

Bioclimatic niches of selected endemic *Ixora* species on the Philippines: predicting habitat suitability due to climate change

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Received: 19 June 2014 / Accepted: 21 August 2015 / Published online: 28 August 2015
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Abstract The pantropical genus *Ixora* is highly diverse, with several species endemic to the Philippines. Owing to their endemic nature, many of these species are endangered and little is known about their basic biology. This study aimed to establish baseline information about the bioclimatic niches of *Ixora* species endemic to the Philippines, determine suitable areas and potential range shifts under future climate conditions, and identify priority areas for conservation and future research. Locality records of 12 endemic *Ixora* species from the Philippine archipelago were analyzed, with a particular focus on the five most

abundant species *I. auriculata*, *I. bartlingii*, *I. cumingiana*, *I. macrophylla*, and one island endemic species, *Ixora palawanensis*. Bioclimatic variables from the WorldClim database at 2.5' resolution were used, with a focus on annual means and seasonality of temperature and precipitation as well as precipitation of the warmest quarter. Analysis of the relationships of the species locations with the bioclimatic variables showed that the bioclimatic niches of the five focal *Ixora* species generally had narrow temperature and wider precipitation niches. Species distribution modeling with the model Maxent suggested that *I. auriculata* and *I. bartlingii* will likely shift their geographic distributions southwards under predicted levels of climate change, while *I. cumingiana* and *I. macrophylla* were found to likely expand their ranges. *Ixora palawanensis*, in contrast, was predicted to decrease its potential distribution with future climate

Communicated by Joseph Paul Messina.

Electronic supplementary material The online version of this article (doi:10.1007/s11258-015-0512-6) contains supplementary material, which is available to authorized users.

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change. Further, results of species distribution modeling for the rare endemic *Ixora* species *I. bibracteata*, *I. chartacea*, *I. ebracteolata*, *I. inaequifolia*, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii* were presented, which, however, had much less observation points and therefore only provide a first estimate of potential species distributions. The generated potential habitat suitability maps can assist policy makers in designing conservation strategies for the species and in identifying areas with potential to withstand climate change until at least 2080.

Keywords Climate change · Species distribution modeling · Endemic · *Ixora* · Maxent · Rubiaceae

Introduction

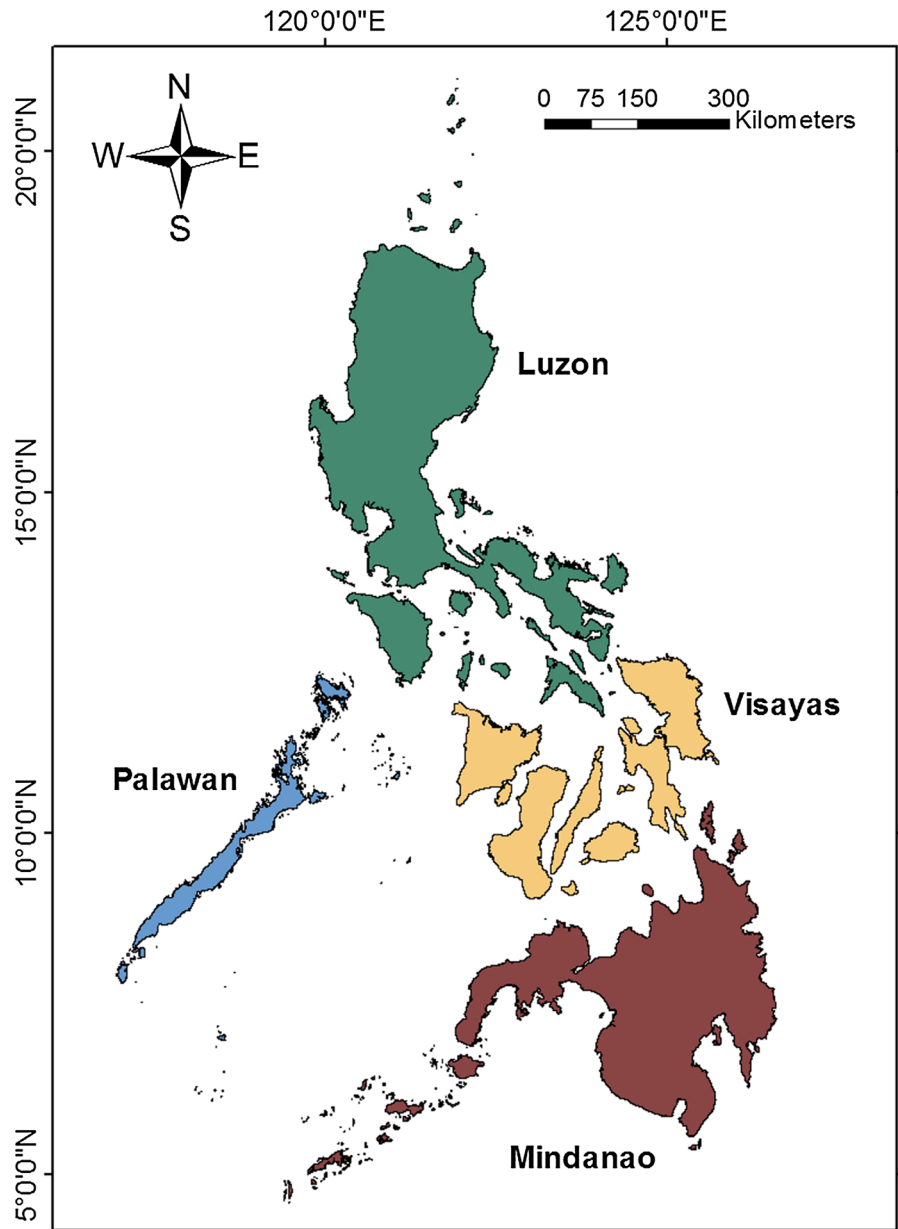
Climate is considered a primary factor constraining distributions of plant species (Cox and Moore 2000; Woodward 1996; Vetaas 2002). Changes in climate are expected to affect distributions of plant species negatively if climatic conditions diverge from climatic optima (Miller and Urban 1999; Ferranini 2012). Over the coming decades, the global climate is predicted to warm significantly due to increasing greenhouse gas concentrations (Parry et al. 2007) and will most likely cause shifts in species composition of plant communities (Niu and Wan 2008; Yang and Rudolf 2010). These shifts can result from differential growth responses to higher temperature, from changes in plant interactions, or a combination of both (Llorens et al. 2004). Warming directly affects the rate of plant respiration, photosynthesis, and other biogeochemical processes and could limit plant growth directly via heat stress (White et al. 2000) or indirectly via water shortage resulting from increased evapotranspiration (De Boeck et al. 2008). All these effects may cause range shifts of various individual species (Huntley 1991; Prentice and Jolly 2000; Davis and Shaw 2001; Walther et al. 2005; Parmesan 2006; Thuiller et al. 2008; Trisurat et al. 2011) and consequently lead to changes in the composition of plant communities in a warmer environment (Llorens et al. 2004).

