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Cover: The nine vultures of India, digital art made on Krita by Dupati Poojitha.

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REVIEW

MaxENT tool for species modelling in India: an overview

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Abstract: MaxENT has been the preferred choice for exploring the patterns and processes related to species distribution and niche models. Across the world, many researchers have used it and here we present the usage trend from the Indian context to identify the different aspects in which it is deployed including the spatial scale, geographical realm, thematic groups, and data sources. Of the 210 papers from India accessed from Web of Science (WoS), only represents 4% of the MaxENT-based papers across the globe. Plants especially trees (24%) and herbs (19%), followed by mammals (16%) while lichens (<1%) as well as corals (<1%) were the most, and least studied taxonomic/ thematic groups from India, respectively. This work highlights the important facets of ecological niche modelling / species distribution modelling (ENM/SDM) like the intensity of occurrence data used and various environmental datasets incorporated during the modelling process. This overview provides insights into ENM/SDM-based research works.

Keywords: Conservation planning, ecological niche modelling, environmental variables, geospatial analysis, habitat suitability, niche, process based modelling, occurrence data, species distribution modelling, taxonomic groups.

Hindi: MaxEnt प्रजातियों के वितरण और पर्यावास निच (niche) मॉडल से संबंधित पैटर्न और प्रक्रियाओं की खोज के लिए एक पसंदीदा उपकरण रहा है। विश्वभर में कई शोधकर्ताओं द्वारा इसका उपयोग किया गया है, और इस लेख में हम भारत में इसके उपयोग के प्रवृत्तियों को प्रस्तुत करते हैं, जिसमें इसके उपयोग के विभिन्न पहलुओं जैसे स्थानिक पैमाना, भौगोलिक क्षेत्र, विषयगत समूह और डेटा स्रोत शामिल हैं। Web of Science से प्राप्त भारत से संबंधित 214 शोधपत्रों में से, ये केवल वैश्विक MaxEnt-आधारित शोधों का 4% प्रतिनिधित्व करते हैं। पौधों में विशेषकर वृक्ष (24%) और औषधीय पौधे (19%) सबसे अधिक अध्ययन किए गए, जबकि स्तनधारी, लाइकेन और कोरल सबसे कम अध्ययन किए गए विषय रहे। यह अध्ययन ENM/SDM मॉडलिंग के महत्वपूर्ण पहलुओं जैसे कि प्रयुक्त उपस्थिति डेटा की तीव्रता और मॉडलिंग प्रक्रिया में शामिल विभिन्न पर्यावरणीय डेटासेट्स को उजागर करता है। यह अवलोकन ENM/SDM आधारित शोध कार्यों की समझ को गहराता है।

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INTRODUCTION

Ecological niche modelling (ENM), also known as species distribution modelling (SDM) or habitat suitability modelling, is a computational approach used in ecology, conservation biology, and biogeography to predict the potential geographic distribution or habitat suitability of a species or ecological niche under various environmental conditions. There is a rising opinion that both ENM and SDM vary in certain aspects (Melo-Merino et al. 2020); yet these concepts have been used extensively in the disciplines of ecology, biogeography, and conservation to forecast how a changing climate may affect species. ENM/SDM has also been used to manage invasive species, plan protected area management, and estimate the effects of climate change in evolutionary biology and ecology. The greater accessibility of digital data, user-friendly software, and instructional resources, as well as the growing interest & focus on these techniques, have supported the development of this field. Recent developments in data analysis and information technology have provided an edge to ecologists and conservationists to use this computational approach to a greater extent.

The origins of this ecological approach can be found in earlier works that connected biological patterns with environmental changes like geographic gradients. Also, the studies that showed how individuals, rather than groups, responded differently to environmental factors, inspired the creation of methods to represent individuals as species. In order to provide a picture of possible distributions of species at the landscape level, ENM/SDM infers correlations between species distributions (as records of occurrence or abundance), and environmental characteristics at selected study sites. These models have also been referred to in the literature as habitat models, climate envelopes, range maps, ecological niche models (ENMs), resource selection functions (RSFs), correlative models, and spatial models.

The occurrence data on species, environmental covariates, and a modelling technique are three important components that can influence the SDM outputs. Typically, the modelling is done at two levels—a) single model algorithm technique and b) ensemble technique. The foundation of ensemble modelling is the idea that each model algorithm exhibits some meaningful “signal” regarding relationships in the real world, as well as some noise brought on by the data and the limitations of the algorithm. As a result, ensemble modelling uses many models to separate the signal from the noise more effectively. Therefore, the choice of algorithm matters and the algorithms are categorised (Rathore & Sharma 2023) as

i) Regression Models - Generalized Linear Models (GLMs), Generalized Additive Models (GAMs), Multivariate Adaptive Regression Splines (MARS)

ii) Classification Models - Flexible Discriminant Analysis (FDA) and Classification and Regression Tree (CART)

iii) Complex Models - Random Forest (RF), The Genetic Algorithm for Rule-set Production (GARP), The Maximum Entropy (MaxENT) method, and Artificial Neural Network (ANN).

