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continued on the back inside cover

Cover: Mugger Crocodile basking on the banks of Savitri River at Mahad in Maharashtra, India. © Utkarsha M. Chavan.

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COMMUNICATION

A comparative analysis of the past and present occurrences of some species of *Paphiopedilum* (Orchidaceae) in northeastern India using MaxEnt and GeoCAT

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Abstract: Members of the genus *Paphiopedilum* are well known for their long-lasting unique flowers. They are becoming rare due to over-collection and habitat loss because of human disturbances and deforestation. The present study aimed to compare the past and present occurrences of the genus *Paphiopedilum* in northeastern India using MaxEnt and GeoCAT. A historical occurrence model (HOM) was prepared using secondary data, and an actual occurrence model (AOM) was constructed with primary field data. The HOM and AOM revealed that bioclimatic factors, topography and precipitation play a significant role in the survival of *Paphiopedilum* populations in northeastern India in both the current and historical distributions. The other vital environmental variables were elevation (h_dem), mean diurnal range (bio_2), annual mean temperature (bio_1), temperature annual range (bio_5) and annual precipitation (bio_12). The results showed a sharp decline in the extent of occurrence and the area of occupancy of *Paphiopedilum* in the study area. The extent of occurrence and area of occupancy for HOM were 170,972 km^2 and 18 km^2. For the AOM, they were 125,315 km^2 and 12 km^2, respectively. The HOM model indicated that *Paphiopedilum* was earlier growing sporadically. On the other hand, the AOM result indicates that it is presently growing sparsely in isolated pockets that are more prone to extinction. *Paphiopedilum* can be conserved successfully using an integrative conservation approach, comprising ecological modeling techniques to search for additional locations, ex situ propagation techniques, and possible reintroduction in selected areas.

Keywords: Ecological niche modeling, environmental variables, lady slipper orchids, orchid conservation.

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Author details: Debonina Dutta is currently pursuing her PhD. Her research interest includes the study of few selected species of *Paphiopedilum* genus in northeastern India and their conservation using biotechnological tools. Aparajita De is a professor. She has specialized in forest ecology, RS, and GIS applications in forest ecology and ethnobiology.

Author contributions: DD carried out the fieldwork and drafted the manuscript. AD provided guidance to conduct the field surveys and has reviewed and corrected the manuscript.

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INTRODUCTION

Predictive habitat distribution models are being used extensively in ecology as they can statistically relate the geographic distribution of species or communities to their environment (Guisan & Zimmermann 2000). These models correlate known species occurrence with climatic data available for relevant areas to determine the boundaries of the multidimensional range of the species. By projecting such conditions onto geographical space, one can predict the potential distribution of the target species. These techniques are applied in a wide variety of studies to: 1. predict the distribution of rare, threatened, or invasive species (Serra et al. 2012; Silva et al. 2013, 2014; Deka et al. 2018), 2. optimize future faunal/floristic surveys (De Siqueira et al. 2009), and 3. inform the establishment of future protected areas (Nóbrega & De Marco Jr 2011).

Studies related to species distribution models have been conducted for the family Orchidaceae by many workers (Kolanowaska & Konowalik 2014; Kolanowska & Busse 2020). Orchids are one of the most threatened group of plants as their complex life history makes them particularly vulnerable to global environmental change. There are more than 1,200 genera of orchids reported in India (Misra 2019; Singh et al. 2019; Schuiteman 2022). The present study tries to model the current distribution of the genus *Paphiopedilum*, family Orchidaceae in northeastern India, and compare it with the historical occurrence data depicting its distribution in the past. The genus *Paphiopedilum* is highly preferred in the horticultural market for its exotic, large flowers on small plants (Cribb 1998). A few species are regarded as threatened or even extinct in the wild due to over-collection from natural areas and large-scale illegal trade (Long et al. 2010). The genus *Paphiopedilum* is listed in Appendix I of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 2022). All the species under the genus *Paphiopedilum* found in India come under the category of Vulnerable to Critically Endangered according to the IUCN Red List of Threatened Species (IUCNredlist.org/2021-3) (Table 1). Due to its high horticultural importance (Zhen et al. 2006), the genus faces extensive collection pressure from the wild. This, along with the rapid degradation of its habitat has led to the drastic reduction in the population of the genus (Cribb 1998).

Nine species of *Paphiopedilums* have been reported from India: *Paphiopedilum druryi* (Bedd.) Stein, growing at an altitudinal range 1,400–1,550 m, *Paphiopedilum fairrieanum* (Lindl.) Stein growing at 200–1,200 m, *Paphiopedilum venustum* (Wall. ex Sims) Pfitzer at 500–1,500 m, *Paphiopedilum wardii* (Summerh.) at 1,200–2,500 m, *Paphiopedilum villosum* (Lindl.) Stein at 1,300–2,200 m, *Paphiopedilum insigne* (Wall. ex Lindl.) Pfitzer at 1,000–1,500 m, *Paphiopedilum charlesworthii* (Rolfe) Pfitzer at 1,200–1,600 m, *Paphiopedilum spicerianum* (Rchb.f.) Pfitzer at 300–1,400 m and *Paphiopedilum hirsutissimum* (Lindl. ex Hook.) Stein at 200–1,800 m. Eight species are found in the eastern Himalaya and northeastern India, and one in southern India (Hajra & De 2009; Chowdhery 2015). All the species of this genus found in northeastern India have been reported to grow at altitudes of 200–2,200 m. Several species of *Paphiopedilum* are found growing in shady vertical/ limestone cliffs at varying altitudes (Averyanov 2007; Averyanov et al. 2014; Gurung et al. 2019).

