Environmental Niche Models Reveal Receding Refugia for Philippine Endemic and Threatened Melastome Trees under Accelerated Climate Change

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Home to exceedingly diverse and highly endemic flora in the Malesian region, the Philippines is highly vulnerable to species loss due to climate change. The lack of baseline ecological and biogeographic information in the country, which are requisites to effective conservation, compounds this problem. To address this, we used maximum entropy modeling to predict suitable habitats of four Philippine endemic trees – *Astronia cumingiana*, and three threatened species, *Astrocalyx calycina*, *Beccarianthus ickisii*, and *B. pulcherrimus* (Astronieae: Melastomataceae) – under current climate conditions. We then predicted changes in their habitats for the years 2041–2060 and 2061–2080 under two future climate scenarios. We also assessed the level of protection that the species receive using the current protected area boundaries. Our models showed potentially suitable habitats for all species outside of their observed occurrence under the present climate, but their niches are generally predicted to shrink and ascend to higher altitudes when projected under future climate scenarios. The overlaps of their suitable niches outside protected area boundaries also increase southward, with Mindanao island possibly harboring the greatest number of unprotected Astronieae species. Our findings contribute to the emerging field of environmental niche modeling in the country and support the need to re-envision the country's protected area system to move towards climate-smart local conservation strategies.

Keywords: Astronieae, climate change, ecological niche modeling, Maxent, Melastomataceae

INTRODUCTION

Accelerated climate change and its associated anomalies are now being felt across the planet. Temperatures have been rising at a minimum rate of 0.14 °C per decade, bringing about an increase in the number of warm days (IPCC 2018). Southeast Asia is experiencing the first signs of precipitation increase as monsoons and tropical cyclones continue to deliver unprecedentedly high rainfall in the past two decades (Loo *et al*. 2015). The Philippines, which is situated at the immediate northwestern periphery of the Pacific, is even more vulnerable to the ongoing shifts in global temperature and precipitation. An average of 0.1 °C rise in decadal mean temperatures, as well as extremely high regional rainfall and slightly less frequent but increasingly intense tropical cyclones, has already been observed in the country (PAGASA 2018). In fifty years, the temperature is expected to rise further by a minimum of 1.3–2.5 °C under moderate and drastic

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climate projections, respectively, while precipitation may exhibit both an extreme drop in predominantly wetter regions while also rising in currently drier parts of the country (PAGASA 2018).

Climate change also poses threats to natural ecosystems and their balance, processes, and the life forms that they support (CBD 2018). The past decades saw drifts in growth rates, phenologies, and distribution of terrestrial vegetation (IPCC 2018). In the Southeast Asian tropics, extended and intensified droughts have had dire effects on flowering and reproduction, and subsequently, dispersal and productivity, particularly in lowland and seasonal forests (Sakai *et al.* 2006; Yusuf and Francisco 2009; Daniau *et al.* 2012). In the Philippines, which is both a center of diversity and a climate change hotspot for rainforest species (Ong *et al.* 2002; Alcala *et al.* 2012), erratic rainfall is known to further alter plant associations and, consequently, forest landscapes (Lasco *et al.* 2008). Other ongoing disturbances, including geological and anthropogenic, may adversely affect Philippine flora in the future, yet the higher inevitability and uncontrollability of climatic factors and their great capacity to drive species loss cannot be overstated (Hughes 2017).

In the Philippines and its over 10,000 plant species, the rare ones – endemic (ca. 50% of the species) and threatened (ca. 10%) – are regarded as more climate-sensitive and at a higher extinction risk (PCARRD 2010; Pelser *et al.* 2011; DENR 2017). While limited habitat ranges and low gene flow naturally pose threats to these species, the risk of loss is compounded by the lack of baseline data that could accurately describe them, especially their habitat and survival requirements (Bentlage *et al.* 2009; Ramos *et al.* 2012). Fortunately, developments in ecological modeling in recent years allow more accurate depictions of species and natural systems. Environmental niche modeling, also known as species distribution modeling, has gained traction in ecology and conservation biology globally (Phillips and Dudík 2008) but local applications have remained sparse (Bentlage *et al.* 2009; Garcia *et al.* 2013; Snelder *et al.* 2013; Banag *et al.* 2015; De Alban *et al.* 2015; Tumaneng *et al.* 2019).

