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# Combining ecological niche modeling with genetic lineage information to predict potential distribution of Mikania micrantha Kunth in South and Southeast Asia under predicted climate change

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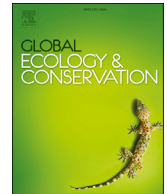
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A B S T R A C T

Ecological niche models (ENM), an effective tool to predict the potential distribution of invasive species, are often built on assumptions of niche conservatism between native and invasive ranges and genetic uniformity of the invasive population. In this study, we have incorporated genetic information with ENM to generate projected distribution of the invasive species *Mikania micrantha* for which two genetic clusters were identified in South and Southeast Asia. Climatic niches were compared between native and invasive ranges, as well as between invasive ranges of two lineages by using multivariate and univariate analyses. Ecological niche models were built with MaxEnt, using occurrence data of two lineages separately, together and also using native range data. Predictive abilities of the models were compared and potential distributions of the two lineages were predicted under present and future climate scenarios. The models were projected on the native range to identify climatically suitable areas for each lineage. Significant differences between climatic niches of the two invasive lineages were found and unique climatically suitable areas for each lineage were identified. A large area of South and Southeast Asia was found to be climatically suitable for both lineages. Under climate change scenarios, pole ward range expansion for one lineage and decrease in range size along marginal areas for another lineage were predicted. However, high amount of niche unfilling for both the lineages indicated that if introduced, the lineages can establish in cold and dry areas of the invasive range. The evidence of niche abandonment between native and invasive ranges indicated presence of other lineages in its native range which are not yet introduced in this region. These findings provided baseline data for implementing management strategies at early stage of invasion and quarantine measures to protect this region from future invasions. Climatically suitable areas in the native range were identified for both lineages which can be prioritized for conducting surveys for identification of source populations and biological control agents. Our study highlights the importance of integrating genetic data in future ENM approaches to have finer scale information of species' distribution, which can be utilized to develop region-specific and climate change-integrated management strategies for invasive species.

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## 1. Introduction

Biological invasions are now considered a major global challenge for the conservation of natural resources and biodiversity (Simberloff et al., 2013). The similarity of climatic conditions between the native and invaded ranges is one of the crucial factors for successful invasion of an alien species (Williamson, 2006). Ecological niche models (ENM) are powerful tools to identify areas in a novel habitat that are climatically suitable for an invasive species (Elith et al., 2006; Elith and Leathwick, 2009) and are frequently used towards understanding the potential distribution of invasive species (Elith, 2017; Mainali et al., 2015; Padalia et al., 2014) under current and future climate change scenarios.

Two fundamental assumptions of classical ENM approaches are niche conservatism and genetic uniformity of a species throughout its range. The niche conservatism hypothesis assumes that a species will conserve its climatic niche over space and time, implying that an invasive species will occupy a similar climatic envelope in both native and invaded ranges (Peterson et al., 1999). The genetic uniformity hypothesis assumes absence of genetic variation in a species across its geographic distribution (Ikeda et al., 2017). While a number of studies on invasive species have confirmed spatial and temporal niche conservatism between native and invasive habitats (Petitpierre et al., 2012), contrasting examples of niche shift were also reported (Atwater et al., 2018; Broennimann et al., 2007). In the case of range-shifting species, assuming niche conservatism between native and invaded ranges may over- or underestimate the predicted distribution under present and future climate conditions (Elith et al., 2010). On the other hand, the influence of genetic diversity on invasion success has been long recognized (Baker and Stebbins, 1965). Genetic diversity may lead to local adaptation, which is defined as the shift of phenotypic traits in response to environmental heterogeneity (Cortés, 2017; Gentili et al., 2018). Locally adapted genotypes could vary in their climatic requirement and therefore, will spread differentially under changing climate conditions (Schierenbeck, 2017). In this context, testing niche conservatism and the incorporation of genetic information whenever available, becomes crucial for predictive accuracy of ENM, especially when predicting the potential distribution of an invasive alien species for future climate change scenarios (Early and Sax, 2014; Ikeda et al., 2017).

A number of studies on tree species [e.g. *Populus fremontii* (Ikeda et al., 2017); *Pinus strobus* (Joyce and Rehfeldt, 2013)] have demonstrated that incorporation of niche and genetic information into ENM has significantly improved model predictive accuracy (Alvarado-Serrano and Knowles, 2014). However, similar application on invasive species is rare (but see Zhu et al. (2017)), suggesting that there is a clear need to increase the numbers of studies by including global invasive species (species with ranges spanning more than one continent) and identifying their potential distribution in developing economies of the world where the majority of the world's biodiversity hotspots are found. The threat of invasive alien species is set to be much higher in the coming decades in the economically developing regions where invasions are least recognized and studied (Early et al., 2016).

To fill these research gaps, the present study has been undertaken to model the invasion potential of one of the hundred worst weeds of the world (Lowe et al., 2000), *Mikania micrantha* Kunth (Asteraceae), under present and future climate change scenarios. Native to Mexico, Central America, the Caribbean and tropical South America, *M. micrantha* has now spread to Oceania, South and Southeast Asian countries and southern Florida (Ellison and Sankaran, 2017). Due to its fast growth rate and creeping growth form, *M. micrantha* smothers other plant species and causes extensive economic and ecological impacts on natural forests, plantations and agricultural systems across its invasive range (Tripathi et al., 2012). Recent molecular studies involving populations from South and Southeast Asia identified two genetic clusters of *M. micrantha* and these two genetic lineages were also presumably introduced from different source populations (Yang et al., 2017) and spread through different routes in its invasive range (Banerjee et al., 2019).

In this context, we can incorporate this genetic cluster information into ENM to generate lineage level projected distributions of *M. micrantha* in South and Southeast Asia (hereafter, invasive range). Previous studies have predicted the potential distribution of *M. micrantha* using ENM at regional (Choudhury et al., 2016), national (Iyer et al., 2019) and global (Day et al., 2016) scales under both present and future climatic situations (Shrestha et al., 2018). We hypothesized that in comparison to the conventional ENM (*i.e.* considering all genotype information together), models built for two lineages separately will provide finer scale estimate of the potential distribution of *M. micrantha* and have better interpretability for guiding its management actions. Many successful invasions were associated with the occurrence of multiple introductions, combining genotypes from differentiated source populations (Bock et al., 2015; Dlugosch and Parker, 2008). Given the wide ecological amplitude of *M. micrantha* (Banerjee et al., 2017b), we can clarify the invasive potential of this species in this region by hypothesizing that both lineages can grow throughout the invasive range. Therefore, this study was undertaken with the following objectives: 1) to test whether the climatic niche of *M. micrantha* was conserved between native and invasive ranges (niche differentiation in environmental space), 2) to compare invasion potential of the two lineages in the invasive range (niche differentiation in the geographic space), and 3) to predict the impact of climate change on the distribution of two lineages in the invasive range.

## 2. Materials and methods

### 2.1. Collection of occurrence data and environmental variables

*M. micrantha* occurrence data from both native and invasive ranges were sourced from the Global Biodiversity Information Facility (GBIF), herbarium databases and previously published research papers (1950−2015). GBIF database was searched using the search string: 'Scientific name: *Mikania micrantha* Kunth'(https://doi.org/10.15468/dl.h4ymbn). We consulted seven herbaria and four literature databases (Invasive Species Specialist Group, CABI, Google Scholar, and PIER) to collect the occurrence records. Considerable ambiguity exists in literature over the identity of the species present in this region due to − 1) synonymous use of three names to identify the species as *M. cordata*, *M. scandens* and *M. micrantha*; and 2) overlapping native range of *M. cordata* (Hainan in China, Indonesia, Malaysia, Myanmar, Philippines, Taiwan, Thailand; CABI Invasive Species Compendium - https://www.cabi.org/isc/datasheet/118575#todistributionTable) with the invasive range of *M. micrantha* in Asia. To avoid any confusion arising from this taxonomic ambiguity, we searched the literature databases using the following keywords: 'Mikania'; 'invasion'; 'invasive plants'. We considered literature reports with the specific epithet '*M. micrantha*' and screened the literature records by - 1) discarding the reports on *M. cordata* from its native range (which overlapped part of our study region) and studies without any species information, 2) considering reports of *M. scandens* (a native of northern USA) and *M. cordata* (outside its native range) as misidentification of *M. micrantha* (Holmes, 1982; Parker, 1972). Each herbarium specimen was checked for possible misidentification (except for digital collections), and location information from label data was recorded. Geographic coordinates (longitude and latitude) were collected from herbarium records (n = 392) and literature reports (n = 160). Locality descriptions and Google Earth™ was used to georeference occurrence data lacking geographic coordinates at a precision level of two decimal degrees. Furthermore, occurrence records collected during our field surveys in part of its invasive range (southern China, east, northeast and south India) were also used. Since our sampling locations did not overlap with the native range of *M. cordata* in Asia, the samples were positively identified as *M. micrantha*. The details of occurrence data sources have been provided in Appendix A and the field sampling locations have been given in Appendix B in Supporting Information.