Among these algorithms, one stands as a popular choice for SDM modelling, i.e., MaxENT. It is an algorithm for general-purpose machine learning that calculates target probabilities by identifying the distribution that is most entropic (i.e., uniform) while adhering to the requirement that each environmental variable’s expected value match its empirical average (i.e., the average value of the variable at a sample of points from species distribution). After the first publication on MaxENT by Phillips et al. (2006), who introduced the MaxENT application as a tool/software based on the maximum entropy method for SDM with presence-only data; there are several publications that have used MaxENT. In this paper, we have made efforts to explore and comprehend the preference and usage trend of SDM in the Indian context with the following questions: i) What is the extent, i.e., number of publications based on MaxENT in India? ii) What are the different aspects where MaxENT has been used and the lessons learnt from it? The extent of publications based on MaxENT in India will indicate the subject area where it was used, while also providing an overall perspective, and insights for using MaxENT in upcoming works.

MATERIALS AND METHODS

The literature corpus was collected from the Web of Science (WoS) database. It was selected owing to its authentic and comprehensive coverage. A keyword search TC= “MaxEnt” or “MaxENT” was used to collect the data from the Web of Science, for the period between 2000–2023 (accessed on 01.x.2023). Considering the broader nature of research publications from different disciplines, it was decided to use a string keyword search. Further, studies involving topic-specific searches have recounted the increased specificity and recovery of information (Aleixandre et al. 2015; Sweileh et al. 2016). The search in WoS yielded 5232 publications from which articles were screened based on the countries, i.e., INDIA – 214 manuscripts were sorted, and 210 manuscript metadata were used in the analysis (Nakagawa et al. 2019). The metadata was downloaded in the BibTeX format and analyzed in R version 4.0.1 along with Rstudio Version 1.3.959 using the bibliometrix R-package (http://www.bibliometrix.org) (Aria & Cuccurullo 2017). It provides a range of tools for importing, cleaning, and organizing bibliographic data, and for conducting various types of bibliometric analysis. The biblioshiny tool based on the bibliometrix R-package was used in the analysis.

RESULTS AND DISCUSSION

Across the timespan, there were 210 scientific publications published in 103 journals with an annual growth rate of 27.81% (Figure 1) and the publications peaked in 2013. About 778 authors contributed with an average of 4.79 authors per document and 32.34 % international collaboration for publishing. There were only three authors who published single-authored scientific documents, which indirectly indicated the level of collaboration among authors. Almost all states were covered with at least 5–10 publications, with hotspots of the studies being Karnataka, Kerala, Tamil Nadu (Western & Eastern Ghats), Uttarakhand, and Jammu & Kashmir (Himalayan region). The least studied will be the western part of India (arid & semi-arid regions). With regard to the spatial scale, the study area in many of the studies has not been confined to selected regions within the state but even pan-India level studies have also been reported. For instance, the invasion potential of the mango fruit borer (Choudhary et al. 2019), prediction of *Boswellia serrata* in the year 2050 for two climate change scenarios - IPSL-CM5A-LR and NIMR-HADGEM2-AO (Rajpoot et al. 2020), and potential area for cultivation of *Melia dubia* (Sundaram et al. 2023) were studied at country level; whereas predicting the potential distribution of *Justicia adhatoda* was carried out at district level (Yang et al. 2013).

It is pertinent to point out that apart from the java based MaxENT software, some of the studies have used MaxEnt tool in other formats like a plugin in the QGIS, an interface based on GRASS GIS, and numerous R packages like dismo, ENMeval, SDMPlay, rmaxent, MIAmaxent, kuenm, ENiRG, and maxlike, which clearly indicatesthe dominance of MaxENT algorithm. There are a good number of scholarly publications that might not be captured in WoS. The usage of a single database (the WoS) and exclusion of articles in other languages may have hampered the accessibility of all research papers. Yet, the wider coverage in Web of Science reduces the "indexer effect", thus making the findings significant (Orimoloye & Ololade 2021). Figure 2 shows the number of publications on MaxENT from India indexed in different databases. As evident, the total number of publications using MaxENT from India was only 4% of the global output as recorded in the WoS. However, we can presume that there will be more publications related to Niche Modelling or Species Distribution Modelling using the MaxENT tool in the future. Lotka's law is used to assess productivity levels by examining the relationship between several authors and the number of articles published. The constant and beta coefficients of Lotka's law were 0.61 and 2.77, respectively. The goodness of fit test (Komogorov-Smirnoff) value was 0.91 and the p-value was 0.541 (Figure 3). This implies that Lokta's law is valid and thus there is a good possibility for an increase in the number of publications in the future (Rathinam et al. 2022).

To understand the changes in the MaxENT-based studies based on institutes, keywords, and journals over the last two decades, the three-field plot from bibliometrix tools was used (Figure 4). The left side indicates the top 20 institutes in India; the right side indicates the name of journals and the middle field indicates the keywords. Figure 4 provides a bird's eye view of the interlinkage in the published studies between 2000 and 2023. It reveals that ecological informatics, ecological engineering, and current science are some of the journals where dedicated research on ENM/SDM based on MaxENT in India is being published. The central segment indicates sides the keywords from the published papers; it is clear that the Western Ghats and Himalayas are two significant regions where SDM-based studies are being carried out.