The Melastomataceae Juss. are a large family of predominantly tropical herbs, shrubs, woody climbers, and trees that are typically distinguished by their opposite leaves with checkerboard-patterned veins and flowers with elaborate anthers (Renner 1993; Clausing and Renner 2001). In the Philippines, melastomes comprise over 180 native species in 15 genera and are mostly shrubs, some of the most popular being the ornamental favorite *Medinilla* Gaudich. (Sonerileae Triana/Dissochaeteae (Naudin) Triana group) and the common secondary forest pioneer, the type genus *Melastoma* L. (Melastomateae Bartling). A smaller group of large shrubs to massive

trees, the Astronieae (Decne.) Triana, exhibits high diversity and endemism in the country yet remains poorly documented among the melastomes (Penneys 2013). All of the 25 species that occur in the country but one are endemic (Maxwell and Veldkamp 1990a, b), some of which are common – if not dominant – components of forest understories (Barcelona *et al.* 2008; Buot 2009; Balete *et al.* 2013). A few poorly known members of this tribe have recently been included in the latest national list of threatened plants (DENR 2017), and recent collecting expeditions suggest that the conservation status of some is underestimated (Fritsch *et al.* 2020). Despite their high evolutionary and ecological significance, information about the distribution and suitable habitats of Astronieae species remains inadequate (Reginato *et al.* 2020), impeding any directed conservation effort.

To help address this, we used environmental niche modeling to locate suitable habitats of select endemic and threatened Astronieae species under the present Philippine climate, then projected their suitable habitats under two future climate change scenarios. We analyzed the future lateral and vertical movements of the suitable habitats, and also determined priority areas for the protection of these melastomes based on their niche overlaps. We hypothesized the species' potential distributions to be nationwide but mostly concentrated in the eastern Philippine track and in Mindanao island. We also anticipated the contraction of environmental niches of all modeled species proportional to the intensity of climate change, with movement towards higher altitudes as temperatures continue to increase in the lowlands (Kelly and Goulden 2008; Randin *et al.* 2009). We also predicted the melastomes' niche areas to be most likely not completely protected at the moment, especially in Mindanao – the supposed center of diversity and endemism for the tribe in the country (Mancera 2017).

