewness, indicating a more symmetrical distribution that could suggest more consistent predictions. Kurtosis assesses the 'tailedness' of a distribution, with negative values indicating a platykurtic distribution, where more probability mass is concentrated around the shoulders (one standard deviation from the mean) and less around the tails (extreme values), making such distributions less likely to generate outliers, whereas distributions with high kurtosis are more prone to producing outliers. In this work, we observed that the GBM and GAM displayed the lowest kurtosis values, implying flatter distributions with fewer outliers compared to models like CTA, which retained some extreme values (predicted species distribution values that were significantly above average compared to other predictions made by the model). The RF model showed moderate skewness and relatively low kurtosis, suggesting that it captured variability effectively while remaining robust against outliers. The ANN also presented a good option with higher skewness than RF but slightly lower kurtosis, indicating its capability to model complex relationships while managing extreme values reasonably well. Models such as GLM and MAXENT, with their lower skewness and kurtosis, were suitable for scenarios where extreme values were less prevalent, providing stable predictions overall. Finally, the ensemble approach offered a balanced method by combining multiple models to enhance predictive performance and reduce uncertainty, making it a very viable option. This result aligned with Tripathi et al. (2024), who advocated for ensemble approaches to study the effects of climate change on biodiversity in India's biogeographic zones.

The RF model effectively captures nonlinear relationships and interactions among environmental variables without predefined functional forms, aligning well with complex species–environment dynamics (Hao et al., 2019). This flexibility enhances model fit and generalization across varying conditions. RF also performs well with imbalanced, limited, or presence-only datasets, offering reliable predictions where data are sparse (Valavi et al., 2021). By averaging multiple decision trees, RF minimizes variance and over fitting, producing stable results even with noisy inputs (Kaky et al., 2020). Species distributions often form clusters, reflecting inherent spatial structure and autocorrelation rather than random placement, and certain habitats naturally provide more suitable conditions than others. In this context, RF excels because it can process many environmental predictors without being troubled by collinearity and can easily capture nonlinear species–environment responses (Chiaverini et al., 2023). Its accuracy remains high even when occurrence data are spatially clumped, and it reliably identifies influential variables while maintaining temporal stability despite correlated climate inputs (Unnithan Kumar et al., 2021; Hanberry, 2024). At the broader methodological level, ecological systems show

Table 2

Comparative account of the variable contribution (in percentage) of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), Random Forest (RF) and Ensemble model.

Variables	ANN	CTA	FDA	GAM	GBM	GLM	MAXENT	RF	Ensemble
Bio2	13.287	19.579	16.26	14.058	14.275	33.318	20.964	14.984	17.659
Bio7	11.487	10.626	5.714	5.222	3.599	24.17	7.305	10.082	4.285
Bio10	21.365	33.168	31.813	29.749	53.259	3.947	38.095	26.852	38.377
Bio12	17.164	15.023	28.602	31.273	16.438	5.196	19.777	15.753	23.88
Bio15	14.244	8.193	13.083	12.358	8.177	32.275	8.948	16.4	10.707
Bio19	16.299	10.337	2.897	3.254	3.688	0.636	2.919	10.645	3.384
Human footprint	3.118	2.092	0.841	1.861	0.471	0.018	1.006	3.262	0.913
LULC	3.036	0.982	0.791	2.225	0.095	0.44	0.986	2.021	0.395