The present work deals with the following objectives: estimation of the past and the present distribution status of some *Paphiopedilum* orchids in northeastern India, estimation of changes in the area and the extent of occurrence of *Paphiopedilum* spp. (if any), and determination of the environmental variables that are vital to the distribution of the genus.

Study area

Northeastern India comprises the eastern part of the Himalayan range, intercepted by plains, valleys, and hilly terrains (Yadava 1990). Our study was carried out in Meghalaya, Mizoram, Arunachal Pradesh, Sikkim, Nagaland, and Assam (Figure 1). The following species of *Paphiopedilum* were recorded in the present study, viz, *P. spicerianum, P. venustum, P. insigne, P. fairreanum*, and *P. hirsutissimum*.

MATERIALS AND METHODS

Study design

Ecological niche models (ENM) were prepared using maximum entropy modelling (MaxEnt) of species geographic distributions (Phillips et al. 2006). The version 3.3 of MaxEnt was used for the current study. We executed two models for our study. Past and present data were divided into historical occurrence points and actual occurrence points. Model 1 was executed using the Historical occurrence points. Historical occurrence data of *Paphiopedilum* were obtained from the recorded historical data such as herbarium records (Kew Herbarium catalogue 2022; Museum National D histoire Naturelle 2022; GBIF 2022; Natural History Museum 2022) and published literature (Table 2). We have named

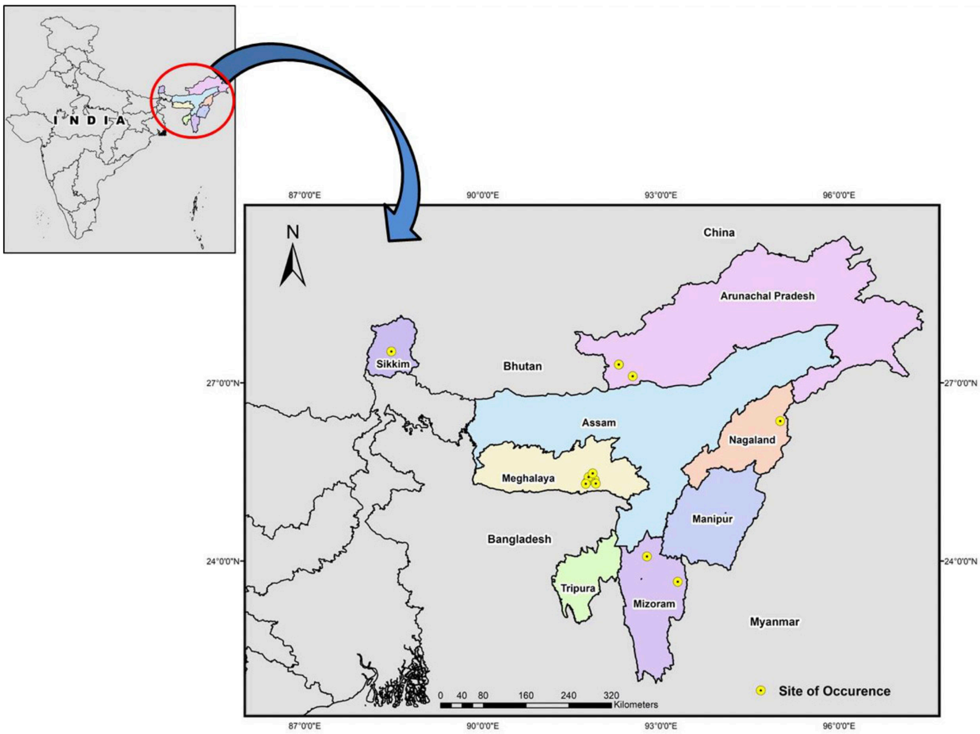

Figure 1. The study area.

it as historical occurrence model (HOM) in this paper. Model 2 was executed using the actual occurrence data (Table 3). Therefore, model 2 is referred to as the actual occurrence model (AOM).

The results obtained from the ecological niche model were verified in the study area during the period of 2015–2021. The details of the historical presence sites and actual presence sites are given in the Table 2 & 3. Based on the ENM observations, the area of occupancy (AOO) & extent of occurrence (EOO) of historical and actual occurrence data of *Paphiopedilum* were estimated. The estimation of AOO & EOO were performed using Geospatial Conservation Assessment Tool (GeoCAT), calculated at a 1 km^2 area cell size. Figure 2 gives the details of the study design.