To understand the different aspects where MaxENT has been used, the publications were sorted out on the thematic study subjects (Figure 5). SDM modelling was widely used to study trees, herbs, and mammals in the Indian context. More particularly, the MaxENT tool has been also used for some landscape-level studies. For instance, Pandey et al. (2020) assessed the landslide susceptibility along riven models along the Tipari to Ghuttu highway corridors in the Garhwal Himalaya by coupling MaxENT output with DEM, NDVI, Slope, Aspect, and drainage density datasets. Unlike SDM models for flora or fauna where the presence locations of the species of interest are deployed along with environmental parameters such as temperature and rainfall, the studies on landscape (Pandey et al. 2020),

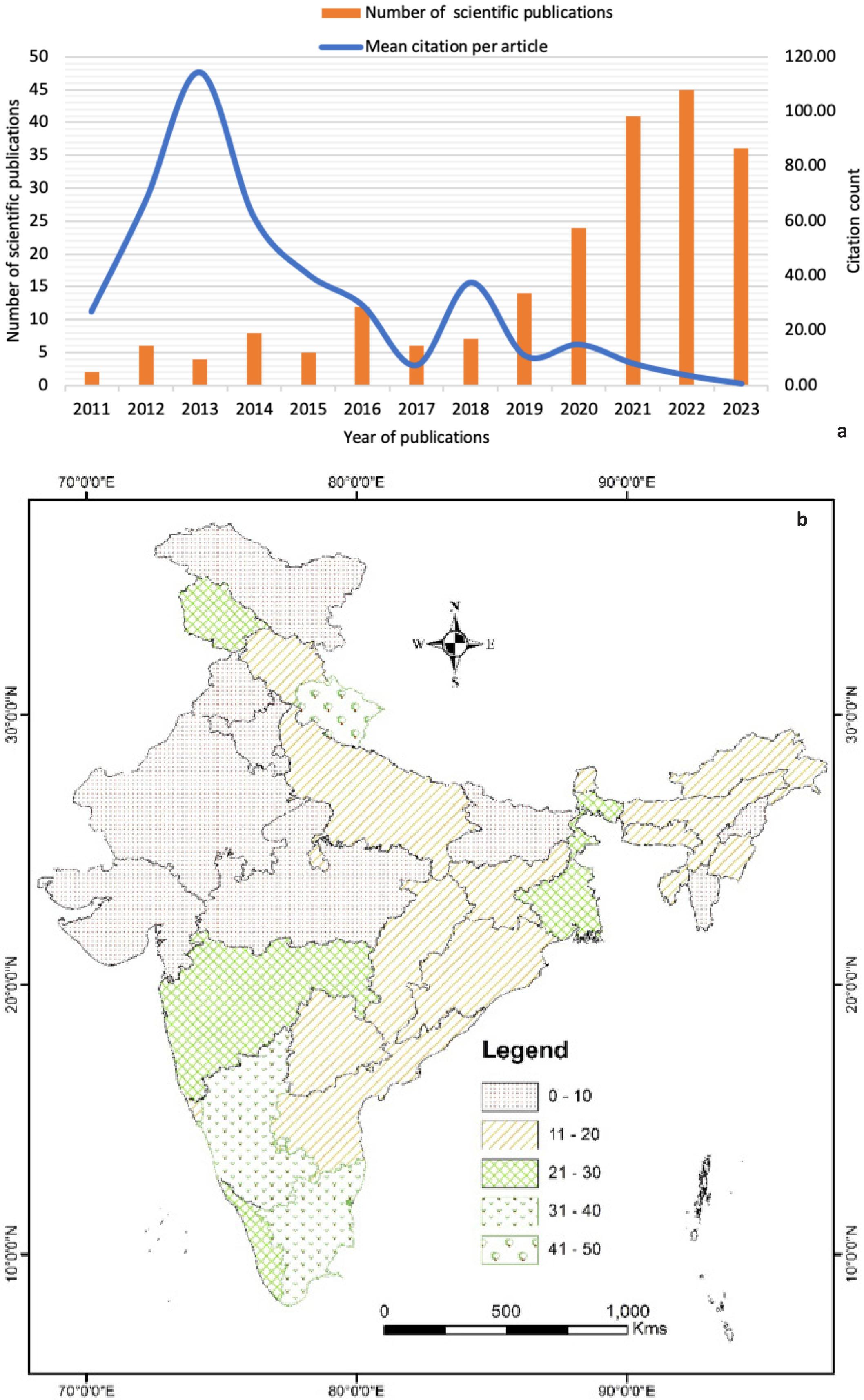

Figure 1. Scientific publications based on MaxENT over the years: a—across timescale | b—across the country.

forest fire prediction (Banerjee 2021), and transition in lagoon ecosystem (Santhanam et al. 2022) are some of the new methodologies by tuning the MaxENT tool with additional remote sensing & GIS datasets to meet the desired objectives. It is pertinent to point out that all of the studies were carried out after 2020 which indicates that new horizons using MaxENT are being explored and there will be more publications, as indicated by Lotka's law. All studies focus on the fundamental principle, i.e., the MaxENT model/tool is based on theory of statistical mechanics, and information concept which gives an approximation of a likelihood phenomenon based on known events.