The invasive range occurrences were subset for the study region and we considered occurrence records only from those countries in South and Southeast Asia for which genetic information and invasion routes of *M. micrantha* are available. Occurrence records were further screened for duplicates and were spatially rarefied [using SDMtoolbox 2.3 in ArcMap 10.2 (Brown, 2014);] by selecting a single point per grid cell (cell size of 10 km) to avoid model over-fitting and to ensure the validity of statistical analysis. A total of 879 occurrence records were retained for the native region and 352 records for the invasive range. The occurrence records of the invasive range were divided into two lineages − lineage 1 (n = 202) and lineage 2 (n = 150) based on previous genetic information and invasion routes of *M. micrantha* in South and Southeast Asian countries. Consequently, populations from Indonesia, Malaysia, Singapore, Taiwan, south India, Hainan province of China, Sri Lanka, Brunei and Timor-Leste were considered as lineage 1 whereas populations from east and northeast India, Myanmar, Thailand, Philippines, southern China, Hong Kong and Macao formed lineage 2 (Fig. 1). The geographical locations of the occurrence records have been provided in Appendix C in Supporting Information.

Nineteen bioclimatic variables were downloaded from the WorldClim database version 1.4 (http://www.worldclim.org/) (Hijmans et al., 2005), averaged for the 1950−2000 period, at a spatial resolution of 5 arc minutes (approximately 9 km resolution at the equator). We used FactoMineR package (Lê et al., 2008) in R to perform a principal component analysis and visualized the correlation between the bioclimatic variables. Six bioclimatic variables namely 1) Annual mean temperature (Bio01), 2) Temperature seasonality (Bio04), 3) Minimum temperature of the coldest week (Bio06), 4) Temperature annual range (Bio07), 5) Annual precipitation (Bio12), and 6) Precipitation seasonality (Bio15) were chosen based on their non-collinearity and contribution to the overall environmental variation (Appendix D). For future climate projections, we used two representative concentration pathway scenarios of IPCC (RCP 2.6 and 8.5) for the two time periods (2050 and 2070). Since the primary objective of this study was to assess the performance of genetically informed ENM and not entirely focused on mapping potential distribution of *M. micrantha* under changing climate, we considered one general circulation model (GCM), namely the Hadley Global Environment Model 2-Atmosphere Ocean (HADGEM2-AO), to map the potential distribution of the two lineages in the study area.

### 2.2. Niche characterization

The hypothesis of climatic niche conservatism of *M. micrantha* was tested using a modified Principal Component Analysis (PCA-env) following Broennimann et al. (2012). In this approach, environmental niche was characterized by the first two axes of the PCA built with the bioclimatic variables. By applying a kernel density function, the occurrence points of both ranges were converted to smoothed densities of occurrences. We spatially intersected the known occurrence points of *M. micrantha* (both native and invasive lineages) with the Köppen−Geiger climate layer (available from CliMond database, https://www.climond.org/Koppen.aspx) and the climate classes where the species is currently occupying were identified. In each region (native, invasive lineage 1 and lineage 2), we included only those areas with the previously identified climate classes. We used these areas as available environment (background) to the species under the assumption of unlimited dispersal. Environmental niches were compared by estimating niche overlap and testing niche similarity between native and invasive ranges, as well as the two lineages in the invasive range. Niche overlap between two ranges was estimated using Schoener's index of
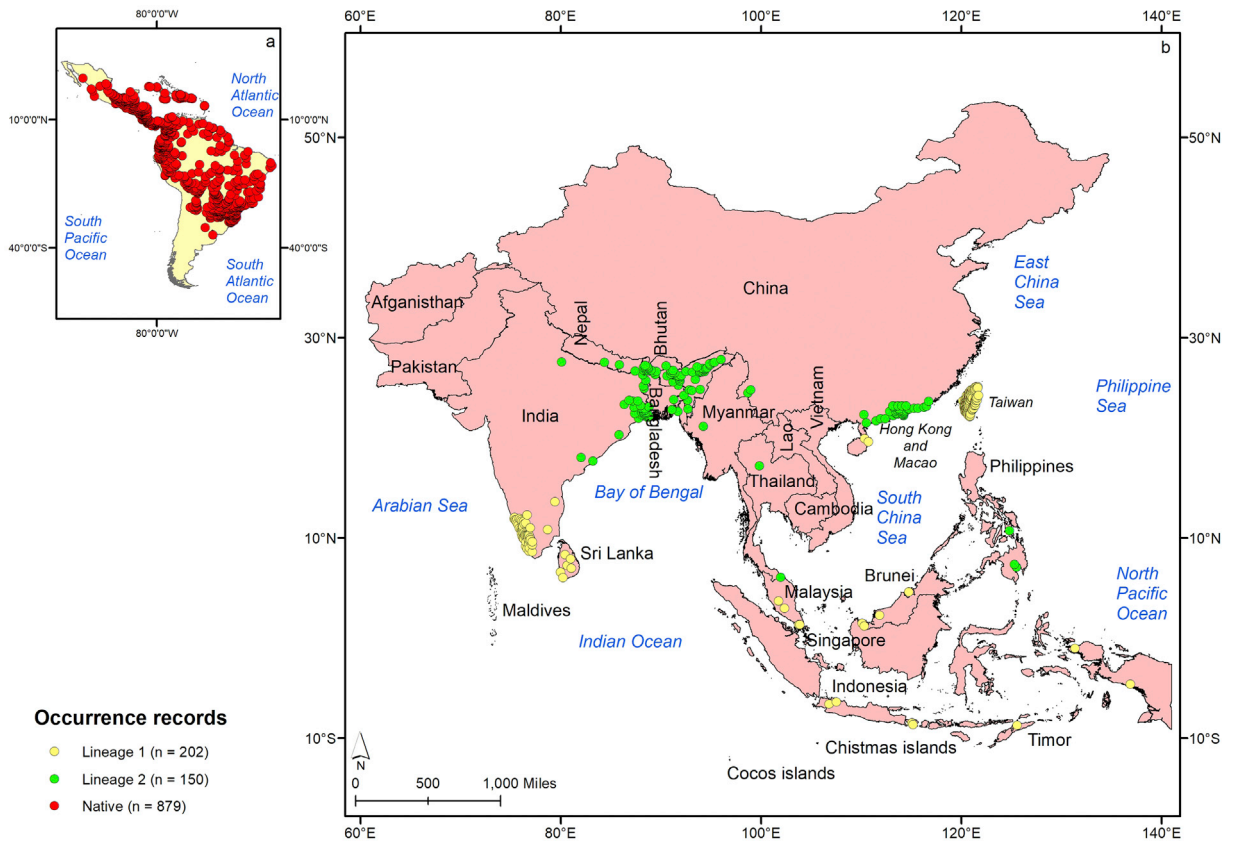
**Fig. 1.** Maps of (a) native and (b) invasive (South and Southeast Asia) ranges of *M. micrantha*. Small circles depict spatially unique occurrence records in native range, and of two lineages in invasive range.

niche breadth (D). Niche similarity tests were performed at 95% confidence intervals to test a null hypothesis of similar niches between ranges. In a niche similarity test, observed D is compared with simulated D which is generated by randomly allocating known occurrences of any one range (Broennimann et al., 2012). Following the recommendation of Guisan et al. (2014), we identified the effect of non-analogous climates on niche comparison by estimating niche overlap and testing niche similarity for each individual climate variable. In the univariate analysis, we compared niche estimates by considering − 1) all the climates available in both the ranges; and 2) climates common to both the ranges after eliminating 25% of the marginal climates. Finally, by overlapping environmental spaces of native and invasive ranges, we measured species niches by estimating - unfilled niche of native range (U), overlapping niche of both the ranges (O), and expanded niche in the invasive range (E) (Guisan et al., 2014; Petitpierre et al., 2012). These analyses were performed using the ecospat package version 3.0 (Broennimann et al., 2012) in R.