Table 1. The threat category of genus Paphiopedilum (IUCN: Ver.2021–3)

Name	Threat category	Population trend
P. druryi	Critically endangered	Decreasing
P. fairrieanum	Critically endangered	Decreasing
P. venustum	Endangered	Decreasing
P. wardii	Endangered	Decreasing
P. villosum	Vulnerable	Decreasing
P. insigne	Endangered	Decreasing
P. charlesworthii	Endangered	Decreasing
P. spicerianum	Endangered	Decreasing
P. hirsutissimum	Vulnerable	Decreasing

Data collection

Historical data were collected from various herbaria (both offline and online) and literature sources. Occurrence data of *Paphiopedilum* was obtained from herbaria of the Botanical Survey of India, ERC, Shillong (Assam), Global Biodiversity Information Facility (GBIF), Central National Herbarium (CAL), Forest Research Institute, Dehradun (DD), Botanical Survey of India, Arunachal Pradesh Regional Centre (ARUN), Natural History Museum (NHM), Museum National d'Histoire Naturelle (MNHN) and Kew herbarium (KEW) (Table 2). The previous occurrence reports were also noted from the literature survey (Pradhan 1971; Pradhan 1975; Pradhan 1976, 1979; Kataki et al. 1984; Bose et al. 1999; Lucksom 2007; Misra 2007; Russel 2008a,b; Mao 2010; Bhattacharjee et al. 2018). The records obtained from literature reviews were used for cross-referencing with the reported locations of herbarium collections. Further the herbaria collections having location information (nearby village name or landmark) were tagged and digitized with the help of Google Earth following Milagros & Funk (2010).

AOM was prepared from the primary data. The primary data were collected from field visits to respective localities of different states (Table 3). The field surveys were conducted by snowball sampling method (Spreen 1992; Johnson 2014). The flowers of each species growing on the cliff were identified using a binocular. Geo -coordinates of the location were recorded using GPS (Garmin etrex 20) and the habitat features were recorded. The accessible sites were thoroughly surveyed for a closer view of the habitat.

Environmental variables

The dataset for ENM include NDVI (Normalized differential vegetation index), bioclimatic variables, and hydrological variables (i.e., slope, aspect, topography, and elevation). A total of 12 environmental variables were selected for the study. Table 4 shows the list of the final selected variables for the present study.

The environmental variables were applied with principal component analysis (PCA) to avoid multi-co linearity (correlation among the variables that could create redundancy in models) (Chaudhary et al. 2021). The bioclimatic layers in ASCII format were used with a resolution of 30 ARC seconds for this study. The variables for the area of interest were obtained by masking the bioclimatic rosters with the boundary of northeastern India using ArcView. Highly correlated variables were excluded by performing a Pearson correlation test of variables exhibiting a value of $r < 0.9$ (i.e., 90%). A total of 12 environmental variables were used post correlation (Table 4).

RESULTS

A total of 40 specimens were obtained from various herbaria in India and other countries (Table 2). During the present study, we located five species of *Paphiopedilum* in different sites of the study area (Table 3). They were *P. spicerianum*, *P. insigne, P. fairreanum, P. venustum*, and *P. hirsutissimum.* A total of 16 actual occurrence sites were recorded for the five species. Image 1 shows the habitat of a few *Paphiopedilum* species. The two ecological niche models were executed based on this data and the results obtained are given as follows.

Historical occurrence model and actual occurrence model

Two models were obtained using the historical occurrence data and actual occurrence data. The ENM models are represented in Figure 3. Model 1 or HOM represents the historical occurrence distribution of *Paphiopedilum*, and model 2 or AOM represents the actual occurrence distribution of *Paphiopedilum* in northeastern India.

AUC and jackknife interpretation

The model calibration test for *Paphiopedilum* yielded satisfactory results for both models. The red line shows the 'fit' of the model to the training data, and the blue line indicates the 'fit' of the model to the testing data (Figure 4). The area under the curve (AUC) value of each model aids in the assessment of the model quality. In the jackknife of AUC, the blue line depicts the real test of the predictive power of the MaxEnt model. An AUC value above 0.9 (closer to 1.0) indicates a good model performance. The AUC values for HOM (AUCtest = 0.972 ± 0.015) and AOM (AUCtest = 0.942 ± 0.015) therefore indicated that the model performance was good in both cases.

The significance of environmental variables on each model was assessed by interpretation of the jackknife of AUC (Figure 5). The contribution of the environmental variables on the model build was assessed from the percent contribution of variables and permutation importance (Table 5). Among all the variables, bio_2 (mean diurnal range) and bio_1 (annual mean temperature) were the most influential variables in the build of HOM as evident from the percent contribution of the variables in model build. The variable bio_2 contributed 46.6% and bio_1 contributed 19.3% respectively on HOM (Table 5). According to the internal jackknife of AUC for HOM, bio_1 (annual mean temperature) has the highest contribution to the model, followed by h_dem (elevation) (Figure 5). Jackknife of AUC shows the contribution of environmental variables in both models. The variables collectively contributed 100% to the HOM. Aspect (h_aspect) and topographic index (h_topoind) contributed 19.1% and 0.7% (Table 5). Considering the permutation importance, bio_5 contributed the highest (55.3%) to the model, followed by h_dem (27. 5%) and bio_2 (8. 9%) (Table 5). The variable bio_2 was the most influential environmental variable in the model build of HOM.

The percent contribution of variables in the model build of AOM revealed that bio_12 (annual precipitation) and bio_2 (mean diurnal range) were most influential in the model build. Bio_12 contributed 41.9% and bio_2 contributed 29.1% to the model build. The variable bio_2 was followed by bio_5 (max temperature of the warmest month) that contributed 24.4%, and h_topoind contributed 3.9% to the AOM. Considering the permutation importance, bio_5 contributed 53.1%. Jackknife of AOM infers the highest contribution of h_topoind and bio_14 (precipitation of driest month),

Table 2. Historical occurrence records of *Paphiopedilum* spp.