Future climate change is likely to intensify endangerment and extinction particularly of species with limited ranges or narrow ecological niches, and limited dispersal capabilities (Convention on Biological Diversity [CBD] 2010). Among species with narrow ranges, endemic species are of particular concern since they are confined to a particular geographic area and may have small population sizes associated with relatively high risk of extinction (Ndayishimiye et al. 2012; Fischlin et al. 2007; Vié et al. 2008). Endemic species are more likely dispersal limited than other species, and may be less able to respond rapidly to changing climate (Morueta-Holme et al. 2010). It has been estimated that 20–30 % of plant and animal species, globally, will be at higher risk of extinction due to global warming and that a significant proportion of endemic species may become extinct by 2050 or 2100 as a consequence of the increase in global mean temperatures exceeding 2–3 °C above pre-industrial levels (CBD 2010; Fischlin et al. 2007). Endemic species are particularly sensitive to climate change, as such, an understanding of climatic and ecological requirements and distribution constraints of endemic species is crucial in developing effective conservation strategies that are robust to future climate changes (Svenning and Skov 2007; Ohlemüller et al. 2008; Fløjgaard et al. 2010; Morueta-Holme et al. 2010).

The Philippines (Fig. 1) is identified as one of the world's biologically richest countries and ranks second among the biodiversity hotspots in the world, next to Madagascar (Myers et al. 2000). The country hosts about five percent of the world's species of flora; more than half of its 10,000 vascular and 14,000 non-vascular plants are endemic to the archipelago (Ong et al. 2002). For the Rubiaceae family alone, 83 % of the 535 species found in the Philippines are endemics (Davis et al. 2009). However, due to anthropogenic activities as well as natural disturbances, the country continues to lose its rich biodiversity resources (Conservation International [CI] 2012). Aside from anthropogenic habitat alteration, climate change has been identified as one of the major threats facing biodiversity worldwide (CBD 2010; Parry et al. 2007). In 2009, Yusuf and Francisco identified the Philippines, together with Indonesia and Malaysia, as among the climatically most vulnerable countries in Southeast Asia, due to the high exposure to frequent droughts, cyclones, landslides, and floods. As

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Fig. 1 Map of the Philippines with colors indicating the main island groups



evidenced by the increasing mean temperature observed over time, climate change is apparently affecting the Philippines and future climate change will likely have a substantial impact on the Philippine flora and fauna (Philippines Atmospheric, Geophysical, and Astronomical Services Administration [PAGASA] 2011). Hence, there is a greater risk of extinction for species that are already vulnerable, particularly those with strict habitat requirements and restricted ranges (CBD 2010).

The pantropical genus *Ixora* L. was chosen as focus in this study for a number of reasons. The genus is almost exclusively restricted to the rain forest, which implies narrow ecological preferences and sufficiently limited dispersal potential of the genus (De Block 1998). This could mean that the endemic species of *Ixora* may be particularly sensitive to future climate change and calls for increased efforts to conserve these species. The genus *Ixora* belongs to the family Rubiaceae, which shows great species diversity across

tropical Asia (Davis et al. 2009; Mouly et al. 2009), and is present in the Philippines with 25 endemic species (Banag et al. in prep.). The Philippine *Ixora* species are of particular interest due to their ornamental value as garden plants and their importance as a potential source of a wide variety of pharmaceuticals (Inouye et al. 1988; Wen et al. 2011; Wahab et al. 2012; Yoga Latha et al. 2012; Rajendra et al. 2013).

In 2007, the Department of Environment and Natural Resources of the Philippines (DENR Administrative Order No. [DAO] 2007-01) established the official list of threatened plant species and identified 99 critically endangered (CR) species, 187 endangered (EN) species, 176 vulnerable (VU) and 64 other threatened species (OTS) of plants in the Philippines. However, no *Ixora* species was included in this list despite the high number of endemic species and the continuing decline in their natural habitat. This could be attributed to the lack of basic information on the Philippine *Ixora* species, concerning their geographic distribution, habitat status, and ecological requirements. Knowing the current and potential distribution and understanding the responses to climate change of endemic Philippine *Ixora* species can inform and help policy makers to facilitate appropriate decision-making for the conservation of *Ixora*.

Preliminary studies on the distribution of Philippine endemic *Ixora* using herbarium records show that most species are single island endemics or are restricted to few islands and only few species are widely distributed across the country. To date, only three studies dealing with potential effects of climate change have been carried out in the Philippines focusing particularly on forest ecosystems (Cruz 1997; Lasco et al. 2008) and selected threatened forest tree species (Garcia et al. 2013). However, no studies have investigated potential impacts of climate change on Philippine endemic *Ixora* species.

With this research gap in mind, and given the potentially drastic climate change in the Philippines, our study aims to establish baseline information about bioclimatic niches of endemic Philippine *Ixora* species and identify the effects of future climatic conditions on Philippine endemic *Ixora*. In particular, our questions are: (1) How does the occurrence of endemic *Ixora* species relate to bioclimatic conditions? and (2) How will climate change affect the distribution of potential habitat of endemic Philippine *Ixora* species?

Materials and methods

The present study aims to derive information on bioclimatic requirements of 12 endemic *Ixora* species of the Philippines. Five focal species (*I. auriculata*, *I. bartlingii*, *I. cumingiana*, *I. macrophylla*, *I. palawanensis*) were selected for the main investigation, since these species had the highest number of observations (≥ 20) and therefore allowed to draw most robust conclusions. The remaining 7 endemic species (*I. bibracteata*, *I. chartacea*, *I. ebracteolata*, *I. inaequifolia*, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii*) (with ≤ 5 observations) were investigated with the same methods, with results shown in the Online Resource 1.