Recently, Rathore & Sharma (2023) reported that SDM can be utilised for forecasting, restoration planning, climate change effect assessment, critical habitat identification, fishing zone identification, pollinator range prediction, disease spread prediction, fire regime, corridor identification, conservation status prediction, conservation planning, habitat range shift prediction, protected area management, hotspot identification, and Invasive species range identification. The recent studies have attempted to diversify the MaxENT analysis coupled with other applications and softwares (He et al. 2024; Asadollahzadeh & Torkaman 2025; Mao et al. 2025; Wang et al. 2025). More specifically, the category 'Others' mentioned in Figure 5 which are based on the application of the MaxENT tool for gully erosion and land subsistence susceptibility mapping, predicting the expansion of dengue vectors, predicting the monkey fever risk, assessing the impact of overuse of groundwater for agriculture, and many other works..

Our results indicate that MaxENT can be used in many other areas and it is up to the researchers to apply the tool with combination of other models or methods. For instance, the fluctuation of ecosystems services owing to conservation of a keystone species has been studied by combining MaxENT with Co$ting Nature and DINAMICA EGO modelling approaches (Hemati et al. 2020). It is also coupled with InVEST models to estimate benefit of conservation effort in Chongqing Municipality (Wang et al. 2024). There are specific R packages like Dismo, Maxlike, and Biomod2. that can perform niche modelling and species distribution (Sillero et al. 2023). Some R package like MIAmaxent is created to improve the predictive performance and ecological interpretability (Vollering et al. 2019) and these packages aim to address the limitations of MaxENT (Yackulic et al. 2013; Renner et al. 2015; Sillero & Barbosa 2021). Even Python based tools are also combined with MaxENT for additional information such as the SDMtoolbox for landscape level genetic and biogeographic model (Brown 2014).

All these studies show that this Java-based software has aided in the application of information theory and related statistical concepts for predicting factors. The use of presence/occurrence-only data (both for continuous and categorical data) has been regarded as one of the MaxENT tool limitations. Jha et al. (2022) have proved that MaxENT performs better than occupancy models which use both presence and absence data.

All the research works have invariably used bioclimatic data from the worldclim (https://www.worldclim.org/data/worldclim21.html) apart from additional datasets like altitude, Digital Elevation Model, NDVI, Enhanced Vegetation Index, Landsurface Temperature, Landuse & landcover, Compounded Topographic Index, Forest Type map & Forest Cover map, Direct Normal Irradiance, evapotranspiration, fraction of absorbed photosynthetically active radiation, water vapour, Leaf Area Index, Ozone, NOx, albedo, aerosol absorbing index, biodiversity indices, hill shade, habitat heterogeneity index, distance from road, soil properties, flow accumulation, Ivlev's index of selection and even human footprint have also been used. All these indicate the flexibility and wider application of MaxENT tools for identifying the niche and distribution of the species in present as well as future climatic conditions. However, the datasets are mostly open-accessible or generated for the particular study site and the inference generated directly depends on the number of occurrences datapoints used. Studies from the Indian context, are primarily accessed from databases like GBIF, Ebird Atlas or data points generated from the field survey. One particular aspect is the range of occurrence data points which can range from ~30 to 3,500 as indicated in Figure 6. It is pertinent to point out that there are a few studies with more than 3,500 occurrence points that are not included here in the figure. For instance, a study assessing the impact of climate change on the 10 hornbill species had about 93,184 points total from GBIF, however only 5,055 points were included for modelling to avoid bias, and cluttering (Sarkar & Talukdar 2023). There are certain taxa such as the Mollusca where the published studies supplement the field survey datasets and therefore mentioning the GPS coordinates in the study reports/publications will be useful in a larger context (Bharti & Shanker 2021).

Studies with small number of occurrence points in MaxEnt have made modifications in settings to prevent overfitting and ensure reliable predictions. For instance, increasing the regularization multiplier from 1 to 1.5 (maximum 3–4) to produce more generalized models