	Species	Year	Location	Herbarium source
1	*P. fairreanum*	1857	NA	Royal Botanic garden, Kew
2	*P. insigne*	1859	Mount Khasia, Meghalaya	Museum National d'Histoire Naturelle
3	*P. venustum*	1893	Sonai, Assam	Natural History Museum
4	*P. venustum*	1893	Sikkim Himalaya	Natural History Museum
5	*P. insigne*	1894	Cherrapunjee, Meghalaya	Central National Herbarium, Kolkata
6	*P. insigne*	1899	Shella, Meghalaya	Central National Herbarium, Kolkata
7	*P. insigne*	1899	Jaintia hills, Meghalaya	Central National Herbarium, Kolkata
8	*P. insigne*	1899	Jaintia hills, Meghalaya	Bavarian Natural History Collections (SNSB-GBIF)
9	*P. venustum*	1899	Lingzah Tolung,North Sikkim	Naturalis Biodiversity Center (GBIF)
10	*P. venustum*	1899	Sikkim	Harvard University Herbaria (GBIF)
11	*P. fairreanum*	1941	Rohlu, Sikkim	Central National Herbarium, Kolkata
12	*P. insigne*	1944	Smit, Meghalaya	Natural History Museum
13	*P. venustum*	1952	Cherrapunjee, Mount Khasia, Meghalaya	Naturalis Biodiversity Center (GBIF)
14	*P. venustum*	1952	Khasia hills, Meghalaya	Museum National d'Histoire Naturelle, ,
15	*P. fairreanum*	1957	Dirang dzong, Arunachal Pradesh	Central National Herbarium, Kolkata
16	*P. hirsutissimum*	1962	Khasi hills, Meghalaya	Central National Herbarium, Kolkata
17	*P. villosum*	1963	Cultivated plant	Central National Herbarium, Kolkata
18	*P. spicerianum*	1972	National orchidarium	BSI-ERC, Shillong
19	*P. fairreanum*	1974	Tenga Valley, Arunachal Pradesh	BSI-ERC, Shillong
20	*P. insigne*	1974	Mount Khasia, Meghalaya	Natural History Museum
21	*P. insigne*	1974	Mount Khasia, Meghalaya	Museum National d'Histoire Naturelle
22	*P. insigne*	1975	Khasia Mountains	Royal Botanic Garden, Kew
23	*P. villosum*	1976	Lunglei, Mizoram	Forest research Institute, Dehradun
24	*P. fairreanum*	1978	Jameri, Arunachal Pradesh	Forest research Institute, Dehradun
25	*P. venustum*	1984	Khasya hills, Meghalaya	Royal Botanic Garden, Kew
26	*P. venustum*	1984	Sikkim Himalaya	Royal Botanic Garden, Kew
27	*P. venustum*	1993	Khasia hills, Meghalaya	Museum National d'Histoire Naturelle
28	*P. hirsutissimum*	2006	Maram, Manipur	BSI-ERC, Shillong
29	*P. insigne*	2016	Sohra, Meghalaya	iNaturalist (GBIF)
30	*P. fairreanum*	2017	Arunachal Pradesh	Wildlife Institute of India (GBIF)
31	*P. venustum*	2019	East Khasi Hills, Meghalaya	University of Michigan Herbarium (GBIF)
32	*P. hirsutissimum*	2019	Senapati, Manipur	University of Michigan Herbarium (GBIF)
33	*P. hirsutissimum*	NA	NA	Royal Botanic Garden, Kew
34	*P. fairreanum*	NA	Rupa bridge, Arunachal Pradesh	Central National Herbarium, Kolkata
35	*P. fairreanum*	NA	Gochum, Rupa	BSI-ERC, Shillong
36	*P. insigne*	NA	Khasiya mountains	Royal Botanic Garden, Kew
37	*P. villosum*	NA	Sairep, Mizoram	BSI-ERC, Shillong
38	*P. insigne*	NA	Khasi hills, Meghalaya	Central National Herbarium, Kolkata
39	*P. spicerianum*	NA	Cachar, Assam	Central National Herbarium, Kolkata
40	*P. hirsutissimum*	NA	Naga hills. Nagaland	Central National Herbarium, Kolkata