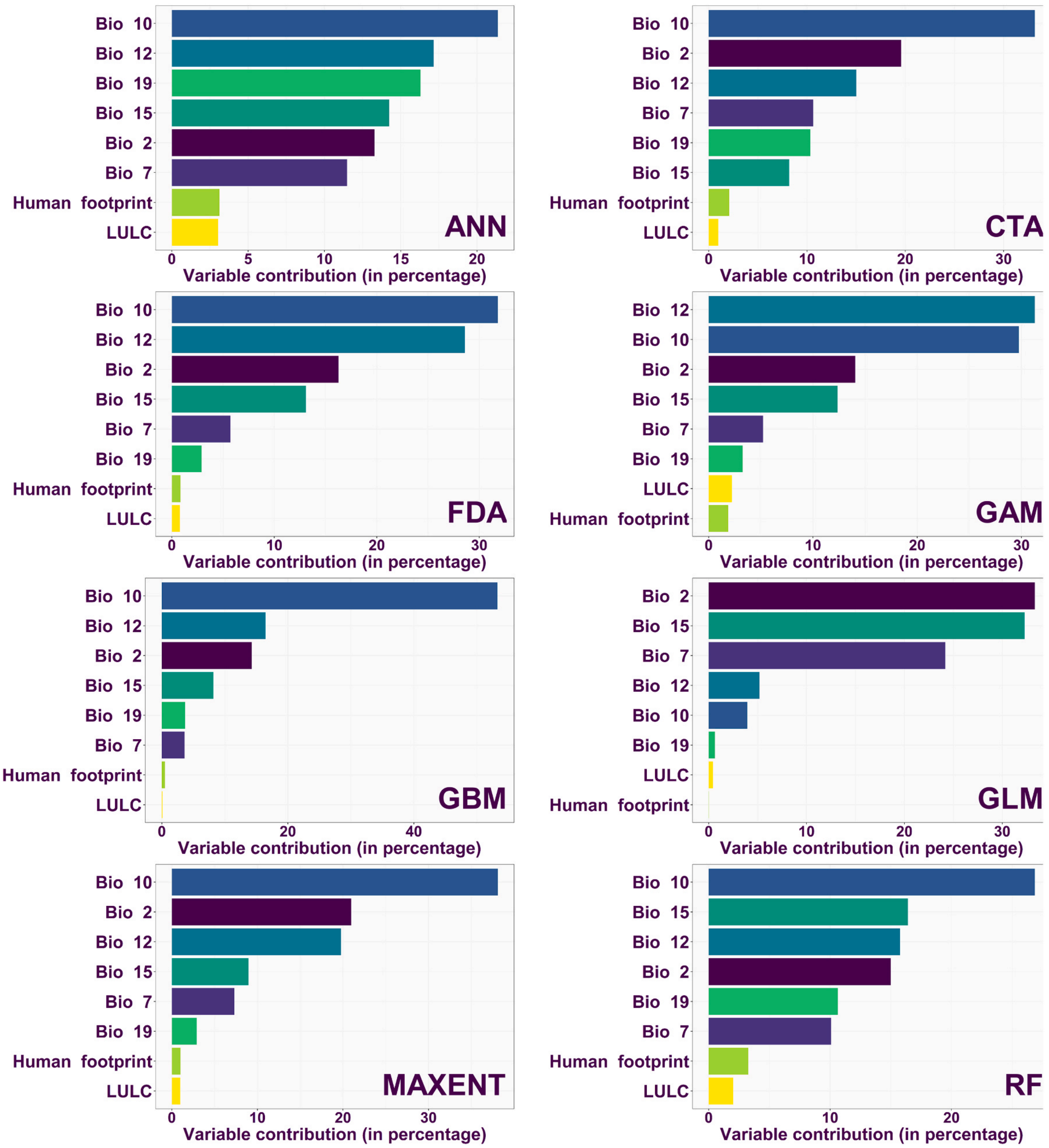

Fig. 8. Comparative account of variable contribution of eight species distribution models (SDMs) – Artificial Neural Network (ANN), Classification Tree Analysis (CTA), Flexible Discriminant Analysis (FDA), Generalized Additive Model (GAM), Generalized Boosting Model (GBM), Generalized Linear Model (GLM), Maximum Entropy Model (MAXENT), and Random Forest (RF).

complementarity when different species use resources in distinct ways, boosting overall performance. Ensemble model mirrors this logic as it fuses multiple individually modest but complementary algorithms so that each compensates for the shortcomings of others which Civantos-Gómez et al. (2021) describe as a "*smart mix of weak models*". Such ensemble integrates method-specific strengths, correct individual biases, and yield higher predictive accuracy and robustness under novel environmental scenarios, while also allowing for explicit estimation of model uncertainty (Araujo and New, 2007). For these reasons, the RF and ensemble model generally outperform other models. Therefore, for effective modeling of Bumblebee distributions in high-altitude areas, prioritizing RF and Ensemble models are advisable due to their favorable statistical properties and robustness against outliers.