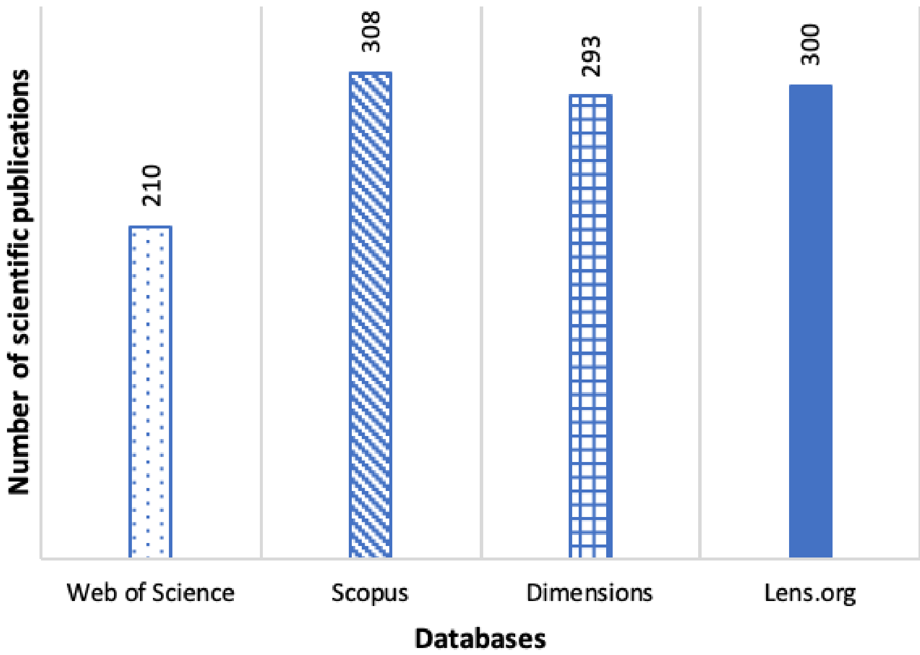

Figure 2. Number of publications in different scholarly databases.

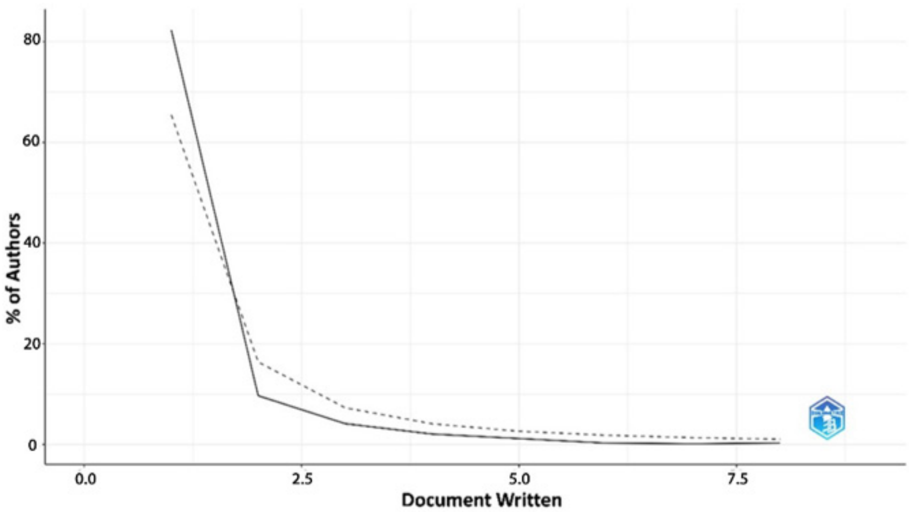

Figure 3. Theoretical and observed scientific productivity (Lotka's law) of research articles published on MaxENT over the years.

(Radosavljevic & Anderson 2014). Feature selection is also refined by restricting complex polynomial and threshold functions, often limiting the model to hinge and linear features for better interpretability.

Cross-validation methods, such as leave-one-out cross-validation (LOOCV), are commonly used in such cases to assess model robustness (West et al. 2016). Additionally, background (pseudo-absence) sampling is fine-tuned by adjusting the number of background points (default ~10,000) and incorporating bias files to correct for sampling effort and presence-only data bias. To improve model reliability with small datasets, cross-validation techniques are essential. LOOCV is particularly useful for small sample sizes (less than 10 occurrences), as it systematically tests each occurrence point while training the model on the remaining data. For slightly larger datasets, k-fold cross-validation (with k = 5 or 10) helps estimate model variance and robustness. These approaches ensure that the model is evaluated effectively despite data limitations. When choosing between logistic and cloglog output functions, logistic output (default) provides probability estimates ranging