In the MESS (multivariate environmental similarity surface) analysis, the environment of grid cells occupied by the species in projection range is compared with that of the calibration range, with respect to the set of selected bioclimatic variables (Elith et al., 2010). The grid cells having a positive value indicates similar environment between the two ranges, whereas grid cells with a dissimilar environment for at least one variable received negative values (Broennimann et al., 2014). We used the dismo package version 1.1−4 (Hijmans et al., 2017) in R to compute the MESS analysis for identifying how similar the invasive and native range projections were in comparison with the four different training datasets (occurrence data of lineage 1, occurrences of lineage 2, all occurrences from invasive range, and occurrences from native range).

### 2.3. Model development and evaluation

We used Maximum Entropy Species Distribution algorithm (MaxEnt version 3.4.1) to develop the ENM for potential distribution of *M. micrantha* in its invasive range. Many studies have reported MaxEnt as one of the highest performing presence-background algorithms (Boria and Blois, 2018; Ma and Sun, 2018; Merow et al., 2013). Being a presence only model, MaxEnt generates probability of species occurrences in a landscape by comparing the probability densities of selected environmental variables from the known occurrence locations to that of randomly selected pseudo-absence (PA) points across selected model background. Geographic extent of a model background can influence a model's predictive ability (Barve

et al., 2011; VanDerWal et al., 2009). Following the BAM (Biotic-Abiotic-Movement) framework proposed by Barve et al. (2011), we considered the Köppen−Geiger climate classes as the climatically suitable regions where the species could occupy under unlimited dispersal and therefore, used these areas as the model backgrounds.

Four MaxEnt models were generated with different occurrence datasets: first, occurrence data of lineage 1 and lineage 2 were separately used in projecting the entire native and invasive ranges (model 1 and model 2); model 3 was developed using all occurrences from invasive range (irrespective of lineages) and projected on the invasive range; and finally, all native occurrence data were used to generate projected distribution in the invasive range (model 4). For simplification of the modeling algorithms, we used the default settings (feature class and regularization) in MaxEnt for each of the four models. Predictive accuracies of different models were tested using both threshold dependent and threshold independent approaches. Predictive accuracy of the three models was evaluated we used ten-fold cross-validation method in which 70% of the occurrence points were used for model training and 30% points were kept for extrinsic evaluation of the model's predictive accuracy. Minimum training presence (MTP) values obtained by training localities were used as thresholds to convert the continuous predictions generated by MaxEnt to binary predictions (pixels identified as suitable or unsuitable). Omission rate (OR = proportion of test points falling in pixels not predicted suitable) was estimated and the average value of OR for 10 replications was used as a metric for threshold dependent test. In addition, we used binomial probability tests (Peterson et al., 1999) to assess the accuracy of predicted distributions of each model. Specifically, Cohen's Kappa statistics were estimated for the threshold which minimizes the sum of sensitivity and specificity on the test data points, and predictive success was estimated based on the proportion of correctly predicted test points for each model. Using the ROCR package (Sing et al., 2005) in R, we calculated Area-Under-the-Curve (AUC) of the receiver-operating characteristics (ROC) plot. To avoid the background size bias on AUC calculation (VanDerWal et al., 2009), fixed area AUC was estimated by generating 10000 random points on the entire Köppen−Geiger climate background.

### 2.4. Mapping potential distribution

All available occurrence data for each genetic lineage was used to generate potential distribution in invasive range and as well as to identify climate suitable regions in native range. For each map, the MTP was used to generate binary prediction. Raster overlay analysis was conducted to identify prediction congruence between the two lineages in both native and invasive ranges. Omission percentage of known occurrence points were used to further classify the binary maps, where 10% omission was designated as low suitability, 10−25% omission as mid low suitability, 25−50% as mid high suitability and >50% omission as very high suitability. Change in climatically suitability areas for *M. micrantha* was quantified for both time periods (2050 and 2070) and for two RCPs (2.6 and 8.5). ArcMap 10.2 was used to perform all these analyses and visualize the outputs.

## 3. Results

### 3.1. Niche conservatism and environmental analogy

The PCA analysis of 19 bioclimatic variables revealed that maximum environmental variations between native and invasive ranges (82.3%) and between the two lineages (87.6%) were explained by the first two PCA axes. From the contribution of the six selected variables, the three most important variables were the minimum temperature of the coldest month (Bio06), temperature annual range (Bio07) and temperature seasonality (Bio04) (Table 1). We found high overlap [according to (Rödder and Engler, 2011)] between the native and invasive ranges (D = 0.597) and low overlap was detected between the invasive ranges of the two genetic lineages (D = 0.361) (Table 2). Without considering lineage information, the niche similarity test revealed that the climatic niche occupied by the species in its invasive range was more similar to the climatic niche of its native range than would be expected by chance (p = 0.019). The high value of niche stability (0.964) between the climatic niches of the native and invasive ranges (Fig. 2) indicated that *M. micrantha* in the invasive range has occupied most of its native niche. However, the null hypothesis of niche similarity was not rejected when climatic niches were compared between the invasive ranges of lineage 1 and lineage 2 (p = 0.059) (Table 2). The observed niche dissimilarity was attributed mostly to niche unfilling (0.449) in comparison to niche expansion (0.147) (Fig. 2).

Individual comparisons of the chosen climatic variables occupied by *M. micrantha* in its native and invasive ranges revealed limited to low overlap for precipitation-related variables and medium to high overlap for temperature related variables. When niche overlap was estimated between lineage 1 and lineage 2, low to medium niche overlap was found for temperature variables, whereas precipitation-related variables showed high overlap. For all the climatic variables, the similarity test revealed that the niches occupied by the species in the two ranges were not similar (p > 0.05) (Table 2). Univariate analysis further revealed niche unfilling (available environment in both ranges, but occupied in native range and unoccupied in invasive range), expansion (available environment in both ranges, but occupied in invasive range and unoccupied in native range), and abandonment (environment available and occupied only in native range) for individual climatic variables (Table 3). For example, occurrence of *M. micrantha* was recorded in annual mean temperature (Bio01) range of 5−10 °C (n = 9) in its native range. The similar climatic condition was within range of available environment for invasive lineage 1 (range = 9.1−29.2 °C) and lineage 2 (range = 7.1−29.2 °C) but unoccupied by both lineages (niche unfilling). Niche abandonment for Bio01 was also observed since a single occurrence at <5 °C was recorded from its native range, which was beyond the limit of the available environment for both invasive lineages (Table 3). Similarly, niche unfilling in the invasive

**Table 1**

Loadings on two PCA axes of climatic variables between native and invasive ranges and between invasive ranges of two lineages.

| Climatic variable | Native and invasive ranges | | Invasive ranges of lineage 1 and lineage 2 | |
|---|---|---|---|---|
| | Axis 1 (63%) | Axis 2 (19.3%) | Axis 1 (67.4%) | Axis 2 (20.2%) |
| Bio01 (Annual mean temperature) | 0.754 | 0.525 | 0.750 | 0.594 |
| Bio04 (Temperature seasonality) | −0.875 | −0.019 | −0.947 | −0.133 |
| Bio06 (Minimum temp of the coldest week) | 0.946 | 0.247 | 0.954 | 0.254 |
| Bio07 (Temperature annual range) | −0.911 | 0.195 | −0.951 | 0.163 |
| Bio12 (Annual precipitation) | 0.771 | −0.214 | 0.725 | −0.384 |
| Bio15 (Precipitation seasonality) | −0.354 | 0.859 | −0.493 | 0.775 |

Values > 0 indicate a positive contribution, whereas, those <0 indicate a negative contribution to the axis. Values in parenthesis denote percentage of variability explained by each axis.