In most bumblebee species, hibernating queens emerge in early spring, coinciding with the blossoming of flowers and late summer, the queens have completed colony reproduction (Mola, 2021). During the summer, bumblebees increase their foraging and flying activity, as temperatures influence their flight capabilities (Martinet et al., 2021). Therefore, the temperature during the summer season plays a critical role in their behavior and survival. In this study, we found that Bio 10, representing the mean temperature of the warmest quarter, significantly influences bumblebee distribution in most SDMs. But, bumblebees are sensitive to heat stress (Goodwin and Wang, 2025), so rising warm-season temperatures may force upward shifts in their suitable habitats. Policymakers can use these insights to designate climate refugia, prioritize high-altitude zones for conservation, and support adaptive land-use policies that anticipate these range shifts. Incorporating thermal suitability thresholds into agricultural zoning and conservation corridor design can prevent habitat fragmentation and ensure pollination continuity under warming trends. Annual rainfall affects

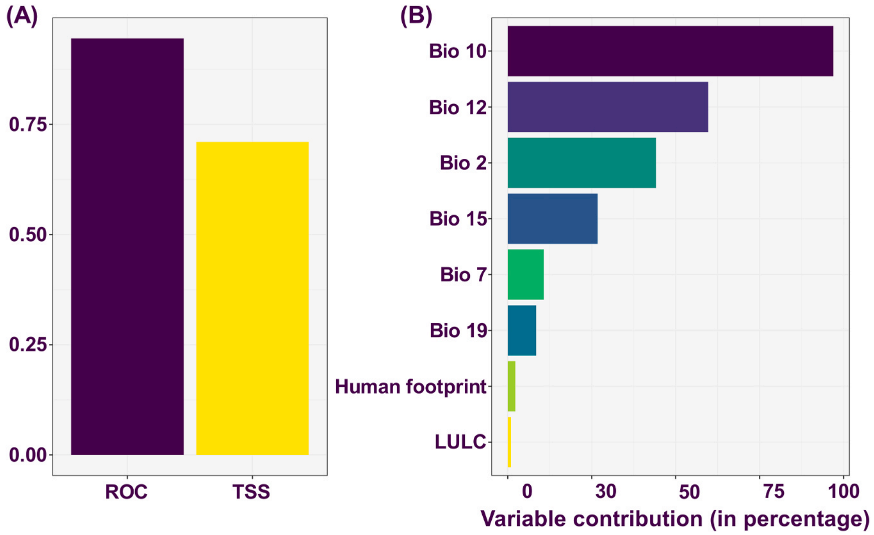

Fig. 9. (A) The receiver operating characteristic (ROC) and true skill statistic (TSS) values of ensemble species distribution model (B) Variable contribution for ensemble species distribution model.

both soil and atmospheric moisture, which plays a critical role in the flowering phenology of nectar plants. Since bumblebees rely on the nectar of these plants for food, changes in flowering patterns due to variations in soil moisture directly impact their feeding resources. As a result, rainfall indirectly influences the distribution of bumblebees by affecting the timing and availability of the nectar plants they depend on. Also, since bumblebees nest in the ground (Sharma et al., 2024), they rely heavily on soil moisture for successful nesting. However, excessive rainfall can threaten their nests, leading to potential destruction. Since atmospheric humidity is proportional to precipitation and influences the flying and foraging activity of bumblebees (Sanderson et al., 2015), their distribution is consequently affected by rainfall. Thus, in this study, we found that Bio 12, which represents Annual Precipitation, plays a crucial role in most SDMs for bumblebees. Also, we would like to point out that because the Eastern Himalayas receive significantly more rainfall than the central and western regions (Nandargi and Dhar, 2011), due to variation in monsoon patterns, the impact of Bio 12 on Eastern Himalayan bumblebee populations may be greater. Policymakers can therefore promote water-efficient agro-ecological practices such as rainwater harvesting, and drought-resilient crop varieties especially in Trans Himalayan region to sustain floral resources and ecosystem services. In mountain ecosystems, the physiology and flowering phenology of angiosperms are sensitive to frost events (Inouye, 2008), which can impact pollinator species like bumblebees. Frost formation is influenced by the difference between maximum daytime and minimum night-time temperatures. Bio 2, representing the mean diurnal temperature range, plays a crucial role in predicting frost events (Zheng et al., 2015; Zohner et al., 2020). Areas with a lower mean diurnal range tend to experience fewer frost events, creating more favorable conditions for bumblebee populations. Thus in this work we observed that in most of the SDMs the Bio 2 plays an important role. In hilly terrain diurnal microclimate is significantly affected by topography (John et al., 2024). High diurnal variation can stress bumblebee, leading to reduced foraging efficiency and altered pollination patterns (Chapman et al., 2022; He et al., 2025). Thus, from a policy perspective, maintaining microclimatic stability through vegetation cover, agro-forestry, and shade management becomes crucial in Himalayas. Local agricultural and forestry programs can integrate such microclimate-buffering strategies to enhance pollinator resilience and productivity.