The analysis began with the investigation of the distributions of species records in the climate space to provide basic information on species' climatic niches, followed by the modeling of the potential species distributions under present and future climatic conditions with the model Maxent (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011).

Study region and distribution data

Locality data of the naturally occurring Philippine *Ixora* were derived from three sources. Herbarium specimens were surveyed at the following herbaria: A, BK, BR, C, CAHUP, K, L, NY, P, PNH, PPC, SAN, and US (Thiers 2013). Data were also downloaded from Co's Digital Flora of the Philippines (Pelser et al. 2011). Finally, data from the first authors' own field surveys during 2008–2012 were included. Owing to the large spatial extent and topographic complexity of the study region, no systematic surveys are available; records were considered as presence-only data with negligible sampling bias with respect to bioclimatic conditions.

In total, 410 locality records of endemic *Ixora* species were collated (Online Resource 2). Records lacking coordinates were georeferenced using World Gazetteer (<http://worldgazetteer.com>) and Geonames (<http://www.geonames.org/export/web-services.html>). All coordinates were carefully checked for plausibility and/or error-corrected using Google Earth (version 7; Google 2013). Notably, a few common species (*I. bartlingii*, *I. auriculata*, *I. cumingiana*, *I. macrophylla*, *I. palawanensis*) dominated these records. *Ixora bibracteata*, *I. chartacea*, *I. ebracteolata*, *I.*

inaequifolia, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii* had between 5 and 16 observations each. Since Pearson et al. (2007) reported good modeling results with Maxent for as few as 5 observation points, we also analyzed the potential distribution for these species (results are shown in Fig. S2a, b, Online Resource 1).

Environmental data

For analyzing species' distributions, bioclimatic variables from the WorldClim database at 2.5' resolution (approx. 3.5 km in the Philippine archipelago) for the period 1950–2000 were considered (<http://www.worldclim.org>; see also Hijmans et al. 2005).

A preliminary analysis also explored human population density in the year 2000 (Center for International Earth Science Information Network [CIESIN] 2013) as an additional predictor. Given the known association of *Ixora* with undisturbed rainforests (De Block 1998), we assumed that human impact would affect the probability of species presence negatively. However, the low spatial resolution of the data (town level) and a possible sampling bias with respect to human impact (sampling concentrated near settled and accessible areas) resulted in unreasonable results indicating higher probability of presence with increasing human population density. We therefore chose to exclude effects of human presence and focus instead on bioclimatic niche space only.

In order to limit the potential effect of collinearity between bioclimatic variables which can reduce predictive power and cause difficulties in the interpretation (Dormann et al. 2013), predictor pairs with Pearson's correlation coefficient $|r| \geq 0.7$ were identified for the 19 bioclimatic variables from the WorldClim database (Table 1).

Since some of the endemic *Ixora* species included in the Maxent analysis had as few as five observation points, we chose to limit the number of bioclimatic variables to five to avoid model overfitting. Five variables with pairwise Pearson's correlation coefficients $|r| \geq 0.7$ were chosen that had good ecological interpretability and were highlighted by the PAGASA report (2011) on climate change in the Philippines for their future importance: (1) annual mean temperature (AMT) and (2) annual mean precipitation (AMP), as the basic variables determining the climatic niche. (3) Temperature seasonality (TS) and (4) precipitation seasonality (PS), as

indicators for seasonal variability, which are of particular importance in a monsoon climate. (5) Precipitation of the warmest quarter (PwarmQ) as an indicator integrating both water and temperature effects.

We visualized the occurrence of each of the species within the climatic space by plotting their relationship between annual means, as well as seasonality values for temperature and precipitation. For better comparability, smoothed density curves were plotted for each climatic variable, using the function *density* ("Kernel Density Estimation" with a "SJ" smoothing bandwidth, R-internal package *stats*, R Development Core Team 2014). All analyses were performed using R Version 3.1.2 (R Development Core Team, 2014) with the packages *raster* (Hijmans 2014), *dismo* (Hijmans et al. 2014), *rgdal* (Bivand et al. 2014), *sp* (Pebesma and Bivand 2005), *rJava* (Urbanek 2013), and *gplots* (Warnes et al. 2013).

For future climate projections, two scenarios (A2 and B1) for the year 2080 from the GCM data portal (<http://www.ccafs-climate.org>, "HadCM3" model results) were chosen. These two scenarios represent a range from low (B1) to high (A2) levels of expected climate change. Scenario B1 assumes the storyline of "clean and efficient technologies" and represents an estimated increase of 1.8 °C global temperature rise. In contrast, Scenario A2 assumes the storyline of a "heterogeneous world" with "slower technological change", resulting in an increase of 3.4 °C (at 2090–2099 compared to reference period 1980–1999; Table TS6 of Parry et al. 2007). In the Philippines, future mean temperature are predicted to rise by 0.9–1.1 °C in 2020 and by 1.8–2.2 °C in 2050, together with a change in temperature seasonality with largest temperature increases predicted for the summer season (June, July, August). Precipitation is predicted to decrease in most parts of the country during the summer season, but will increase during the southwest monsoon season. Drought conditions during the dry months of March to May are likely to become more severe and the wet months of June to November are likely to become wetter. A reduction in rainfall for all seasons is expected across Mindanao, and stronger southwest monsoon winds are anticipated for Luzon and the Visayas (PAGASA 2011). For further details of the IPCC scenarios, see Parry et al. 2007, and PAGASA 2011 for details about climate predictions for the Philippines. The maps of the five bioclimatic predictors (AMT, AMP, TS, PS, PwarmQ) for present and future conditions are shown in Figure S1 (Online Resource 1).