**Table 2**

Values of niche overlap (Schoener's D index) and significance value (similarity test) between native and invasive ranges as well as between invasive ranges of two lineages, as obtained from multivariate (considering all climatic variables together) and univariate (considering each climatic variable separately) analyses.

| | Climatic variable | Niche comparison | | | |
|---|---|---|---|---|---|
| | | Native and invasive ranges | | Invasive ranges of lineage 1 and lineage 2 | |
| | | D | p | D | p |
| Multivariate | All six variables | 0.297 | 0.019 | 0.361 | 0.059 |
| Univariate | Bio01 (Annual mean temperature) | 0.621 | 0.277 | 0.345 | 0.931 |
| | Bio04 (Temperature seasonality) | 0.581 | 0.633 | 0.452 | 0.059 |
| | Bio06 (Minimum temp of the coldest week) | 0.650 | 0.356 | 0.493 | 0.733 |
| | Bio07 (Temperature annual range) | 0.458 | 0.812 | 0.391 | 0.416 |
| | Bio12 (Annual precipitation) | 0.189 | 0.713 | 0.672 | 0.415 |
| | Bio15 (Precipitation seasonality) | 0.346 | 0.990 | 0.686 | 0.376 |

range of lineage 1 was also observed for Bio07, Bio12 and Bio15 whereas niche abandonment was noticed for Bio06. Niche unfilling in the invasive range of lineage 2 was observed for Bio06, Bio12 and Bio15. Niche expansion was only observed in the invasive range of lineage 2 for Bio07 (Table 3).

The MESS analysis revealed varied amount of interpolation in the invasive and native ranges across different training datasets (Fig. 3). Models trained with occurrence data of two lineages separately and native occurrence data alone could not interpolate the environmental values of all invasive and native occurrences. This is evident from the negative values received by invasive occurrences (36.6% using lineage 1 occurrence data, 7.1% using lineage 2 occurrence data and 11.9% using native occurrence data) and native occurrences (28.4% using lineage 1 occurrences, 36.6% using lineage 2 occurrences and 15.9% using combined occurrence of invasive range).

### 3.2. Predicted distribution of M. micrantha

#### 3.2.1. Model evaluation

Comparing the performance of the four models using threshold dependent and independent tests, we found that models built with occurrence data of lineage 1 and 2 could not retrieve climatically suitable habitats for lineage 2 and 1 respectively, as evident from the high values of OR, low predictive accuracies and low AUC scores (Table 4). However, the all lineage model (model 3) predicted the two lineage test points with higher accuracy than the individual models (model 1 and model 2). The model built with native occurrence data (model 4) performed poorly to predict suitable habitat conditions for lineage 2, as evident from high OR (0.005), low predictive success (0.753) and low AUC score (0.819) (Table 4).

#### 3.2.2. Potential distribution under current climate

The potential distribution maps revealed that under present climatic conditions, 20.8% and 36.3% of the total area in South and Southeast Asia are climatically suitable for lineage 1 (Fig. 4a) and lineage 2 (Fig. 4b) respectively. The Western Ghats of southern India, coastal provinces of south China, Taiwan, east coast of Vietnam and Sri Lanka, and part of Philippines are vulnerable to lineage 1 invasion (high suitability). High climatic suitability for lineage 2 was found in the northeast and eastern India, northern Myanmar and southern China provinces. Overlay analysis between binary predictions revealed unique areas which can be predicted from model 1 (lineage 1) and model 2 (lineage 2) (Fig. 4c). Unique areas for lineage 1 are restricted to southwest India, coastal areas in Thailand, Indonesia and the Philippines. Most of the Indian landmass, Thailand, and south and southeast provinces of China are climatically suitable for lineage 2. The all lineage model predicted large amount of suitable areas (47.2%) in the invasive range than the individual lineage models (see Appendix E in Supporting
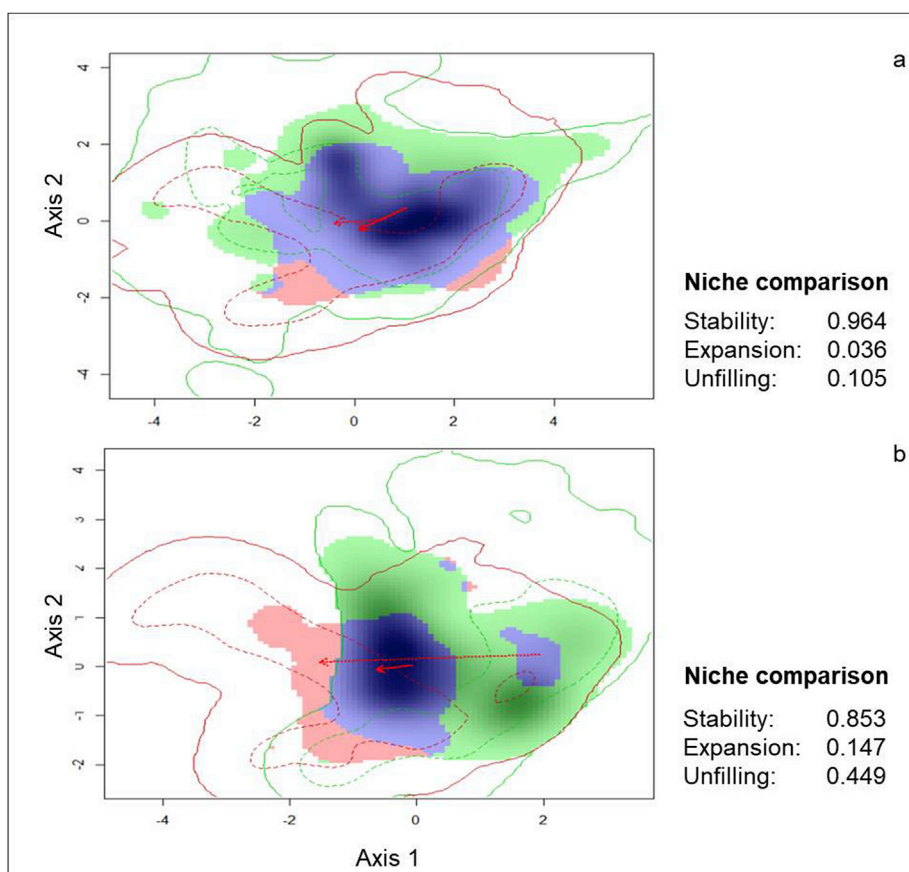
**Fig. 2.** Visualization of climatic niches of *M. micrantha* in - a) native and invasive ranges and b) invasive ranges of two lineages. The green colored areas correspond to the unfilled zone, blue areas represent the overlap zone of the two niches, and the red areas delineate the expansion zone; red arrows represent how the center of the niche has changed between the two ranges. Green contour lines delineate the available niche in native range (a) and invasive range of lineage 1 (b) and the red contour lines indicate the available niche in invasive range (a) and in invasive range of lineage 2 (b). The solid lines represent 100% available environment whereas the dotted lines represent 50% of the same. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Information). On the other hand, model 4 failed to identify all climatically suitable areas (~5% of the suitable areas) for both genetic lineages (see Appendix F in Supporting Information).

The individual models predicted nearly 80% of the habitat in the native range suitable for *M. micrantha* (Fig. 5). Overlay analysis between binary predictions revealed that more than 50% of these areas are climatically suitable for both lineages. However, climatically suitable unique areas for lineage 1 (27.64% of the total suitable area) are restricted in coastal areas of Peru, Chile, Ecuador, Costa Rica, southern parts of Argentina and Venezuela, and eastern part of Brazil (Fig. 5). On the other hand, western Brazil, eastern parts of Argentina and Bolivia, and complete ranges of Paraguay and Uruguay are climatically suitable only for lineage 2 (21.21% of the total suitable area).