In mountainous regions like the Himalayas, it is not feasible to sample every inch of the terrain or collect species data from every location. Sampling efforts are typically concentrated on certain areas and timeframes, which means the absence of a species in collected data does not necessarily confirm its absence in that region. The SDMs are thus built based on the available samples, and as a result, the physical characteristics of sampled regions are emphasized in these models. When certain environmental variables are prioritized over others in the modeling process, it can lead to a skewed understanding of the species-environment relationship. This bias occurs when the algorithm places excessive weight on certain variables, resulting in inaccurate predictions of species distributions by over-representing those influences while neglecting others of equal importance. However, when all relevant variables are treated equally, the resulting models are more likely to be transferable across different regions or conditions, increasing their predictive reliability. In our work, SDMs such as ANN and RF exhibited a more balanced distribution of importance across the environmental variables, supporting the need for equitable consideration of all contributing factors.

The Global Biodiversity Conservation Initiative and the United Nations' SDGs have set targets for biodiversity conservation, particularly within 2030 and 2050. Among these, the '30 × 30 Initiative' aims to designate 30 % of the world's land and oceans as protected areas by 2030 while promoting the achievement of other critical SDGs (De and Dwivedi, 2024a). Biodiversity supports the ecosystem balance and is vital for advancing progress toward the SDGs (De and Dwivedi, 2024b). The Himalayan region, supporting over 50 million inhabitants and providing ecosystem services that benefit more than a billion people, plays a vital role in achieving these objectives (Verma et al., 2021). Pollination, a key ecosystem service, is fundamental to Himalayan ecosystems, and bumblebees are indispensable pollinators in forested and agricultural landscapes of this region. The present study advances a sustainability-oriented understanding of Himalayan pollinator conservation by integrating SDMs with the SDGs. By evaluating eight SDM algorithms for *Bombus* species, our work identifies RF and ensemble approaches as the most reliable tools for predicting pollinator habitats. These models, driven primarily by warm-quarter temperature and annual precipitation, provide spatially explicit maps of habitat suitability that are essential for linking biodiversity science with sustainable development policy in fragile mountain ecosystems. These habitat suitability maps become operational decision-support layers for agricultural advisors (identifying fields at risk of pollination shortfall), protected-area planners (delineating refugia and connectivity corridors), and climate practitioners (targeting micro-refugia and restoration where climatic suitability persists). It was observed that bees have the potential to contribute to 15 of the 17 SDGs and at least 30 specific SDG targets (Patel et al., 2020). The animal pollination can substantially