Table 1 Pearson’s correlation coefficients between bioclimatic variables for the Philippines

	AMT	MDR	ISO	TS	Max TWM	Min TWM	TAR	Mean TwarmQ	Mean TdryQ	Mean TwarmQ	Mean TcoldQ	AMP	PWM	PDM	PS	PwetQ	PdryQ	PwarmQ	PcoldQ
1																			
AMT	1																		
MDR	-0.22	1																	
ISO	-0.02	0.4	1																
TS	0.1	-0.32	-0.93	1															
MaxTWM	0.95	-0.05	-0.19	0.26	1														
MinTWM	0.93	-0.34	0.21	-0.16	0.79	1													
TAR	-0.15	0.48	-0.61	0.63	0.15	-0.48	1												
MeanTwarmQ	0.98	-0.16	-0.04	0.08	0.95	0.89	-0.08	1											
MeanTdryQ	0.96	-0.24	0.16	-0.07	0.85	0.97	-0.35	0.9	1										
MeanTwarmQ	0.98	-0.27	-0.23	0.29	0.97	0.86	0	0.96	0.9	1									
MeanTcoldQ	0.96	-0.13	0.24	-0.2	0.86	0.97	-0.33	0.93	0.96	0.88	1								
AMP	-0.24	-0.26	-0.01	0.06	-0.32	-0.15	-0.21	-0.32	-0.14	-0.23	-0.26	1							
PWM	-0.05	-0.31	-0.4	0.33	-0.02	-0.09	0.12	-0.1	-0.07	0.03	-0.13	0.72	1						
PDM	-0.19	0.2	0.55	-0.32	-0.31	-0.06	-0.34	-0.28	0	-0.29	-0.12	0.49	-0.09	1					
PS	0.16	-0.3	-0.64	0.44	0.27	0.02	0.35	0.19	0.01	0.28	0.05	0.05	0.67	-0.75	1				
PwetQ	-0.06	-0.36	-0.37	0.3	-0.06	-0.08	0.05	-0.12	-0.07	0.01	-0.14	0.78	0.98	-0.05	0.64	1			
PdryQ	-0.2	0.17	0.53	-0.29	-0.32	-0.07	-0.34	-0.3	-0.02	-0.3	-0.14	0.51	-0.09	0.99	-0.76	-0.05	1		
PwarmQ	-0.4	0.1	-0.04	0.05	-0.37	-0.41	0.13	-0.37	-0.41	-0.38	-0.42	0.64	0.44	0.32	0.01	0.45	0.33	1	
PcoldQ	-0.02	-0.17	0.35	-0.17	-0.18	0.13	-0.47	-0.16	0.17	-0.09	0.02	0.58	0.15	0.72	-0.4	0.22	0.72	0	1

Predictors used in Maxent modeling of *Ixora* species are bold-faced. Further details for the bioclimatic variables are given on the Worldclim—Global Climate Data Homepage (<http://www.worldclim.org/bioclim>)

AMT annual mean temperature, MDR mean diurnal range, ISO isothermality, TS temperature seasonality, MaxTWM max temperature of warmest month, MinTWM min temperature of coldest month, TAR temperature annual range, MeanTwarmQ mean temperature of warmest quarter, MeanTdryQ mean temperature of driest quarter, MeanTwarmQ mean temperature of warmest quarter, MeanTcoldQ mean temperature of coldest quarter, AMP annual mean precipitation, PWM precipitation of wettest month, PDM precipitation of driest month, PS precipitation seasonality, PwetQ precipitation of wettest quarter, PdryQ precipitation of driest quarter, PwarmQ precipitation of warmest quarter, PcoldQ precipitation of coldest quarter

Species distribution modeling

Models were developed for *I. auriculata*, *I. bartlingii*, *I. cumingiana*, *I. macrophylla* and *I. palawanensis* using Maxent version 3.3.3 k (<http://www.cs.princeton.edu/~schapire/maxent/>). Maxent is a machine-learning method based on the maximum entropy algorithm (Phillips et al. 2006; Phillips and Dudík 2008; Elith et al. 2011). Maxent estimates the relative density of species occurrences, based on the environmental conditions at occurrence locations, representing the used environmental conditions and at background locations, representing the available environmental conditions (Phillips et al. 2006). It thereby provides an estimate of the species' realized niche, and projects it into geographic space (Phillips et al. 2006). For predicting future climate scenarios, the same relationships between environmental conditions and relative species density are applied to maps of future climate, in order to estimate the species potential distribution under these new conditions.

Maxent is among the most frequently used methods for species distribution modeling and has been shown to generally perform better than many other species distribution models (Phillips et al. 2006; Elith et al. 2006; Fischer et al. 2011). Maxent has furthermore been found to have good predictive ability at low number of species records, making it a suitable model choice for the prediction of distributions for rare species (Hernandez et al. 2006; Pearson et al. 2007; Wisz et al. 2008; Garcia et al. 2013). A detailed description of Maxent is given in Phillips et al. (2006) and Phillips and Dudík (2008).

It has to be noted, that our models only consider bioclimatic variables, further potentially important aspects such as soil conditions, dispersal barriers, and biotic interactions are not taken into account.

Performance of fitted models was assessed using the area under the receiver operator curve (AUC, see also Hanley and McNeil 1982). The AUC provides a measure of a model's discriminatory ability between suitable and unsuitable areas for a species and is a well-established approach for model evaluation (Reineking and Schröder 2006).

Maxent models were run with 5 replicates (based on the lowest number of locality records for the included *Ixora* species). The model settings were kept at default values, except of 'threshold' and 'hinge' features,

which were disabled. Model runs were performed with a Jackknife test of variable importance (which allows to identify the variables with the most useful information by itself, Elith et al. 2011).

Since simpler models can be more appropriate for modeling range-shifting species (Elith et al. 2010), a stepwise backward selection of variables was performed for each *Ixora* species. Starting with all five bioclimatic predictors (AMT, AMP, TS, PS, and PWarmQ), the model was progressively simplified by removing the variable with the lowest test gain (according to the Jackknife test) until the exclusion of a variable did not further improve the Test-AUC, i.e., Test-AUC was maximized.

With these species-specific predictor sets, Maxent simulations were run for present and future climate scenarios B1 and A2 (see previous description and Online Resource S1). Model performance was evaluated with a fivefold cross validation. The result of the selection procedure and the model performance is given in Table 1 for the five main *Ixora* species.

Since model extrapolation into novel climates (which are outside the range of the reference set) can be problematic (Elith et al. 2010), Multivariate Environmental Similarity Surfaces (MESS) were calculated. The MESS calculation provides an index of similarity of a point to a reference set of points for a set of predictor variables (Elith et al. 2010). Sites with at least one environmental variable outside the range of environments over the reference set receive negative values, which indicate novel environments.

All R-Code used to perform the Maxent analysis, the evaluation of model performance and the MESS calculation is provided in the Online Resources 3.