### 3.2.3. Potential distribution under future climate

Potential distribution of the two lineages under future climate change scenarios revealed varied patterns. Under RCP 2.6, an increase in climatically suitable area was noted for lineage 1 by 8.3% in 2050 and by 3.8% in 2070 (Fig. 6), mostly due to the increased number of pixels under mid-low climate classes (see Appendix E in Supporting Information). In South and Southeast Asia, new areas, such as parts of southwest China, Philippines and northern India, were found to become climatically suitable to lineage 1 with the low gas emission increase scenario (Fig. 6c–f). Overall climate suitability was decreased for lineage 2 by 19.2% in 2050 and 2.1% in 2070. Parts of central India, Indonesia and southern China were found to become climatically unsuitable for lineage 2 growth in 2050. However, these areas remain suitable in 2070 (Fig. 6g–j). This pattern was consistent under high gas emission scenarios except for decreased climatic suitability for lineage 1 by 3.3% in 2070. The all lineage model predicted decrease in climatically suitable areas in 2050 and 2070 for both climate change scenarios. Model 4 predicted an overall increase in climatic suitability under RCP 2.6. However, under RCP 8.5, climatic

**Table 3**

Univariate analysis of niche dynamics for individual climatic variables and occupancy (O — number of occurrence records) of climate classes by *M. micrantha* against available climate (B — minimum to maximum) in its native and invasive ranges (two lineages). Absence of occurrence records in invasive range against presence in native range denotes niche unfilling (NU — if the climate is available in the invasive range) or niche abandonment (NA - if the climate is not available in the invasive range) or niche expansion (NE) in case of presence in invasive range but absence in native range. The darker cells indicate absence across all three ranges.

| Climatic variables | Bin | Native O | Native B | Lineage-1 O | Lineage-1 B | Lineage-2 O | Lineage-2 B |
|---|---|---|---|---|---|---|---|
| Bio01 | 5 | 1 | | NA | | NA | |
| | 10 | 9 | | NU | | NU | |
| | 15 | 14 | -2.67 – | 3 | 9.13 – | NU | 7.13 – |
| | 20 | 173 | 29.18 | 27 | 29.23 | 9 | 29.19 |
| | 25 | 369 | | 115 | | 100 | |
| | 30 | 312 | | 50 | | 41 | |
| Bio04 | 0.005 | 512 | | 65 | | 4 | |
| | 0.01 | 228 | | 25 | | 7 | |
| | 0.015 | 135 | 0.00038 | 94 | 0.00038 – | 98 | 0.00066 – |
| | 0.02 | 3 | – 0.026 | 11 | 0.016 | 41 | 0.033 |
| | 0.025 | | | | | | |
| | 0.03 | | | | | | |
| Bio06 | -5 | 3 | | NA | | NA | |
| | 0 | 2 | | NA | | NU | |
| | 5 | 26 | | 2 | | 3 | |
| | 10 | 149 | -14 – | 23 | | 33 | -8.27 – |
| | 15 | 213 | 23.9 | 97 | -0.2 – 24.3 | 107 | 23.32 |
| | 20 | 351 | | 27 | | 4 | |
| | 25 | 134 | | 46 | | 3 | |
| | 30 | | | | | | |
| Bio07 | 10 | 46 | | 11 | | 1 | |
| | 15 | 379 | | 59 | | 3 | |
| | 20 | 323 | 6.18 – | 124 | | 29 | |
| | 25 | 114 | 39.28 | NU | 7 – 29.87 | 109 | 8.9 – 38.2 |
| | 30 | 16 | | 1 | | 7 | |
| | 35 | | | | | 1 (NE) | |
| | 40 | | | | | | |
| Bio12 | 1000 | 60 | | 3 | | NU | |
| | 2000 | 478 | | 33 | | 72 | |
| | 3000 | 253 | | 120 | | 59 | |
| | 4000 | 52 | 0 - 9916 | 39 | 404 - 6708 | 15 | 584 - 7449 |
| | 5000 | 25 | | NU | | 2 | |
| | 6000 | 5 | | NU | | NU | |
| | 7000 | 2 | | NU | | 2 | |
| | 8000 | 3 | | NA | | NU | |
| Bio15 | 0.5 | 446 | | 38 | | 3 | |
| | 1 | 423 | | 139 | | 123 | |
| | 1.5 | 8 | 0 – 2.71 | 18 | 0.04 – 1.56 | 24 | 0.11 – 1.42 |
| | 2 | 1 | | NU | | NU | |
| | 2.5 | | | | | | |
| | 3 | | | | | | |

suitability was decreased by 2.4% in 2050 whereas 5.9% increase in was observed in 2070 (see Appendix G in Supporting Information).

## 4. Discussion

Our study found evidence in support of our hypothesis that incorporating intraspecific genetic information would improve ENM accuracy and predictive ability, under both present and future climate change scenarios. In the context of recent genetic cluster information from invasive range, this study provided first empirical evidence of using genetic information in ENM to characterize the invasion potential of *M. micrantha* in South and Southeast Asia and suggested management implications under current and future climate change.

### 4.1. Identification of niche shift

We estimated niche shift using conventional ENM approach by comparing climatic niches between native and invasive ranges as well as using genetic cluster information in which we compared climatic niches between two lineages present in the invasive range. No significant difference between climatic niches of *M. micrantha* between its native and invasive ranges was found suggesting climatic niche conservatism between the two ranges. This finding is in accordance with other studies on terrestrial invasive species (Petitpierre et al., 2012). The observed niche differences between native and invasive ranges were more likely due to niche unfilling, rather than niche expansion. Niche unfilling as a primary cause of niche shift has been reported for other invasive species as well (Petitpierre et al., 2012; Webber et al., 2012) in which shorter residence time,
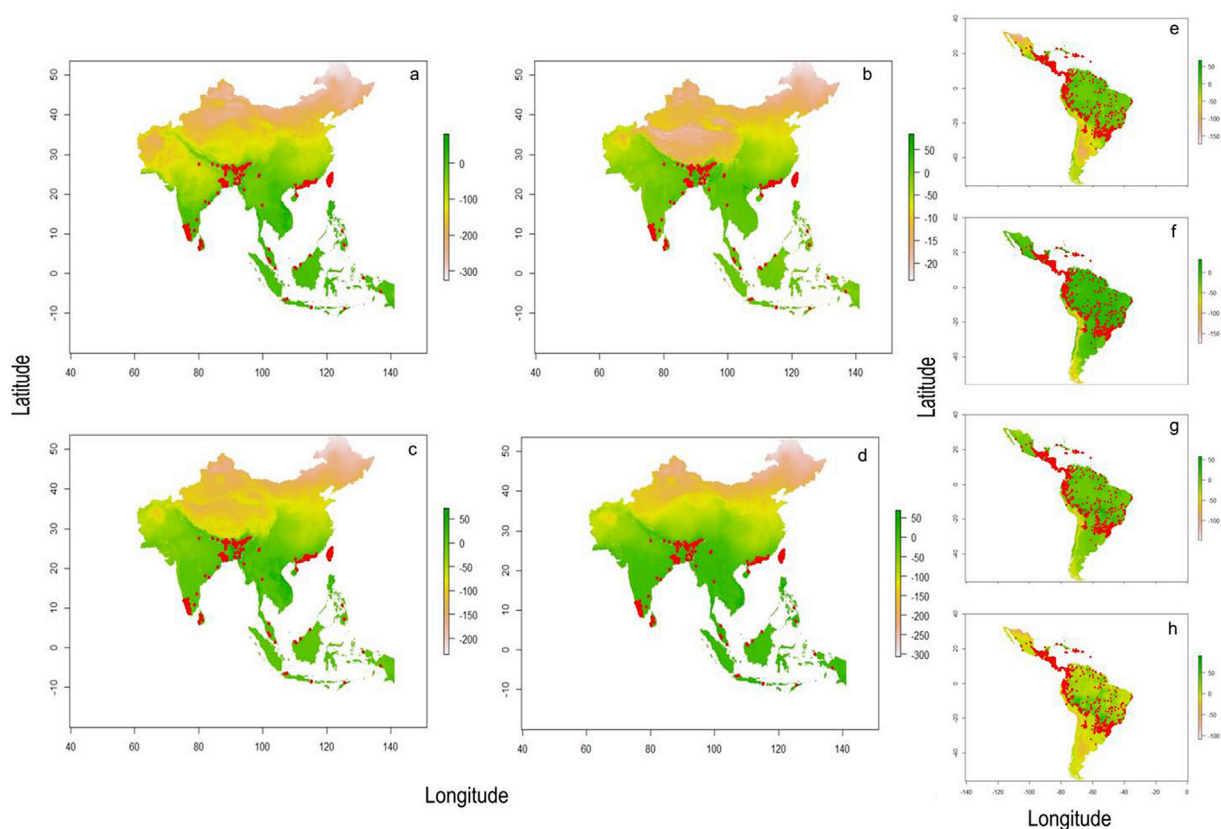
**Fig. 3.** Multivariate environmental similarity surface (MESS) maps of invasive range (a−d) generated using occurrence data of a) lineage 1, b) lineage 2, c) both lineages, and d) native range; and MESS maps of native range (e−h) generated using occurrence data of e) lineage 1, f) lineage 2, g) both lineages, and h) native range. Dark green areas (positive MESS values) correspond to sites in the projection range with similar climatic conditions to the training data points; the yellow to light red gradient (negative MESS values) indicates the degree of dissimilarity in the projection range with the climate of the training datasets. Red dots on the MESS maps indicate geographical position of the invasive (a−d) and native occurrences (e−h). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