MATERIALS AND METHODS

Species Selection and Distribution Data Collection
We selected melastome species for modeling based on their status as threatened species and the availability of their distribution data within the Philippines. We crosschecked all of the locally endemic Astronieae species against the "Updated National List of Threatened Philippine Plants and their Categories" compiled in the Department of Environment and Natural Resources of the Philippines Administrative Order 2017-11 (DENR 2017). From this, we identified three threatened Astronieae species to model: *Astrocalyx calycina* (S. Vidal) Merr. (endangered), *Beccarianthus ickisii* Merr. (vulnerable), and *B. pulcherrimus* (Merr.) Maxw. (vulnerable) (Figure 1). We added another widespread species of "least
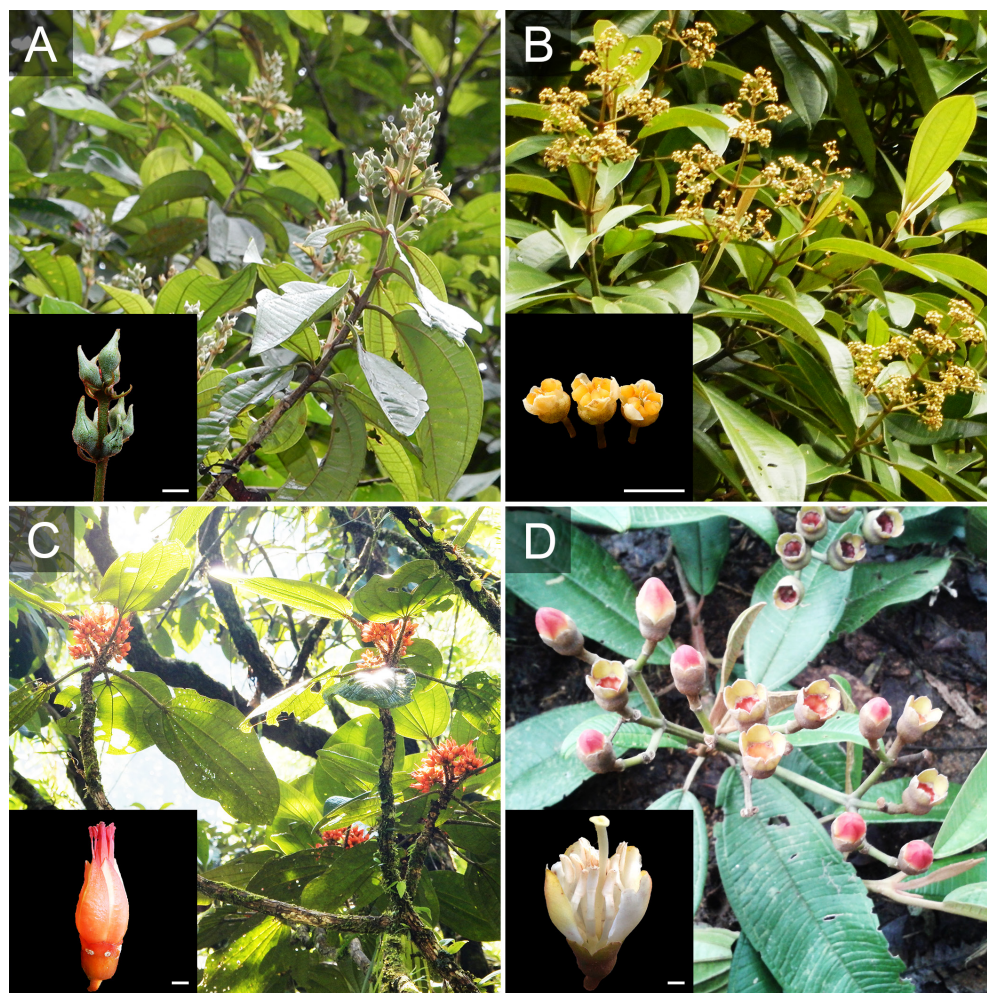
Figure 1. Astronieae species used in the environmental niche modeling: (A) *Astrocalyx calycina* (S. Vidal) Merr., (B) *Astronia cumingiana* S. Vidal var. *cumingiana*, (C) *Beccarianthus ickisii* Merr., and (D) *B. pulcherrimus* (Merr.) Maxw. Insets: flowers at anthesis except A showing flower buds. Scale bar = 5 mm. Photos (c) J.P.M.

concern" status, *Astronia cumingiana* S. Vidal var. *cumingiana*, as a point of comparison. We then compiled their distribution data from field surveys, herbaria, and online databases.

We downloaded occurrence points for all four species from two online databases, *i.e.* the Botanical Information and Ecology Network database ver. 4.1 (https://bien.nceas.ucsb.edu/bien/, accessed on 01 Mar 2019) (Enquist *et al.* 2016; Maitner 2018) and the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/, accessed on 23 Sep 2020) (GBIF 2020). As GBIF points are prone to geolocation errors, such as having species coordinates designated in country centroids or capital cities (Gomes *et al*. 2018), we used the *CoordinateCleaner* (Zizka *et al*. 2019) package in R ver. 3.6.0 (R Core Team 2019) to eliminate erroneous occurrences. To ensure accurate identification of species, physical and virtual herbarium vouchers from seven herbaria with significant

holdings of Philippine flora, obtained from 2014–2017 (*i.e.* A, CAS, L, P, PNH, SING, and U), were used to counter-check entries in the databases. The collections comprised types or non-types determined or annotated by specialists in the family and genera. Within the same period, herbarium visits were conducted at NY, UC, and US, where specimens were examined on-site.