Results

Climatic niche differentiation

Analysis of the relationships of the four widely distributed species (≥ 20 number of observations records), *I. auriculata*, *I. bartlingii*, *I. cumingiana* and *I. macrophylla* and the single island endemic *I. palawanensis*, with the five bioclimatic variables, mean annual temperature (AMT), mean annual precipitation (AMP), temperature seasonality (TS), precipitation seasonality (PS), and precipitation of the warmest quarter (PwarmQ), shows that the

bioclimatic niches of these endemic *Ixora* species generally have narrow temperature and wider precipitation niches (Fig. 2). The occurrences of these species are mainly concentrated in areas where the AMT is within 23–28 °C and AMP between 1500 and 4000 mm. Of these five species, *I. bartlingii* and *I. cumingiana* show generally similar niches in respect to the five bioclimatic variables. *Ixora auriculata* is mainly characterized by high TS and narrow PS while *I. macrophylla* is distributed along a rather wide range of temperature and precipitation regimes. Among these five endemic species, *I. palawanensis* is shown to have the narrowest bioclimatic niches.

Species distribution modeling

The modeling with Maxent shows the most important bioclimatic variables for predicting species distributions of the five endemic species *I. auriculata*, *I.*

bartlingii, *I. cumingiana*, *I. macrophylla*, and *I. palawanensis* (Table 2). Among the bioclimatic variables, TS has the highest percent contribution for *I. auriculata* and *I. bartlingii* followed by PS for *I. auriculata* and Precipitation of the warmest quarter (PwarmQ) for *I. bartlingii*. The main contributor among the bioclimatic variables for *I. cumingiana* is PS followed by PwarmQ, while for *I. macrophylla*, AMP, TS and AMT show the highest percent contribution. PwarmQ and AMP are the two most important bioclimatic variables for *I. palawanensis*.

Model performance for the five species are in an acceptable Test-AUC range (values > 0.7). According to the results of Maxent modeling, *I. macrophylla*, *I. cumingiana*, *I. bartlingii* and *I. auriculata* are found to benefit from future climate while *I. palawanensis* is predicted to experience a decline of suitable habitats.

Suitable areas are identified for *I. auriculata* in northern Luzon and eastern Visayas (Fig. 3a, b). In the year 2080, under both climate scenarios, there will be

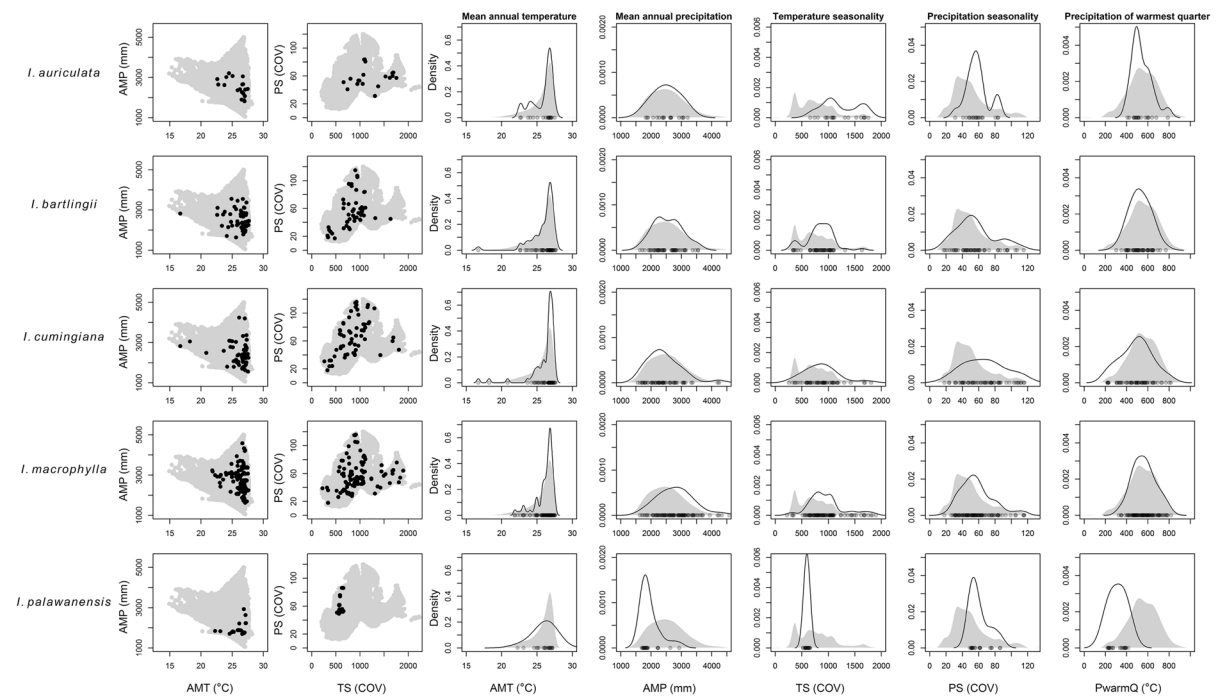


Fig. 2 Scatter plots and Kernel density plots of the five climatic variables for the five endemic Philippine species of *Ixora*. Gray background indicates the climatic space for the entire Philippine archipelago, based on the climatic conditions within each raster cell of the Bioclim-maps. Black points and black density curves

show the distribution of the respective *Ixora* species within bioclimatic space. Temperature seasonality is shown as standard deviation (SD), precipitation seasonality as coefficient of variation (CoV) for all plots

Table 2 Number of species presence records, AUC-values (CV: fivefold crossvalidation), percentage of contribution, permutation importance, and training gain (with and without the respective variable) for the selected bioclimatic variables