altered biotic interactions and dispersal limitations were found to restrict an invasive species to occupy all areas with suitable habitat conditions (Atwater et al., 2018). We found niche expansion only for temperature annual range (Bio07) in the invasive range of lineage 2, indicating that the analogous climate of the invasive range (Bio07>30 °C) is a part of the fundamental niche of the lineage which is presently unoccupied in its native range. Niche shift in non-analogous climate space, in the form of niche abandonment, was also observed in the invasive ranges of the two lineages for annual mean temperature, minimum temperature of the coldest week and precipitation seasonality. However, very few occurrence records (n < 10) in the native range under these climate classes should be considered carefully prior to interpretation of niche shift in non-analogous climate space.

We found a significant difference between the climatic niches of the two lineages which occupied novel climatic spaces in their respective invasive ranges. This variation in climatic niches was mostly explained by the temperature related variables as lineage 2 was found having larger niche breadth and occupying warmer niches than lineage 1. The MESS analysis also revealed that climatic niches of the two lineages of *M. micrantha* are different in the invasive range. This finding is in accordance with other studies which reported climatic niche dissimilarity at the intraspecific level (Ikeda et al., 2017). However, the marginal difference in climatic niche similarity between the two lineages (p value marginally higher than 0.05) might be also due to clustered distribution of the occurrence records of both lineages and limited number of occurrences from certain regions of their distributions. In this context, the observed niche differentiation between two lineages should be interpreted carefully and further investigated with the support of occurrences across the distribution range. Nevertheless, high values of niche unfilling and small differences in climatic similarity between the invasive ranges of the two lineages indicated that a lot of suitable habitat is available for colonization by lineage 2. Given more than 100 years of residence time of *M. micrantha* since introduction (first introduction in the eastern hemisphere dates from 1884; Geng et al. (2017)), this is likely that unfilling will convert to suitability for this invasive species in the near future.

**Table 4**

Evaluation of the four models using three metrics: omission rate of the test points, predictive success of correctly identifying location points as presence (threshold dependent), and AUC values (threshold independent). The metric values were averaged over ten replicate runs.

| Model (occurrence data) | Test points (n) | Threshold dependent tests | | Threshold independent test |
|---|---|---|---|---|
| | | Omission rate (OR) | Predictive success | AUC |
| Model 1 (lineage 1) | Lineage 1 (42) | 0.031 | 0.855 | 0.949 |
| | Lineage 2 (150) | 0.157 | 0.694 | 0.693 |
| | All Lineage (352) | 0.071 | 0.611 | 0.854 |
| | Native (879) | 0.107 | 0.855 | 0.755 |
| Model 2 (lineage 2) | Lineage 1 (202) | 0.161 | 0.625 | 0.745 |
| | Lineage 2 (41) | 0.024 | 0.902 | 0.940 |
| | All Lineage (352) | 0.074 | 0.743 | 0.833 |
| | Native (879) | 0.394 | 0.968 | 0.464 |
| Model 3 (all lineages) | Lineage 1 (202) | 0.0005 | 0.883 | 0.952 |
| | Lineage 2 (150) | 0.0027 | 0.913 | 0.925 |
| | All Lineage (352) | 0.0048 | 0.883 | 0.929 |
| | Native (254) | 0.053 | 0.831 | 0.658 |
| Model 4 (native) | Lineage 1 (202) | 0 | 0.854 | 0.936 |
| | Lineage 2 (150) | 0.005 | 0.753 | 0.819 |
| | All Lineage (352) | 0.002 | 0.611 | 0.854 |
| | Native (254) | 0.002 | 0.754 | 0.819 |

## 4.2. Identification of potential distribution

We considered two models using lineage information to visualize the potential distribution of *M. micrantha* in its invasive range. There are three lines of logic that affirm the validity of our approach. First, although the model built using native occurrence data (model 4) performed well in predicting lineage 1 data, it could not predict all lineage 2 occurrences. Conventional ENM has been trained on native occurrence data based on the assumption of niche conservatism between native and invasive ranges or uses pooled data from all ranges in case of range-shifting species (Broennimann and Guisan, 2008; Elith et al., 2010). However, our findings suggest that even if the climatic niche is conserved between native and invasive ranges, conventional ENM approach based on native occurrence data alone may underestimate the potential distribution of an invasive species in current and future climate conditions. The MESS analysis using native occurrences as training data could not interpolate the available environment for invasive occurrences, thereby strengthening this inference.

Second, although the all lineage model (model 3) was found to have marginally higher prediction accuracies than the individual models and significantly predicted the occurrence records of both genetic clusters, it overestimated current and future suitable habitat (Ikeda et al., 2017) and cannot discriminate the climatically suitable areas for individual lineages. An overall decrease in climatically suitable areas under future climate change scenarios was observed for the all lineage model, similar to the findings for many invasive species (e.g. (Bezeng et al., 2017; Wan et al., 2016)). However, the genetic clusters may vary in their responses to climate change scenarios, which might be scale-dependent or due to intraspecific variability in responses to a changing environment. For example, climate may not be a limiting factor at the small scale at which range expansion of lineage 1 was observed (Bellard et al., 2018). The predicted increase of lineage 1 was found towards higher altitude; similar to that reported for other plant species (Bellard et al., 2013) and *M. micrantha* as well (Banerjee et al., 2017b). This pole ward shift is restricted for lineage 2 due to the oceanic barrier around the geographic range which might explain the predicted decrease in range size of this lineage (Bellard et al., 2018). On the other hand, climate change-driven other factors like land use, nutrient variables, propagule pressure and anthropogenic activities may also influence the potential distribution of an invasive species. Numerous studies have demonstrated that species' response to these factors can be influenced by genetic diversity in the invaded range in which rapid selection of populations showing greater fitness may lead to local adaptation and subsequent invasion success (Lavergne and Molofsky, 2007; Roman and Darling, 2007). In case of genetic depletion of the invaded population, as frequently observed due to demographic bottleneck, plasticity of ecologically relevant traits of a genotype is increased for taking advantage of a wider ecological niche leading to successful invasion (Spens and Douhovnikoff, 2016; Walls, 2010). In *M. micrantha*, for example, common garden experiments revealed that dispersal-related traits (plume loading, seed mass and pappus radius) were under genetic control during range expansion of this species (Huang et al., 2015). A large number of studies also reported plasticity of functional traits in response to environmental factors (Banerjee et al., 2017a; Prabu et al., 2014; Song et al., 2009). These findings are indicative that the two lineages may respond differently to climate change and effect of these intraspecific variations on species' distribution in the invaded range can be masked in conventional ENM approach if all lineage information is considered together.