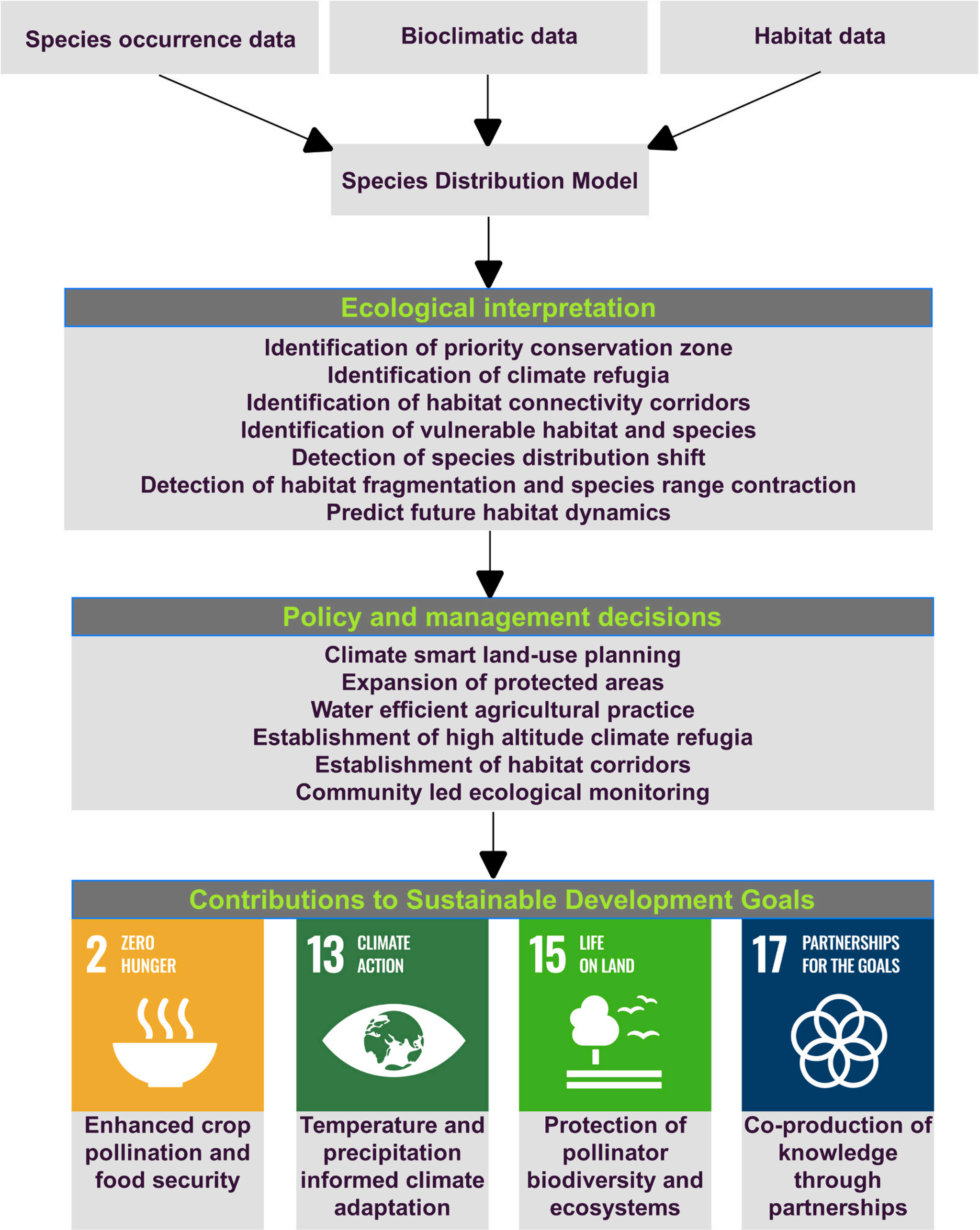

Fig. 10. Schematic representation of how species distribution models of pollinators can help achieving sustainable development goals in the Himalayas.

increases yield stability and reduces variability across years, a service that is especially valuable under climatic uncertainty. Thus, SDMs linking pollinator habitat and climate drivers equip managers and communities with the spatial foresight necessary to safeguard food security, enhance the resilience of socio-ecological systems, and protect biodiversity (Fig. 10). Our work contributes directly to SDG 2 (Zero Hunger) by revealing where pollination services are most vulnerable, thereby supporting food security through targeted agro-ecological interventions, crop diversification, and habitat restoration. Reliable pollinator mapping enables planners to safeguard insect-dependent crops and sustain local livelihoods dependent on fruits, vegetables, and medicinal plants. For SDG 13 (Climate Action), the study demonstrates how pollinator SDMs can identify climate refugia and anticipate upslope range shifts under warming scenarios. This information underpins adaptive management strategies such as protecting high-elevation habitats, enhancing floral resources, and developing climate-resilient agricultural practices to mitigate the effects of climate change on pollination services. In relation to SDG 15 (Life on Land), the research supports biodiversity protection by highlighting priority zones for pollinator conservation that also preserve vital plant–pollinator networks in alpine meadows and forest systems. These efforts maintain ecological integrity and ensure the continued provision of ecosystem services. Through SDG 17 (Partnerships for the Goals), the study emphasizes the role of collaborative monitoring, citizen science, and capacity building in improving SDM inputs and promoting community engagement. The SDMs for insect pollinators can translate directly into spatially explicit guidance for conservation zoning, agro-ecological planning, and Himalayan regional policy by mapping present and future habitat suitability under land-use and climate scenarios. By SDM high suitability and climatically persistent areas can be identified for bumblebees and other pollinators and such areas can be prioritized as core conservation zones, ecological corridors, or climate refugia within

Himalayan protected area networks and community-managed forests. In high altitude agricultural landscapes, SDM outputs can be overlaid with cropping patterns and pollination-dependent crops allow planners to target agri-environment schemes, floral strips, and reduced pesticide zones where pollinator richness and ecosystem service potential are highest. The Himalayas, spanning India, Nepal, Bhutan, and China, host diverse pollinator communities distributed across steep altitudinal and climatic gradients. Because these species occur across multiple national boundaries, their conservation requires multi-scale governance frameworks that promote policy harmonization throughout the region. In this context, SDMs can serve as a unifying scientific tool, enabling joint monitoring systems, coordinated identification of connected conservation areas, and shared climate-adaptation strategies. By aligning national land-use plans with predicted pollinator movement pathways and phenological shifts, the Himalayan countries can collaboratively safeguard pollination services essential for biodiversity, agriculture, and mountain livelihoods.