Variable	Nr. records	AUC (CV)	AUC (Test)	AMT	AMP	TS	PS	PwarmQ
<i>I. auriculata</i>	20	0.78	0.82					
Contribution (%)				–	0.158	99.842	–	–
Perm. importance				–	0.146	99.855	–	–
Training gain without				–	0.505	–0.010	–	–
Training gain with only				–	–0.010	0.505	–	–
<i>I. bartlingii</i>	57	0.66	0.71					
Contribution (%)				–	–	72.509	–	27.491
Perm. importance				–	–	77.703	–	22.297
Training gain without				–	–	0.012	–	0.104
Training gain with only				–	–	0.104	–	0.012
<i>I. cumingiana</i>	77	0.71	0.72					
Contribution (%)				–	–	–	62.542	37.458
Perm. importance				–	–	–	61.225	38.775
Training gain without				–	–	–	0.105	0.201
Training gain with only				–	–	–	0.201	0.105
<i>I. macrophylla</i>	120	0.7	0.75					
Contribution (%)				23.562	38.523	31.736	6.180	–
Perm. importance				18.386	32.592	36.510	12.512	–
Training gain without				0.185	0.149	0.199	0.279	–
Training gain with only				0.043	0.078	0.141	0.036	–
<i>I. palawanensis</i>	25	0.97	0.97					
Contribution (%)				1.492	6.835	14.864	4.211	72.597
Perm. importance				1.708	25.358	49.288	15.218	8.428
Training gain without				2.289	1.988	1.799	2.069	2.359
Training gain with only				0.009	0.698	1.273	0.268	1.589

Variables without any values (indicated by –) were removed by the variable selection procedure (see “[Species distribution modeling](#)” section of the [Materials and methods](#)) due to low predictive power

AUC-values are a threshold-independent model quality criterion and range from 0 to 1 (perfect fit). Useful models yielded AUC-values above 0.7. Training gains are determined by Jackknife test for the specific variable in isolation (training gain with only) and in exclusion (training gain without)

an increase of some moderately suitable areas in Luzon and in the western and southern parts of the country (Fig. 3c, d). Current suitable climatic areas were identified for *I. bartlingii* mostly in central and southern Luzon and the Visayas, with isolated patches in northern Luzon (Cordillera Administrative Region) and Mindanao (Surigao del Sur) (Fig. 3e, f). However by 2080, under both climate scenarios, most areas in Luzon are predicted to be no longer suitable for the species in the future, and the model shows a general southward shift of suitable areas for *I. bartlingii* (Fig. 3g, h).

The extent of suitable habitat areas for *I. cumingiana* and *I. macrophylla* are likely to increase in both climate scenarios by 2080. Some moderately suitable habitat areas for *I. cumingiana* (Fig. 3i, j) particularly in Zambales are predicted to become highly suitable for the species in the future. Furthermore, model results show an increase in moderately to highly suitable areas in some provinces of Mindanao for the B1 scenario but not in the more severe A2 climate scenario (Fig. 3k, l). Current suitable areas for *I. macrophylla* (Fig. 3m, n) are predicted to increase from moderately to highly suitable habitat for the

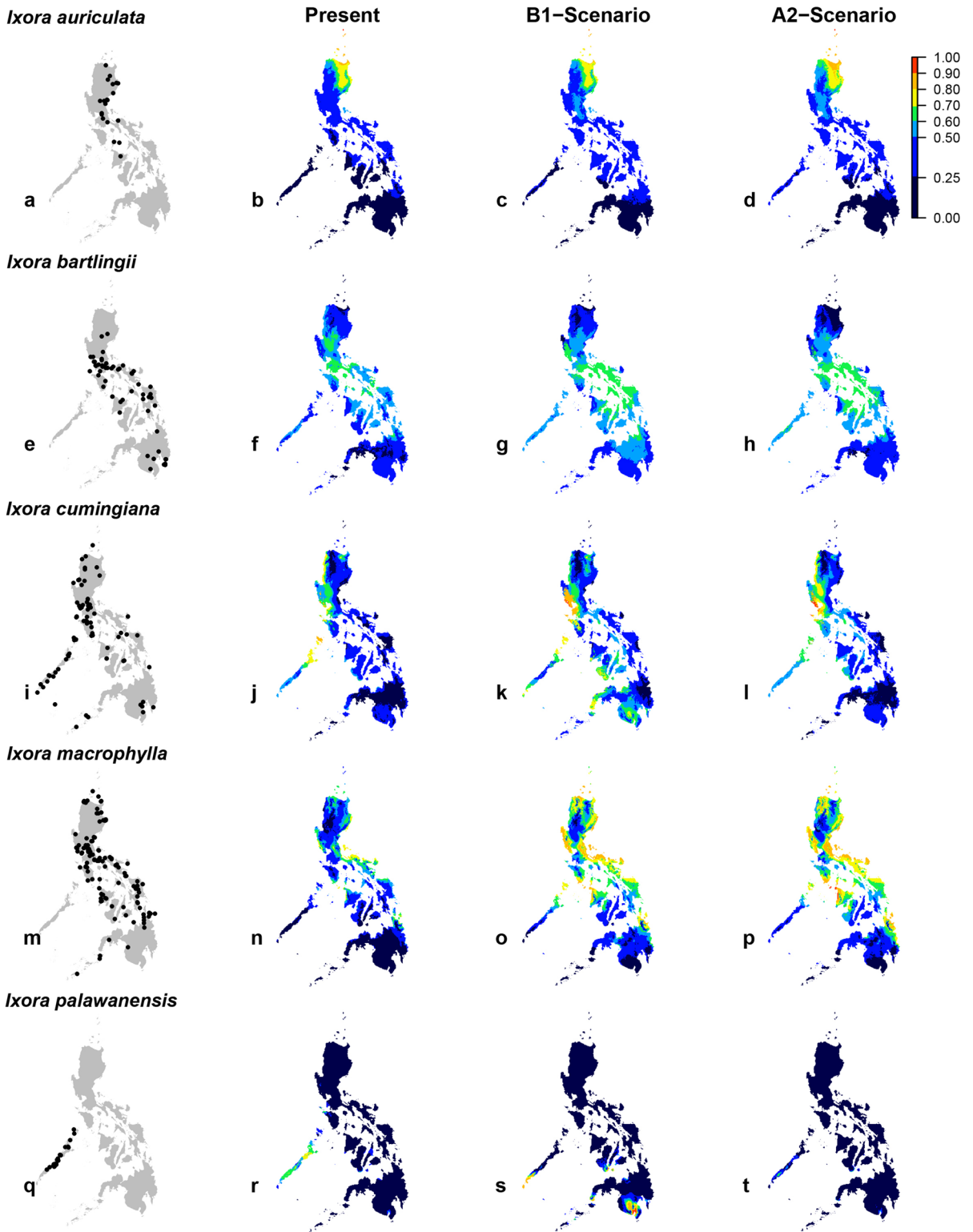


Fig. 3 Maps of habitat suitability (expressed as probability of presence) of **a–d** *Ixora auriculata*, **e–h** *Ixora bartlingii*, **i–l** *Ixora cumingiana*, **m–p** *Ixora macrophylla*, **q–t** *Ixora palawanensis* under current conditions and predicted climate change conditions for the two emission scenarios (B1 and A2 from Parry et al. 2007) for 2080 using the model Maxent

species, particularly in the eastern part of the country with appearance of moderately suitable habitat in Mindanao for both climate scenarios (Fig. 3o, p). *Ixora palawanensis* is only found in Palawan and is shown to be the species that will be affected most by future climate change. Model results predict a decrease in habitat suitability on Palawan, but also show the potential of newly occurring suitable areas outside the areas (Fig. 3).