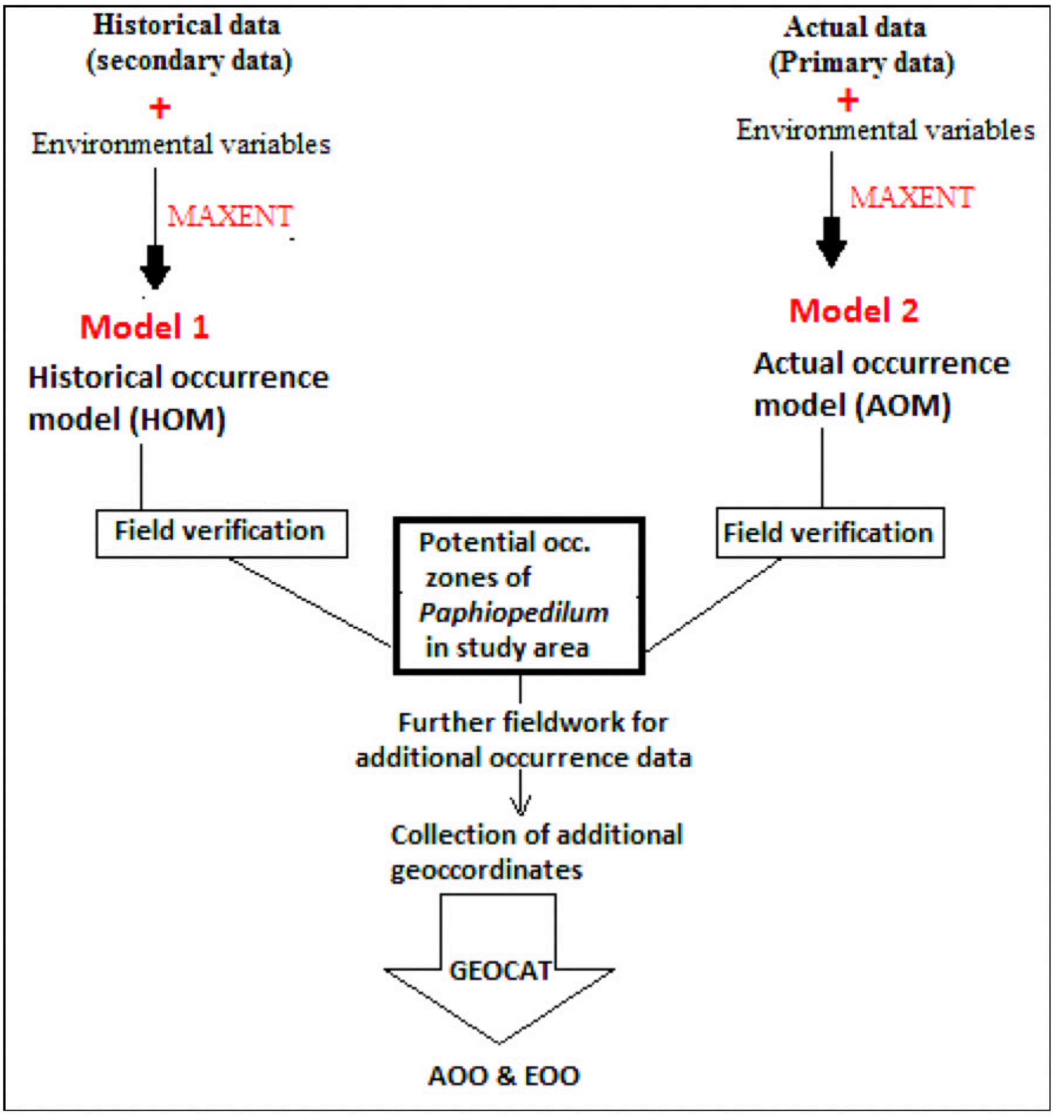

Figure 2. Flowchart of the study design.

Image 1. i—Cliff habitat site of *Paphiopedilum insigne* | ii—Habitat of *Paphiopedilum insigne* | iii— Habitat of *Paphiopedilum fairrieanum* | iv—Habitat of *Paphiopedilum spicerianum*. © Debonina Dutta.

Table 3. Actual occurrence records of *Paphiopedilum* spp.

	Species	State	Locality	District
1.	*P. spicerianum*	Mizoram	Lengpui	Mammit
2.	*P. insigne*	Meghalaya	Laimotsiang	East Khasi Hills
3.	*P. insigne*	Meghalaya	Latara	East Khasi Hills
4.	*P. insigne*	Meghalaya	Mawlyndiar	East Khasi Hills
5.	*P. insigne*	Meghalaya	Mawlyndiar (Liewla)	East Khasi Hills
6.	*P. insigne*	Meghalaya	Sohra (Nohkalikai)	East Khasi Hills
7.	*P. venustum*	Arunachal Pradesh	Dirang	West Kameng
8.	*P. venustum*	Meghalaya	Sohra	East Khasi Hills
9.	*P. fairreanum*	Arunachal Pradesh	Dirang	West Kameng
10.	*P. fairreanum*	Arunachal Pradesh	Dirang	West Kameng
11.	*P. fairreanum*	Arunachal Pradesh	Tenga	West Kameng
12.	*P. fairreanum*	Arunachal Pradesh	Rupa	West Kameng
13.	*P. venustum*	Sikkim	Upper Dzongu	North Sikkim
14.	*P.hirsutissimum*	Nagaland	Tobu	Mon
15.	*P.hirsutissimum*	Nagaland	Meluri	Phek
16.	*P. venustum*	Sikkim	Mangan	North Sikkim

Table 4. List of environmental variables.

	Variable	Description
1.	Bio_1	Annual mean temperature
2.	Bio_2	Mean Diurnal Range (mean of monthly (max temp – min temp))
3.	Bio_3	Isothermality (P2/P7)*(100)
4.	Bio_4	Temperature Seasonality (standard deviation *100)
5.	Bio_5	Max temperature of the warmest month
6.	Bio_12	Annual precipitation
7.	Bio_14	Precipitation of Driest Month
8.	Bio_15	Precipitation of Seasonality (coefficient of variation)
9.	h_dem	Digital elevation model
10.	h_ topoind	Topographic index
11.	h_aspect	Aspect
12.	h_slope	Slope

followed by bio_2 (mean diurnal range) and bio_12 (annual precipitation). Amongst the bioclimatic factors, bio_12 showed the highest contribution to the build of AOM (Table 5).

Potential habitat areas and actual habitat areas of *Paphiopedilum* spp.