This study contributes uniquely to pollinator biogeography by showing that Himalayan bumblebee distributions are primarily shaped by warm-season temperature (Bio10) and annual precipitation (Bio12), which is consistence with global findings that climatic thresholds strongly control *Bombus* range dynamics (Kerr et al., 2015; Cameron and Sadd, 2020; Soroye et al., 2020). Unlike most SDM studies that model single species, this work integrates all *Bombus* species at the genus level, capturing the ecological coherence of high-elevation assemblages and offering a system-wide perspective particularly relevant for the world's major alpine biodiversity hotspot. The comparison of eight algorithms, complemented by histogram-based skewness and kurtosis evaluation, provides a methodological advance seldom used in pollinator SDMs. By identifying RF and ensemble models as most robust, the study strengthens climate-adaptation planning for Himalayan pollinators.

The present study, while providing insights into *Bombus* habitat suitability across the Himalayas, is subject to some limitations that should be acknowledged when applying the results to conservation planning. The reliance on opportunistic field sampling and heterogeneous literature-derived occurrences can introduce spatial sampling bias, as surveys were concentrated along accessible valleys, roadsides, and stream corridors, while vast high-altitude or remote habitats remained unsampled. Such sampling increases the likelihood that pseudo-absences, although randomly generated, may inadvertently fall in environmentally suitable but unsurveyed areas, potentially reducing model discrimination and inflating model sensitivity. Extracting coordinates from local descriptions can introduce positional uncertainty, which can misrepresent fine-scale climatic or land-use conditions in steep Himalayan terrain. The use of genus-level pooling may obscures species-specific niche differences and underestimate microhabitat specialization, especially for narrow-ranged taxa. Though the models provide a broad-scale foundation for identifying potential conservation priorities, their outputs should be interpreted with caution and complemented with targeted field validation, species-level surveys, and finer-resolution environmental data before informing site-level management decisions or protected-area expansion.

7. Conclusion

The SDMs of pollinators offer a strategic approach to conserving biodiversity by identifying key habitats and anticipating environmental changes. By understanding where pollinators thrive, SDMs help guide habitat restoration and protection efforts, ensuring ecosystem resilience. These models support local livelihoods by identifying areas where pollination services can enhance crop yields, providing economic benefits to rural communities. Integrating climate forecasts, SDMs promote adaptive land-use planning, aligning conservation with sustainable agricultural practices. In this work we evaluated eight SDM algorithms, using genus *Bombus* as the taxonomic unit to analyze bumblebee distribution in the Himalayas because genus-level models are also valuable for identifying critical habitats and understanding biodiversity patterns, especially in the context of climate change and habitat alteration. Seven algorithms (ANN, CTA, FDA, GAM, GBM, MAXENT, RF) performed well based on ROC and TSS scores but they vary in skewness and kurtosis. Among single algorithms, the RF stood out as the most effective model for predicting bumblebee distribution due to its robust statistical properties. However, the ensemble approach proved superior overall in terms of accuracy and reliability. Given the variability in model performance, we urge researchers to evaluate all available models before selecting the most appropriate one based on study area, number of species, sample size, and spatial variables. Adopting a model without thorough evaluation may lead to incorrect predictions that could hinder conservation efforts. The best-practice standards that incorporate biodiversity theories, abiotic and biotic factors, trait-based approaches, meta-ecosystem frameworks, and field observations should be established and validated by the scientific community to ensure robust model evaluation, decision-making, and policy development in biodiversity conservation and achieving SDGs.

CRediT authorship contribution statement

Amar Paul Singh: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation. **Kritish De:** Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Virendra Prasad Uniyal:** Writing – review & editing, Validation, Supervision, Resources, Project administration. **Sambandam Sathyakumar:** Writing – review & editing, Validation, Supervision, Resources, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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