For the species with lower numbers of occurrences (and thus less robust model results), potential bioclimatic habitats tend to increase with future climate for seven species (*I. bibracteata*, *I. chartacea*, *I. ebracteolata*, *I. inaequifolia*, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii*) as shown in Fig. S2a, b (Online Resource 1).

Similarity between current and projected climate for both B1 and A2 scenarios are analysed using Multivariate Environmental Similarity Surfaces (MESS) within Maxent (see Elith et al. 2010) and are presented in Fig. S3a, c (Online Resource 1). The highest similarity in projections is indicated for the southern part of the country in Mindanao as well as for eastern part of Luzon, whereas the lowest similarity exists for most parts of Luzon and eastern Visayas.

Discussion

Climatic niche of endemic Philippine *Ixora*

Our results provide for the first time an estimate of the bioclimatic relationships of the endemic Philippine *Ixora* species. As shown in Fig. 2, *Ixora* species appear to have a narrow temperature and wider precipitation niche. Because the genus *Ixora* is pantropical in distribution, it is not surprising that the Philippine endemic species are concentrated on areas with AMT between 23 and 28 °C. In the Philippines, essentially no difference in mean annual temperature occurs between Luzon, Visayas, or Mindanao. Based on the average of all weather stations in

the Philippines, the mean annual temperature is 26.6 °C (excluding Baguio City with a mean annual temperature of 18.3 °C). January is the coolest month with a mean temperature of 25.5 °C while May is the warmest month with a mean temperature of 28.3 °C (PAGASA 2011). Thus, with respect to temperature requirements of *Ixora* [20–30 °C (according to Chen et al. 2003)], the Philippines provide an optimum condition for the genus.

Model results indicate an adaption of *Ixora* species to the monsoon seasons in the Philippines based on the species preference toward areas with higher annual precipitation seasonality. This is of particular importance as it was reported by PAGASA (2011) that the Philippines will most likely experience a substantial difference in terms of seasonal rainfall change in most parts of the country in the future, and climate change will probably lead to an active southwest monsoon in Luzon and Visayas. This will most likely be due to future increases in rainfall mostly in the months of June to August and a reduction in rainfall in most provinces during the summer season making the usually dry season drier, and increasing the likelihood of both droughts and floods (PAGASA 2011).

Looking at the individual species' response to specific bioclimatic variables, most species showed a substantial niche overlap which suggests that *Ixora* species may react in a similar way to climate change. This result supports the assumption by Warren et al. (2008) that although some factors (e.g., range size, habitat and distribution) differ among species, closely related species tend to share similar climatic niches (Warren et al. 2008; Wiens et al. 2010; Pearman et al. 2014).

Information regarding the important bioclimatic variables of Philippine *Ixora* was to this date not available. Here, our results present a first estimate of the bioclimatic niches of endemic *Ixora* species with respect to AMT, AMP, TS, PS, and PwarmQ, however, it should be emphasized that these bioclimatic variables are not necessarily the only and main environmental factors determining the occurrence of *Ixora* in the Philippines, as species distributions are affected by further environmental factors and biotic interactions (Gaston 2003). Nevertheless, knowledge of the baseline information about climatic variables to which plants are adapted is necessary to design future experiments and model simulations investigating vulnerability of terrestrial plants to climate change.

Furthermore, knowledge of the plants' response to specific environmental conditions such as climatic variables is needed to explain their specialized traits that allow them to occupy and survive in a particular habitat (Körner 1998, 2003; Körner and Basler 2010). For the case of Rubiaceae, such studies on the ecological requirements of species are scarce and mainly restricted to *Coffea* (Teketay 1999). For *Ixora*, in situ experiments with the ornamental *I. coccinea* from India have revealed that floral initiation was promoted at temperatures between 10 and 20 °C and inhibited at 30 °C (Chen et al. 2003). Similar experimental approaches using the endemic Philippine species are suggested to elucidate the specific requirements of the Philippine endemic *Ixora* species.

Species distribution modeling

Four out of the five focal species of *Ixora* (*I. auriculata*, *I. bartlingii*, *I. cumingiana*, *I. macrophylla*) considered in the species distribution modeling (Fig. 3) have a wider distribution and have been recorded in several provinces across the country. *Ixora palawanensis* on the other hand, is considered as a single island endemic and is only found in Palawan. The other endemic species of *Ixora* (*I. bibracteata*, *I. chartacea*, *I. ebracteolata*, *I. inaequifolia*, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii*, see Fig. S2a, b Online Resource 1) have limited distribution and are only found in one or few provinces or localities in the Philippines. When considering species distributions, it is important to take into account the crucial role of the areas that have been accessible to the species via dispersal over relevant periods of time (Barve et al. 2011). Given that the *Ixora* species included in the present study are Philippine endemics, our study considers the whole country as the area of these *Ixora* species and did not focus on a particular island or province.

According to the results of the Maxent modeling, the predicted current and future ranges of habitat of the endemic *Ixora* species are likely to be positively and negatively affected by future climate. Maxent predicted gains in suitable habitat for *I. auriculata* in northern parts of Luzon, in Cagayan, Isabela, and Nueva Vizcaya provinces (Fig. 3). Suitable habitats for *I. bartlingii* are predicted to increase in Mindanao, particularly in the provinces of Misamis Occidental, Zamboanga del Sur, and Zamboanga del Norte, but a loss of habitat in northern Luzon, in the Cordillera

Administrative Region (CAR), and Pampanga, Bulacan, and Bataan provinces (Fig. 3). Both *I. cumingiana* and *I. macrophylla* are likely to experience an increase in suitable habitats in the future. Model results suggest generally a greater risk of loss of suitable habitats in Palawan for *I. palawanensis*.