Finally, the individual lineage models (model 1 and 2) predicted native occurrence points with high accuracy compared to that of all lineage model (model 3) and identified climatically suitable unique areas in the native range for both lineages. These findings are in accordance with previous molecular studies on *M. micrantha*. For example, genetic diversity parameters of populations collected from south India, Malaysia, Indonesia and Taiwan (*i.e.* lineage 1 populations of this study) were found to
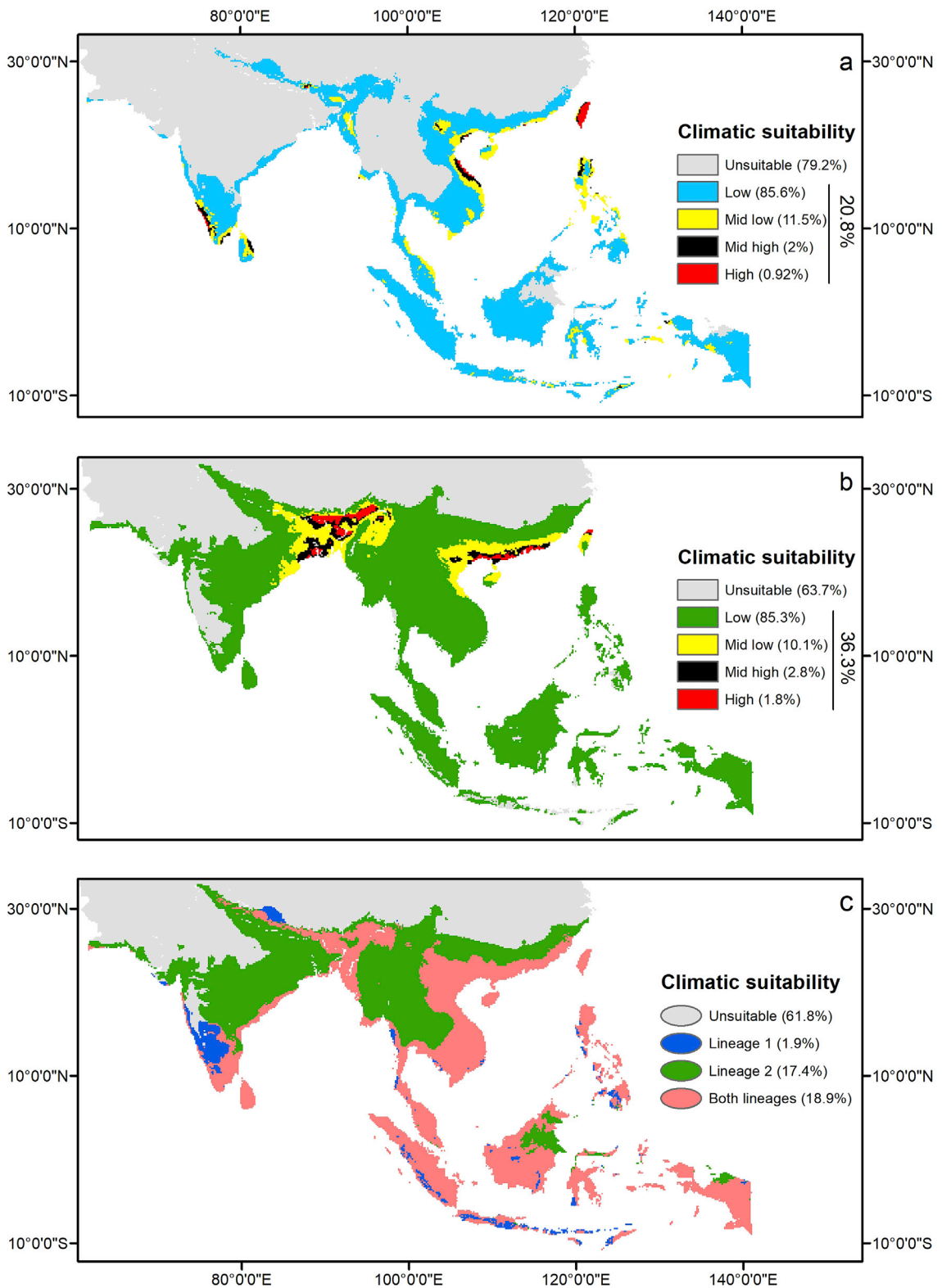
**Fig. 4.** Projected distribution of two lineages of *M. micrantha* in South and Southeast Asia − a) lineage 1, b) lineage 2, and c) overlay map of binary projections of the two lineages. Legends in 'a' and 'b' depict five climate suitability classes based on thresholds calculated in terms of minimum training presence of known occurrences; legend in 'c' indicate the areas in the invasive range found climatically suitable for lineage 1, lineage 2, both lineages, and not suitable.
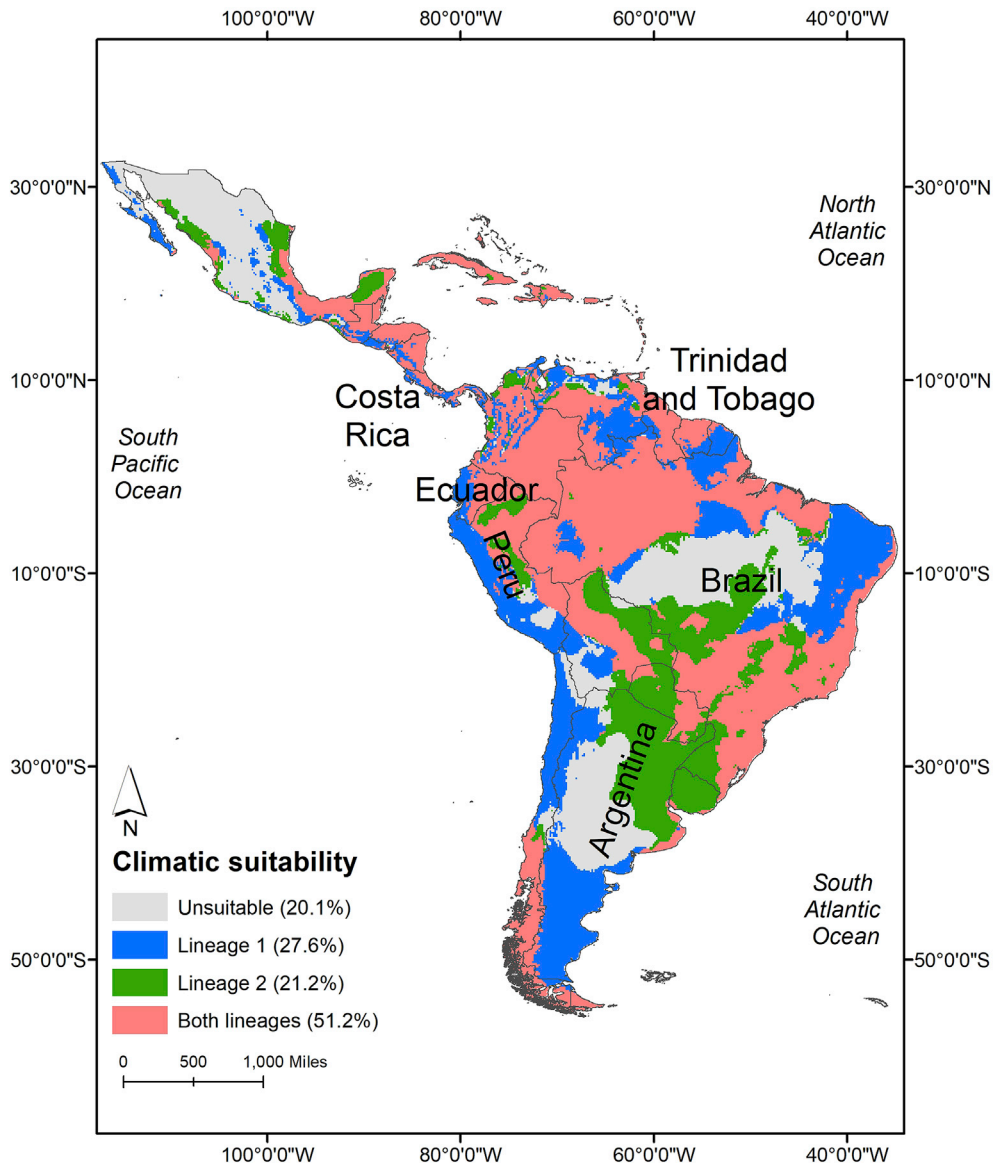
**Fig. 5.** Overlay map of binary projections of two lineages of *M. micrantha* on its native range − Central and South America, and Caribbean islands. Legends depict the areas in the native range found climatically suitable for lineage 1, lineage 2, both lineages, and not suitable. The countries from where classical biological control agents have been released in the South and Southeast Asia have been identified.

be similar to populations sampled from Costa Rica (Yang et al., 2017), where climatically suitable areas were found to be unique for lineage 1.