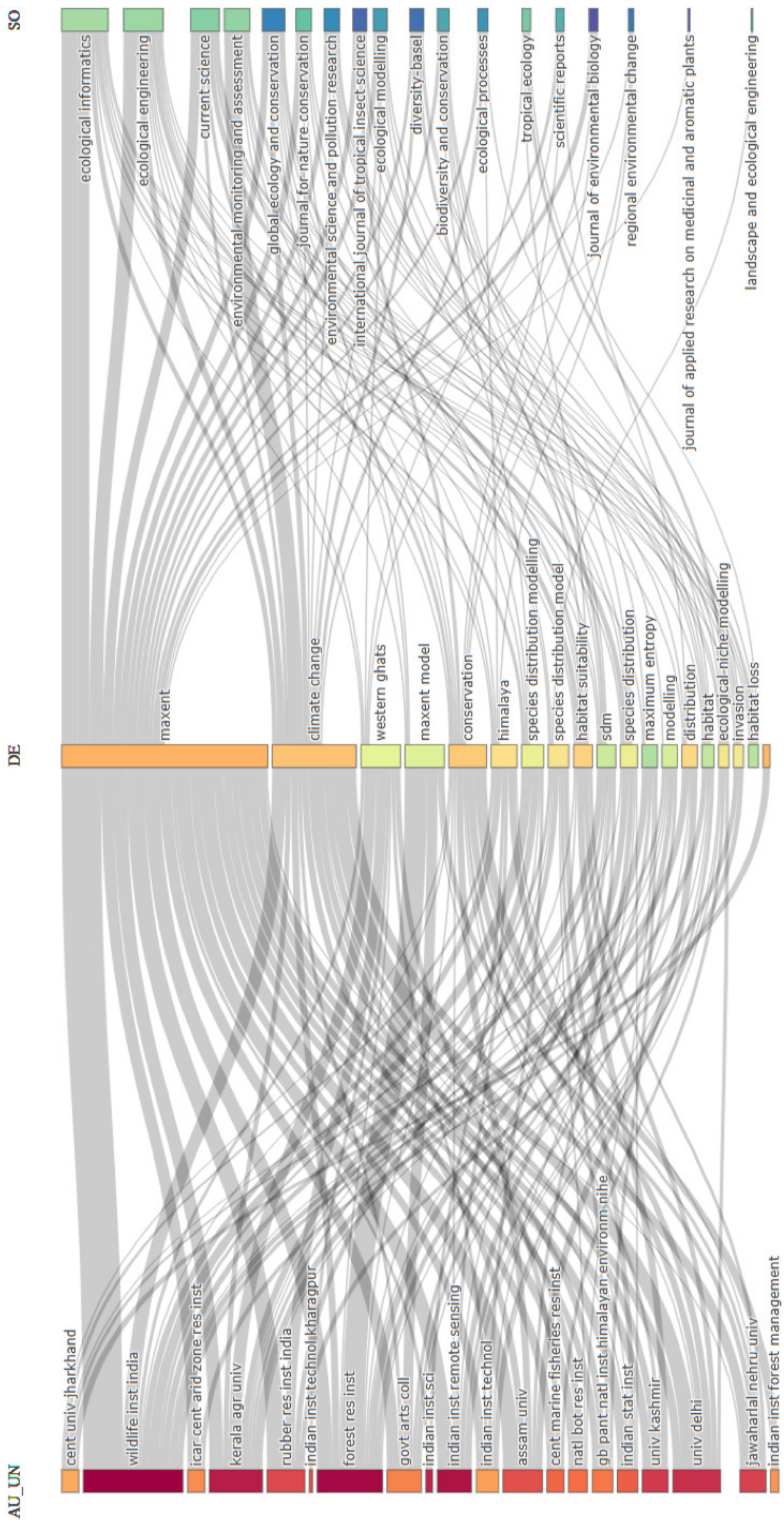

Figure 4. Three-field plot depicting linkage of the top 20 institutes, keywords, and journals for MaxENT-based studies 2000–2023.

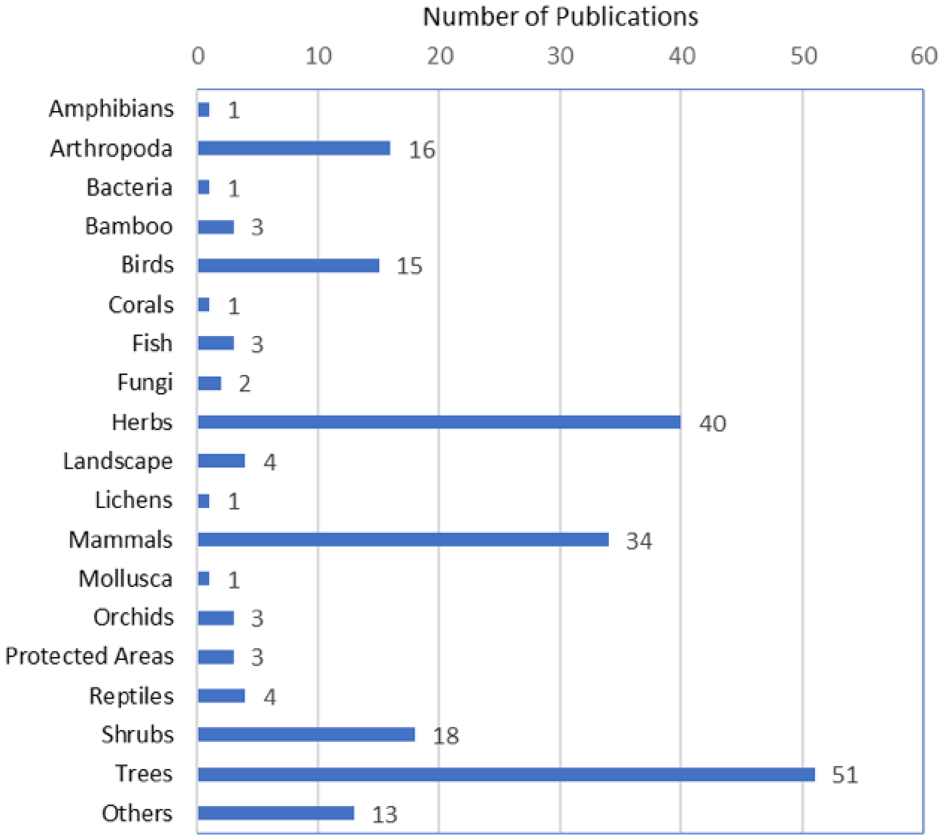

Figure 5. Different thematic groups and their corresponding number of publications from 2000 to 2023.