Figure 3 shows the Ecological niche model for HOM and AOM. The figure depicts the probable habitats in different colours. Areas in red are the highest potential areas for the distribution of *Paphiopedilum*. Yellow represents areas with medium potential whereas the low potential areas are represented by green; 40 secondary occurrence records (historical occurrence records) were recorded from literature and herbarium sources (Table 2). However, the field survey results revealed 16 actual occurrence records of the *Paphiopedilum* spp. in the study area (Table 3).

EOO & AOO of the genus *Paphiopedilum*

HOM shows the distribution regions of *Paphiopedilum* in Assam, Mizoram, Meghalaya, Sikkim, Arunachal Pradesh, Nagaland, and Manipur. However, according to AOM, the distribution of *Paphiopedilum* is found in all the states of northeastern India, found in HOM except Assam (Table 6). The EOO and the AOO for HOM of *Paphiopedilum* were 170,972 km^2 and 18 km^2. EOO and AOO for the AOM were 125,315 km^2 and 12 km^2.

DISCUSSION

Ecological niche modeling has efficiently predicted the potential population areas of the genus in this study. The high AUC values for training and testing (> 0.90) infer the high efficiency of the niche model to differentiate between presence and absence areas for the species.

In the Table 6, a comparison between the historical presence sites and actual presence sites obtained through ENM survey is presented. This comparison revealed the high predictive value of the model. It, therefore, provides a check on the accuracy and reliability of the ENM model in the present study.

Significant environmental variables determining the distribution of *Paphiopedilum*

According to the jackknife model and the percent contribution of variables in model build, the parameter bio_2 (mean diurnal range) shows the highest contribution to the build of HOM (Table 5). The variable bio_2 infers to the mean of monthly temperatures (max temperature-min temperature). It contributes 46.6% to the model build of HOM, indicating the high importance of the mean temperature in the growth of the orchids of this genus.

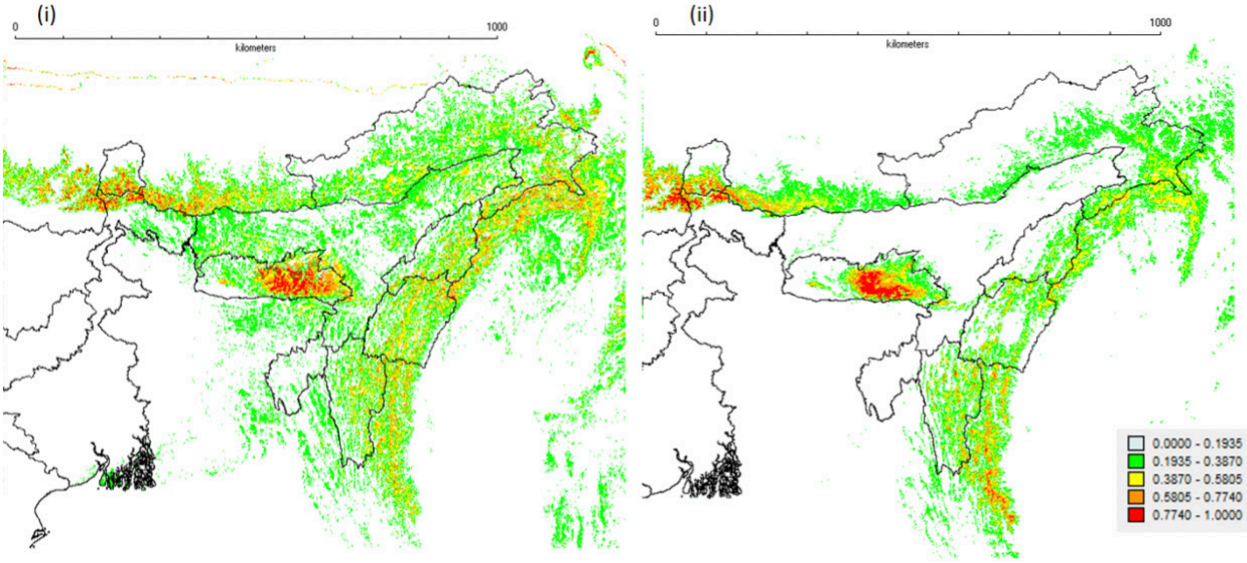

Figure 3. ENM Models representing: i—Historical distribution of *Paphiopedilum* (Model 1) | ii—Actual distribution of *Paphiopedilum* (Model 2) in study area.