### 4.3. Management implications

A considerable amount of research has demonstrated that predictive modeling is an effective management tool for invasive alien species. Our study added novel dimensions by integrating genetic cluster information in the ENM approach and found evidence which showed that genetically informed ENM can improve model interpretability and have important management implications.

Successful management of an invasive species often depends on accurate identification of current and future suitable habitat to be colonized by it. A large area of South and Southeast Asia was identified as climatically suitable for invasion of *M. micrantha*. In addition, potential distribution of lineage 1 was found to move pole-ward under climate change scenarios whereas niche unfilling of lineage 2 was mainly observed for cold temperature (Bio01 and Bio06) and dry environment (Bio12). These findings suggest that if introduced, the lineages can establish in cold and dry areas of the invasive range. The
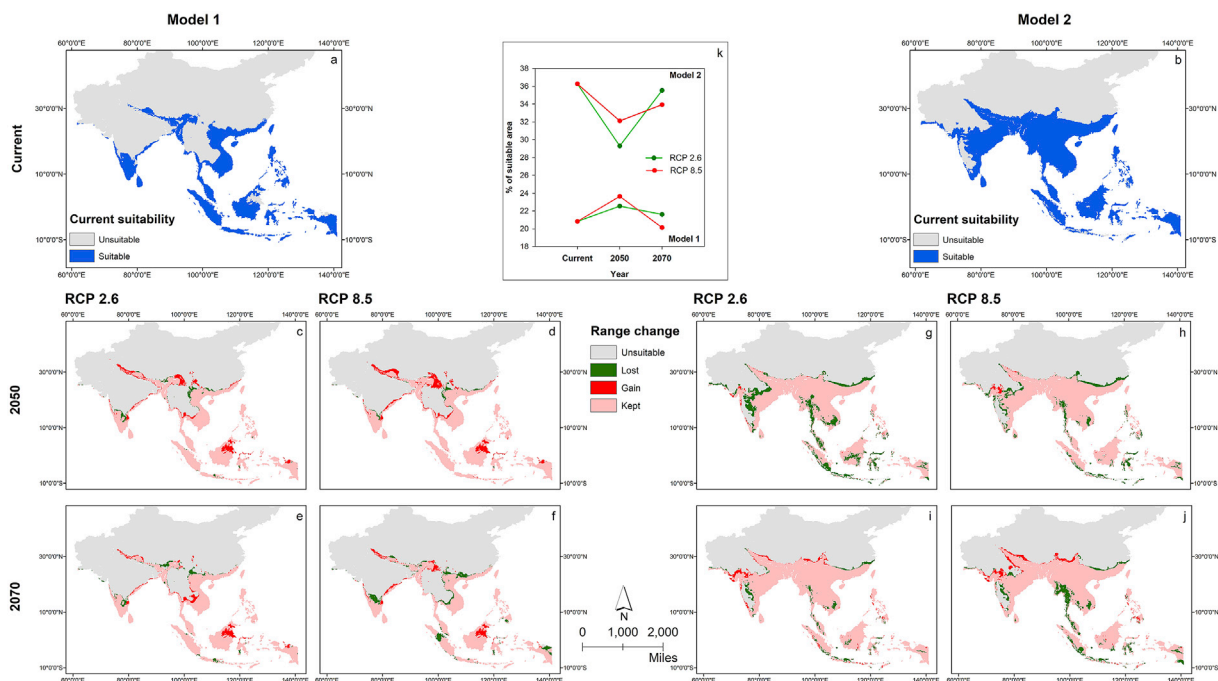
**Fig. 6.** Current and future potential distribution of *M. micrantha* in South and Southeast Asia, according to two different climate change scenarios (RCP 2.6 and RCP 8.5); a–b: binary predictions for lineage 1 and lineage 2 under current climate conditions; c–f: overlay map showing changes in the predicted distributions of lineage 1 by 2050 according to RCP 2.6 (c) and 8.5 (d) and by 2070 according to RCP 2.6 (e) and 8.5 (f); g–j: overlay map showing changes in the predicted distributions of lineage 2 by 2050 according to RCP 2.6 (g) and 8.5 (h) and by 2070 according to RCP 2.6 (i) and 8.5 (j); k: Changes in percentage of current suitable area for both lineages in 2050 and 2070 under two future climate scenarios.

introduction of *M. micrantha* in these climate classes seems likely given the anthropogenic activities in this region. This information can provide a baseline for implementing early detection and rapid response strategies for new invasions (Barbet-Massin et al., 2018; Crall et al., 2013; Ervin and Holly, 2011) and devising scientifically informed site-specific management policies at an early stage of invasion (Clements et al., 2019). The evidence of niche abandonment for cold environment (Bio1 and Bio6) between native and invasive ranges indicates presence of other lineages in its native range which are not yet introduced in this region. In this context, quarantine measures should be implemented to protect this region from invasion of new lineages from its native range.

This study provides preliminary evidence that climate matching technique may be useful to identify probable source populations of the two lineages of *M. micrantha* which were presumably introduced in this region from different source populations at different times. Previous studies have also indicated that climate matching technique may provide valuable insights in the introduction and evolutionary pathways of invasive species (Chown et al., 2015). This information may also be used to identify areas in native range for sampling classical biological control (CBC) agents of *M. micrantha* (e.g. *Puccinia spegazzinii, Dietelia portoricensisa*). While the susceptibility of the CBC agent to the target invasive species is the primary requisite for successful biological control operations (Ellison et al., 2008), climatic compatibility between the areas of origin and introduction can influence successful establishment and/or vigorous population growth of the CBC agent [(Robertson et al., 2008) and references therein]. Indeed, a growing number of studies have used climate matching techniques to identify the potential sampling areas of CBC agents (Dhileepan et al., 2006; Mukherjee et al., 2011; Sun et al., 2017; Sutton, 2019). The information of climatic niche difference of the two lineages of *M. micrantha* in its invasive and native ranges can be used to fine-tune the sampling areas of the CBC agents after host specificity of the agent for the particular lineage is confirmed.

### 4.4. Limitations and future directions

Although the methodological approach of this study is applicable for other invasion scenarios, we identified scopes of further improvements and addressed these uncertainties for consideration in future endeavors. First, in spite of known distribution of *M. micrantha* throughout South and Southeast Asia (Ellison and Sankaran, 2017), the occurrence data found in the databases was clustered around certain regions (e.g. Taiwan) and could not be exhaustive for its entire invasive range. Although consultation of key herbaria and literature reports addressed this issue to some extent in this study, future ENM approaches should consider using occurrences from data deficient regions (e.g. from local herbaria) to characterize climatic niches and identify potential distribution of an invasive species in its invasive range. Second, we considered one future

climate change scenario in this study to assess the performance of genetically informed ENM over conventional approach. Given the differential responses of the two lineages of *M. micrantha* in future climate condition and wide variability in rainfall and temperature patterns across different climate change scenarios for this region, it would be interesting to explore the species' responses across a range of representative concentration pathways and more realistic general circulation models. Third, our study emphasized that future ENM should use genetic information from both native and invasive ranges and consider the response capacities of the genetic lineages across the environmental gradient for a better understanding of the potential distribution. This may help to identify new lineages of an existing invasive species to be introduced in a region, assess their potential distributions, and implement proactive management strategies. Toward this end, controlled experiments should be conducted to identify species' response to environment (local adaptation and/or phenotypic plasticity) and evolution of competitive ability of different genetic lineages in the invaded range. This information will further help to validate the potential distribution of the species under present and future climate scenarios. Finally, the climate matching technique can be applied to identify climatically suitable areas for the host and the susceptible CBC agent in the native range and overlapping their distributions may help in prioritizing regions in the native range to conduct future surveys for CBC agents (Trethowan et al., 2011).

## Declaration of competing interest

No conflict of interest declared.

## Acknowledgement

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.gecco.2019. e00800.

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