from 0–1 and is widely used for species distribution studies. The cloglog function is preferred when adjusting for background prevalence, especially when dealing with spatial bias in small datasets. The accuracy of predictions tends to decrease when using limited presence data, as smaller sample sizes increase model uncertainty, reduce generalizability, and may lead to overfitting. This can also create challenges in transferring predictions to new environments (Merow et al. 2013; Renner et al. 2015; Pasanisi et al. 2024).

With regard to the MaxENT modelling techniques, the feature class and regularization multiplier are the two parameters that can be modified to reduce complexity and overfitting of the model prediction (Warren & Seifert 2011). Typically, the MaxENT prediction output is a distribution of a function of the occurrence datapoint and environmental variables for each grid cells of the study area. The auto features enable selection of the output distribution having the maximum entropy from the series of output generated. Studies have indicated the need for defining the feature class and regularization parameters according to the objectives of the study (Morales et al. 2017). In this regard, only 25.25% of studies from India have customised the regularization multiplier value for better interpretation of the results. The regularization values are tuned to give good predictive performance on a large collection of species from diverse regions. There is quite a variation and some discrepancies in the occurrence data, and a fair amount of diversity in the environmental data, so the default regularization values should be reasonable for the data to be analyzed.

A critical aspect will be usage of error-free occurrence data for MaxEnt modelling, as it depends on the rigorous validation, and preprocessing of occurrence data. Poor-quality inputs, such as duplicate records, spatially biased samples, or misaligned raster layers, can lead to misleading predictions, and overfitting. Ensuring spatial thinning of presence points, harmonizing environmental variables, and using an appropriate background extent or bias file are crucial for model reliability. Another important aspect of MaxEnt modelling is the number and type of predictor variables (i.e., environmental variables) used. Most studies typically employ 19 bioclimatic variables, often supplemented with other environmental, and anthropogenic factors such as