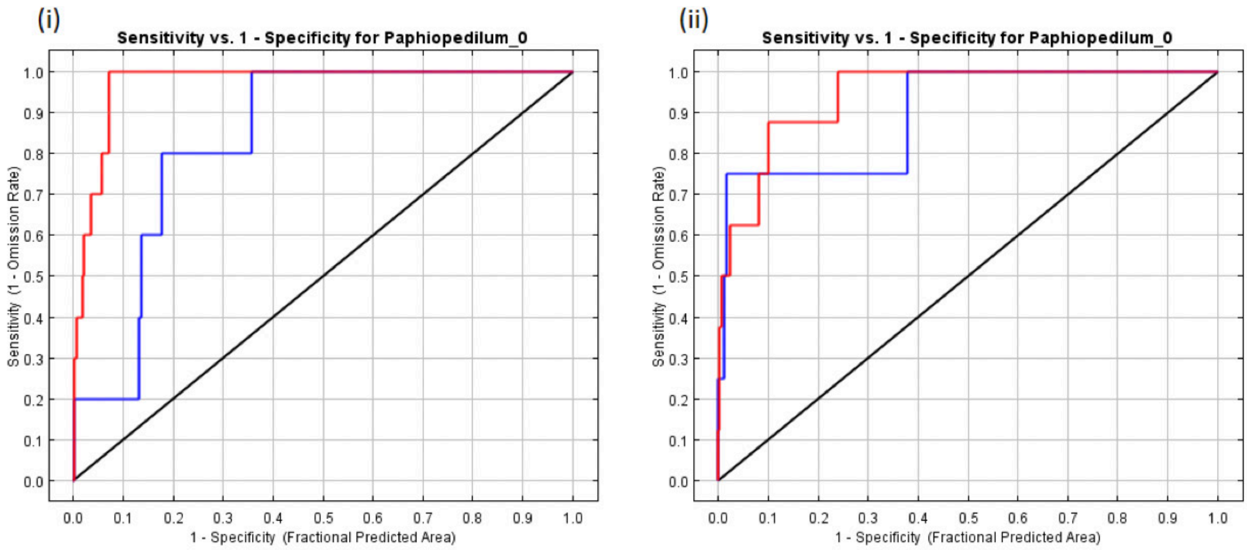

Figure 4. AUC: i—Historical occurrence model | ii—Actual occurrence model.

In the AOM, bio_12 is the most significant variable in the jackknife interpretation of the model (Figure 5). The variable bio_12 indicates the annual precipitation in the model build. The bio_12 variable is followed by bio_2 (mean diurnal range) and bio_5 (max temperature of the warmest month). These results indicate that temperature and rainfall are two important contributors that determine the availability of the members of genus *Paphiopedilum*. The field observations also correlate the importance of precipitation and temperature requirements of *Paphiopedilum*.

All the species of this genus found in northeastern India are found between an altitude of 200–2,200 m, which shows importance of h_dem (digital elevation model) being one of the highest contributing variables of the internal jackknife of HOM (Figure 5, Table 5). Similarly, mean temperature, mean diurnal range, max temperature of the warmest month and annual precipitation play a significant role in the model execution of *Paphiopedilum* in both HOM and AOM.

Other workers have also studied the dependence of the survival, reproduction, and germination of different plant species on temperature and precipitation. For instance, Wilkie et al. (2008) reported the influence of

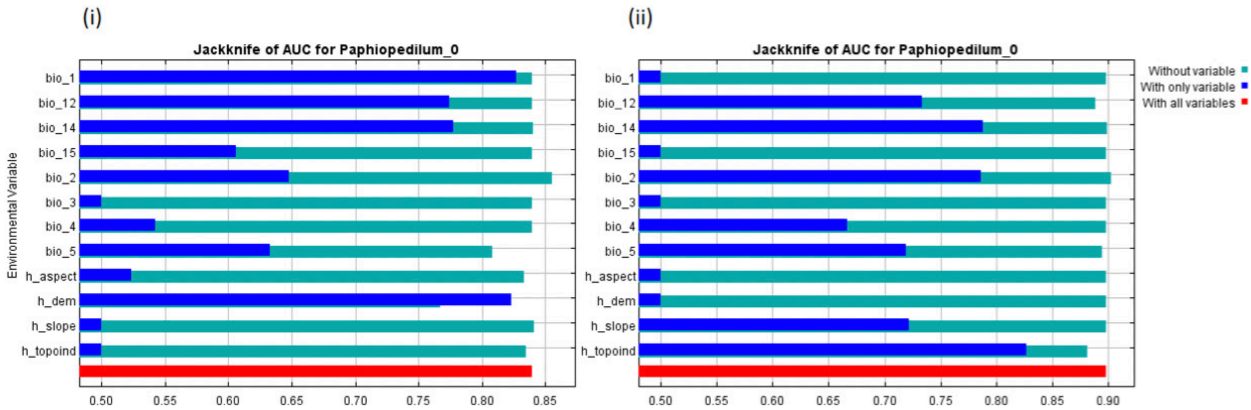

Figure 5. Jackknife of environmental variables: i—Historical occurrence model | ii—Actual occurrence model.

Table 5. Percent contribution of variables in model build.

Percent contribution of variable in Historical occurrence model			Percent contribution of variables in Actual occurrence model		
Variable	Percent contribution	Permutation importance	Variable	Percent contribution	Permutation importance
bio_2	46.6	8.9	bio_12	41.9	0
bio_1	19.3	0	bio_2	29.1	43.1
h_aspect	19.1	6.6	bio_5	24.4	53.1
h_dem	6	27.5	h_topoind	3.9	3.8
bio_14	4.3	0.2	bio_14	0.7	6.7
bio_5	3.7	55.3	bio_15	0	0
h_topoind	0.7	1.3	h_slope	0	0
bio_12	0.3	0	h_dem	0	0
h_slope	0	0	h_aspect	0	0

low temperatures (vernalization), seasonal variations in temperature, photoperiod, and water stress on the flowering of plants (Wilkie et al. 2008). In another study, inadequate temperature conditions during endodormancy compromised flowering or led to erratic and longer flowering duration with morphological disorders and flower necrosis (Rodrigo & Herrero 2002).

AOO, EOO concerning the past and present distribution of *Paphiopedilum*

Comparison of both models shows that the species distribution of *Paphiopedilum* has undergone a sharp decline over the past two decades. Field observations also indicate highly fragmented populations. All the species of this genus have very few individuals in the study area. A reduction in the extent of occurrence (EOO) and area of occupancy (AOO) was observed in the AOM compared to the HOM. During the field survey no species was located in the earlier reported sites of Assam (Table 6).