For the species with lower numbers of occurrence points, the increasing potential habitat of the species *I. bibracteata*, *I. ebracteolata*, *I. chartacea*, *I. inaequifolia*, *I. longistipula*, *I. luzoniensis*, and *I. macgregorii* imply a similar positive effect of the predicted changes in climate. However, it has to be noted that due to the low sampling size, results for the species shown in the appendix are less robust and therefore need to be considered with much care. Further sampling efforts are clearly necessary in order to improve the understanding of the climatic niches of these endemic species.

Species projected to experience shrinkage or shift in geographical range under climate change are considered as the most sensitive (Midgley et al. 2003). The loss of suitable areas in Luzon and shift of potential distribution toward the western Visayas and Mindanao for *I. bartlingii* is an indication of the species' sensitivity to climate change, as predicted with Maxent. Most of the predicted future suitable habitats for Philippine endemic *Ixora* species are found in Visayas and mostly in Mindanao. This finding is supported by recent analyses of climate projections in the Philippines, emphasizing that extreme rainfall is likely to increase in Luzon and Visayas only (PAGASA 2011). The expected decline of suitable areas in Luzon also coincides with results of a study by Yusuf and Francisco (2009), who point out that the northern Philippines will show highest vulnerability to climate change owing to exposure to tropical cyclones.

Furthermore, the key risks associated with future climate change include the occurrence of novel climates and disappearance of extant climates (Williams et al. 2007). The results of the MESS analysis reveal novel climates (portions of climate space that do not presently occur in the Philippines but may appear with future climate change) by the year 2080 that would affect the distribution of the *Ixora* species. Among the five focal species, *I. macrophylla* and *I. palawanensis* are predicted to be affected most by novel climates, thus conclusions about predicted range shifts need to be drawn with additional care.

In general, this study together with that of Garcia et al. (2013) on 14 threatened forest tree species, demonstrate that species distribution modeling with Maxent provides a strong tool to improve our understanding of climate related range shifts in areas like the Philippines.

Relevance to Conservation

Although scientific knowledge of the Philippine biota has improved substantially over the recent years, basic biological information for many species remains incomplete (Posa et al. 2008). These gaps become evident in the present study, as only 12 of the 25 Philippine endemic *Ixora* species had a sufficient number of known occurrences to permit species distribution modeling. More studies like the present one are required to understand the distributional potential of endemic species to improve information for better conservation management plans.

Despite the possible expansion of new suitable habitats for the endemic species, it is important to be aware of the likely loss of habitats in areas where species currently occur (e.g., *I. palawanensis* in Palawan). It is therefore necessary to establish measures that prevent the loss of the suitable habitats and to conduct future studies to ensure that these habitats can actually be occupied by the species. Aside from identifying these habitats, it is important to investigate whether the species will be able to overcome dispersal and other environmental barriers and whether they will be able to successfully compete with other species (Soberón 2007; Hirzel and Le Lay 2008; Olalla-Tarraga et al. 2011). The Philippine archipelago consists of several islands and the sea between them poses a potential dispersal barrier for successful population of suitable areas. In general, the dispersal potential of the genus *Ixora* is limited as their fruits are eaten by frugivorous birds and small mammals, which can only disperse the seeds within the local habitat (De Block 1998). The actual occurrence of the species may therefore deviate from the predicted suitable habitats since the model prediction did not account for landcover changes (e.g., deforestation, agriculture). Furthermore, niche saturation could prevent the species from establishing (Davis et al. 2012). Given the limited dispersal abilities of *Ixora* species and the archipelagic nature of the Philippines, assisted migration (Davis et al. 2012) may become a necessary future

conservation strategy for Philippine endemic *Ixora*. However, field surveys and experiments should be conducted in advance to test for any adverse effects of introductions to a given area and to assess its probability of success.

Lastly, we hope that the assessments emerging from this study may be useful in future modeling studies and development of conservation strategies particularly for endemic species in the Philippines. Our model results can be used to assist the design of conservation strategies for the species, as they identify areas predicted to have potential to withstand climate change until at least 2080, and represent assessment priorities for in situ conservation.

Limitations of the study

Criticisms of the bioclimatic approach include the fact that many other factors beyond climate play a role in structuring species' distributions, such as plant to plant interactions, pollinator availability, dispersal ability, and plant plasticity (Pearson and Dawson 2003; Heikkinen et al. 2006; Hijmans and Graham 2006; Oney et al. 2013). Other environmental variables that might be potentially important to *Ixora* like soil type, topography, vegetation type, and anthropogenic factors (in particular possible future changes in landuse) are therefore suggested to be considered in future modeling studies (Trisurat et al. 2011; Ndayishimiye et al. 2012). We therefore emphasize the need for improving the data situation at a sufficient spatial (and temporal) resolution in order to enhance model predictions for *Ixora* and other Philippine endemic species.

Owing to the paucity of locality records available for the Philippine endemic *Ixora*, only five species were considered in detail. Data points (especially of the rare species) most likely do not cover the entire niche of the species. This problem calls for a need of better primary documentation of plant distributions in the country. Thus, the resulting distribution maps should not be interpreted as representing the actual limits to the range of the species (Pearson et al. 2007), rather, these models tried to identify regions that have similar bioclimatic conditions where the species could possibly maintain populations with respect to the current and future climate conditions.

Finally, the present study did not consider the impact of population density, land use, and habitat

fragmentation, so in the wake of strongly increasing land use and population in the future, the actual fraction of suitable areas is likely to be substantially lower. The improvement of the data situation, in particular in respect to species occurrence and human landuse changes, are recommended to test the implications from the present study and to draw more general conclusions on the ecology of endemic *Ixora* species on the Philippines.

Acknowledgments We are grateful to the following herbaria and their staff for providing loans and/or access to collections: A, BK, BR, C, CAHUP, K, L, NY, P, PNH, PPC, SAN, and US. Dr. A. Townsend Peterson, for his helpful comments in the earlier drafts of this paper. The present work is part of the doctoral dissertation of C.I. Banag, for which financial assistance was obtained from Philippine Commission on Higher Education (CHED), NAGAO Natural Environment Foundation (NEF), DAAD STIBET Grants for Doctoral Studies, and the Katholischer Akademischer Ausländer-Dienst (KAAD).

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