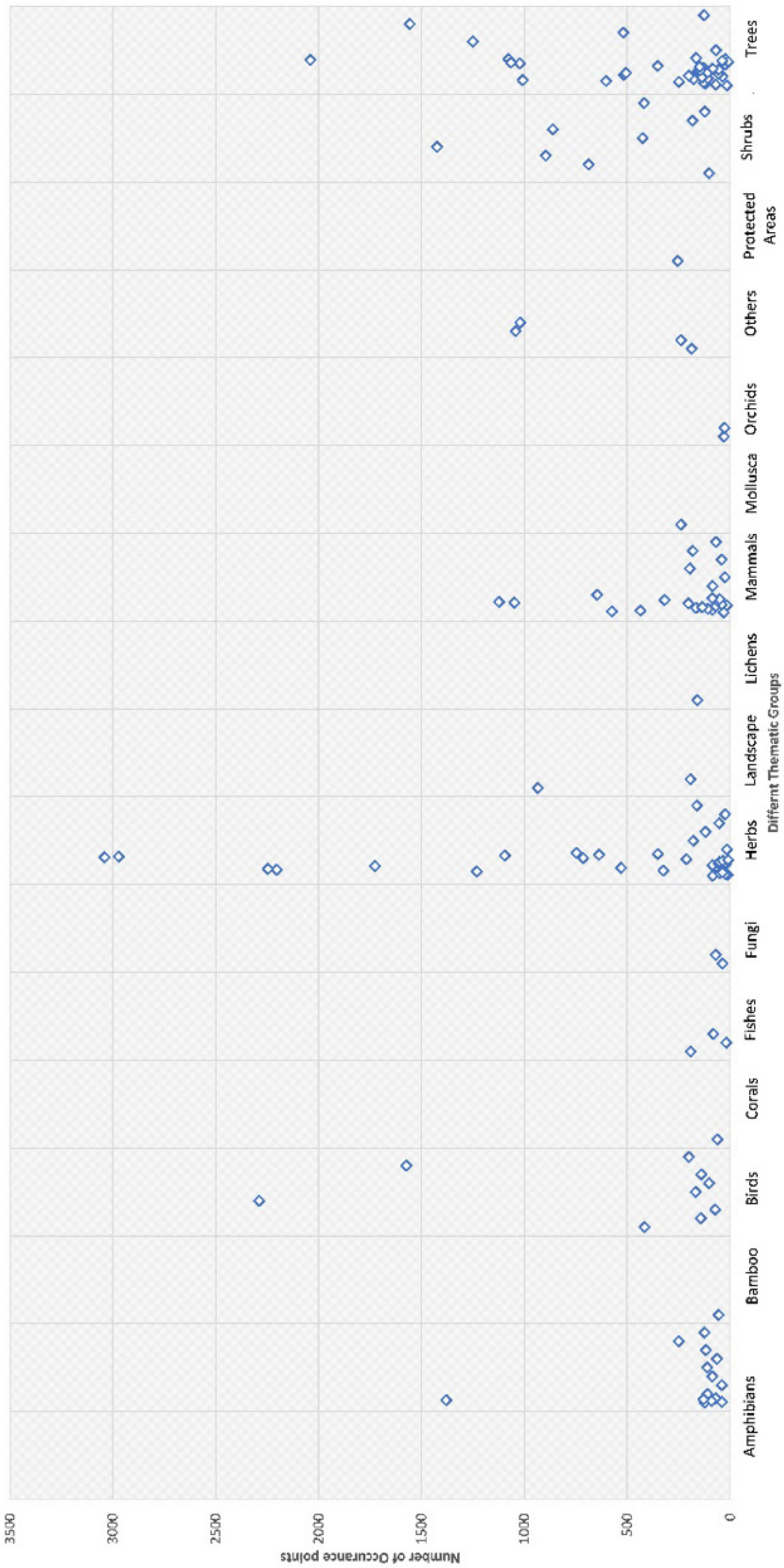

Figure 6. Overview of occurrence data points used for Indian studies.

slope, aspect, elevation, soil type, proximity to water bodies, human settlements, roads, and fire frequency. It is important to note that including a larger number of predictor variables does not necessarily lead to a better-fitting model. A key concern arises when these variables are correlated—an issue known as multicollinearity. Among the 210 publications reviewed, the number of predictor variables used varied depending on the target species. For instance, Banerjee et al. (2017) used only six bioclimatic variables for modelling *Mikania micrantha*, selecting them based on the specific climatic requirements of the species. In contrast, Thakur et al. (2021) initially considered 41 variables—a combination of bioclimatic, topographical, and land cover parameters. After testing for multicollinearity using cluster analysis based on Spearman's rank correlation (ρ) and the average agglomeration method, the list was refined to just seven variables. While many researchers are selective in their variable choice, several studies still fail to adequately address multicollinearity, raising concerns about biased estimates, overfitting, and reduced model interpretability. It is worth noting that the issue of multicollinearity in ecological niche modelling predates the widespread adoption of niche modelling (Benito et al. 2009). Feng et al. (2019) offer a nuanced perspective, challenging the assumption that multicollinearity significantly hampers MaxEnt model performance. Disputing the commonly held belief that correlated predictor variables significantly undermine model performance. They argue that MaxEnt has an inherent mechanism for handling redundancy among predictors during the training process, which enables it to maintain robustness even in the presence of high multicollinearity. This robustness has its limits—particularly when models are projected across different spatial or temporal contexts. In such cases, shifts in environmental conditions and changes in the relationships between variables (i.e., collinearity shifts) can introduce uncertainty. To address this, the authors recommend that researchers explicitly quantify and assess these shifts to better interpret model outcomes. Interestingly, they also note that the frequent strategy of removing highly correlated variables may have minimal impact on model accuracy or predictive power, given MaxEnt's capacity to down-weight redundant information, and the lack of a direct link between predictor multicollinearity, and transferability-related issues. These insights suggest that while variable selection remains important, MaxEnt's design inherently mitigates some of the challenges posed by multicollinearity during model calibration. Nevertheless, many studies continue to assess multicollinearity among predictor variables, and incorporating such analysis into the niche modelling process requires relatively little additional effort. Thus, it can be inferred that this capability may be one of the reasons behind the widespread preference for the MaxEnt.

It is also recommended that while projecting a species for different regions or climate conditions, there is a need to make some adjustments to the default regularization, and feature types (Sutton & Martin 2022). The other aspect of MaxENT modelling will be the choice of global climate system (GCM) and the scenario selection. Typically, the 2 GCM models under different climatic scenarios are taken up in MaxENT based studies and similar trend was also seen MaxENT based studies in the Indian context. Predominantly, studies have used the Representative Concentration Pathways (RCPs) for their studies, and few studies have used the Shared Socioeconomic Pathways (SSPs). Given that SSP was adopted for the Sixth IPCC assessment report (2023), it is not being applied widely. Accounting for the influence of parameters like population, economic growth, education, urbanization, and the rate of technological development in the future greenhouse gas emission is the advantage of SSPs compared to the RCPs, in the number of scenarios used for modelling matters for better understanding, and planning for conservation, and management.

The museums, herbariums, and institutional collections have been reported as sources for occurrence data points, and there is a need to bring these occurrence datasets into a common platform. Given that many of the environmental predictors and other predictors are available in open-access platforms, ensuring the easy accessibility of the dataset will pave robust application of ENM/SDM in real-time decision-making. Relying on a single dataset might be regarded as limitation of this study. This work provides an overview as well as insight for beginners on ENM/SDM.

Supplementary files

The metadata of the publications used in the analysis is listed in supplementary file S1 <https://www.threatenedtaxa.org/index.php/JoTT/$$$call$$$/api/file/file-api/download-file?submissionFileId=69590&submissionId=8916&stageId=5>.

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