The reduction in AOO could be due to factors like over-collection, climate change, urbanisation, unplanned development, and habitat fragmentation. An increased frequency of large-scale disturbances caused by extreme weather events is known to cause increasing gaps and an overall contraction of the distribution range, particularly in areas with relatively low levels of spatial cohesion (Paul & Wascher 2004).

Effects of habitat fragmentation on the persistence of populations and species play a major role in conservation biology (Reed & Frankham 2003). Limitations of plant species dispersal also affect plant colonization (Olivier et al. 2002). Small population sizes, lead to decreased population fitness and eventually make the small population sizes more vulnerable to extinction (Reed & Frankham 2003; Reed 2005, 2008). The field studies revealed that the populations of *Paphiopedilum* had very few individuals. The habitat was also highly fragmented. These factors are further exacerbating the risk of extinction of the genus.

It was observed that *Paphiopedilum* grew in the rock crevices of east-facing slopes of the habitats situated

Table 6. Comparison between historical occurrence data and actual presence data.

Species	State	Locality	Source	Nearby Positive sites as per field findings
P. spicerianum	Mizoram	Mammit district	Literature review	Present
	Assam	Cachar, Sonai river Bank, Barak river bank, Narpuh WS.	Literature review Herbarium data ENM depiction	Not found
P. fairrieanum	Sikkim	Tinkitam	Literature review	Previously presence reported. Habitat Destruction due to ongoing agricultural practices (Jhum cultivation)
P. insigne	Meghalaya	Cherrapunjee, Mawsynram, East Khasi hills	Literature review, Herbarium data, ENM depiction	Present
P. venustum	Sikkim	Beh, Tong, Sanklang (Sikkim)	Literature Review, Herbarium data	Present
	Meghalaya	Jaintia Hills	Literature Review, Herbarium data	Not found
P. fairreanum	Arunachal Pradesh	Gacham village, Rupa, Tenga valley	Herbarium data	Present
P. fairreanum	Arunachal Pradesh	Jameri village	Herbarium data	Absent
P. villosum	Mizoram	Sairep, Theiriat, Lunglei	Herbarium data, ENM depiction	Present
P. hirsutissimum	Manipur	Maram	Herbarium data	Not found

in the hilly terrains (Image 1). They also grew in the space between tree roots and rock layers of the habitat substratum. The prolonged filling of the conjoining rock fissures between the rock crevices and tree roots by the dry leaves and soil organic matter of the forests provide an excellent growth medium for these orchids in the otherwise soil-deprived cliff sides (Phillips 2017).

CONCLUSION

In this study, the present status of *Paphiopedilum* in northeastern India has been determined using ENM-based surveys combined with historical data. The herbarium data provided location history from 1857 onwards (Table 2), while the field data helped in the present assessment of the genus. There was a significant reduction in the EOO and AOO in the actual model as compared with the historical model. The results of the model reveal that temperature and precipitation are the highest contributing factors determining its availability. We were unable to locate the plants in many locations that were earlier mentioned by previous workers. Therefore, it can be inferred that change in the temperature and precipitation patterns in many locations have led to its scarcity. However, this inference needs to be further corroborated with detailed records of the climate parameter.

These orchids are becoming increasingly rare mainly due to over collection from the wild, rising urbanization causing habitat destruction and also global warming (Swarts & Dixon 2009; Seaton et al. 2010; Barman & Devadas 2013; Ye et al. 2021). Favorable climatic conditions, access to wild habitat sites, and a conducive environment are important for the survival of plants (Hulme 2005; Ballantyne & Pickering 2015; Wraith & Pickering 2018; Li et al. 2020; Ye et al. 2021). The comparison of environmental requirements of the distribution of *Paphiopedilum* over the years imparts an understanding of the adaptability of these orchids with changing environmental conditions. The dwindling population size of the various species under the genus is increasing the risk of extinction of the already sparse populations in the study area. The over-collection of the *Paphiopedilum* flowers from the wild for its high market demand results in further habitat loss. Forest road constructions and urbanization also cause further degradation of the *Paphiopedilum* habitats in different areas of Northeast India. Such reasons have caused the *Paphiopedilum* orchids to become increasingly rare with time.

Ex situ conservation techniques for mass production of the species with higher market demand could reduce collection pressure on already dwindling wild populations in northeastern India. *Paphiopedilum* orchids are being propagated elsewhere in the world using various techniques (Huang 1988; Hong et al. 2008; Ng & Saleh 2011). Various individuals have been reintroduced into other suitable habitats by various workers in China (Yang et al. 2020; Gao et al. 2020). Since, in situ conservation is not a viable approach in many locations due to their habitat degradation and other developmental pressures, reintroduction into potential habitats will aid in conservation of the species. We recommend that reintroduction of *Paphiopedilum* orchids should be conducted on a large scale by both government and non-governmental agencies in northeastern India. We recommend the conservation of *Paphiopedilum* orchids using an integrative conservation approach of ecological niche modeling to search for additional locations, ex situ propagation techniques, and possible reintroduction in selected areas. Such schemes can be helpful to meet the market demands of *Paphiopedilum* orchids and boost the conservation of wild populations in northeastern India.

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