For occurrence entries with no coordinates but with physical herbarium vouchers or their corresponding high-resolution images available for inspection, coordinates were carefully georeferenced by counter-checking legacy literature such as taxonomic monographs or historical expedition accounts for more accurate locality description following Ramos *et al*. (2012). Within a municipality or a village, additional ecological filters reflecting microhabitats for the Astronieae as observed in field surveys – such as proximity to ridges and water bodies, available forest cover, and average observed

elevation range – were employed to ensure that the resulting coordinates are more representative of the species' distribution, following Oleas *et al*. (2019). Final georeferencing was done via Google Earth ver. 9.120.0.2.

Finally, primary geographic data from recent botanical expeditions to natural parks in Luzon and Mindanao islands in 2011, 2014, and 2015 spearheaded by CAS, CAHUP, and CMUH, and in Mindanao island in 2019 led by BRIT, WNC, SIU, and CMUH, were added to our list of coordinates. After compiling all the points, we removed duplicates within each species to avoid spatial bias when modeling distributions. A total of 57 unique points was compiled for the four species (Figure 2). Despite our best efforts, we could only get a maximum of 18 unique

Figure 2. Altitude map of the Philippines with species occurrences and protected area boundaries.

occurrences for a species, attesting to their rarity.

Bioclimatic Data

To create distribution models, we utilized bioclimatic variables from the CHELSA v.1.2 database (http://chelsa-climate.org/, accessed on 23 Sep 2020) that summarizes

mean temperature and precipitation patterns from the period 1979–2013 (Karger *et al.* 2017). We resampled the original 30 arc-second resolution of the climate data to 2.5 arcminutes (around 4.5 km in the Philippines), as the lower resolution could already effectively capture the distribution of tree species in a study extent as wide as the Philippines (Banag *et al.* 2015). After cropping and masking the climate data to country boundaries, we then performed Spearman's rank correlation to assess which bioclimatic predictors are highly collinear (Table 1). It is recommended that predictor pairs with high correlations be dropped in order to achieve parsimonious models (Merow *et al.* 2013). For our models, we chose to retain bioclimatic predictors ecologically important to plants with Spearman's $r \leq 0.75$ and were underscored by the Intergovernmental Panel on Climate Change (IPCC 2018) and the Philippine Atmospheric, Geophysical, and Astronomical Services Administration (PAGASA 2018) as variables that would change reasonably under future climate projections. These are mean annual temperature (MAT) and annual precipitation (AP) as basic climate niche variables, temperature seasonality (TS) and precipitation seasonality (PS) as variability indicators, and precipitation of coldest quarter (PCQ) as a predictor that represents the interaction between temperature and precipitation. An earlier analysis included altitude data obtained from CGIAR-CSI (Jarvis *et al.* 2008, accessed on 01 Sep 2020) as one of the parameters, but it was found to be highly correlated with MAT ($r = –0.97$), so we dropped it from the final runs. To derive each species' minimum, maximum, and average values for each variable, we extracted the bioclimatic data at each species point. The cropping, masking, and extraction steps were performed using the *raster* (Hijmans 2019) package in R.

For future climates, we utilized three different CMIP5 Earth system models (ESMs), CNRM-CM5, GFDL-CM3, and MPI-ESM-LR, which have been previously rated as satisfactory in projecting Southeast Asian climate (McSweeney *et al.* 2015; Kamworapan and Surussavadee 2019). We chose two representative concentration pathways (RCPs) – RCP2.6 and RCP8.5 – which represent the lowest and highest greenhouse gas concentration scenarios designated by the Intergovernmental Panel on Climate Change (IPCC), respectively (van Vuuren *et al.* 2011). We projected each RCP onto two time steps available in CHELSA – 2041-2060 and 2061-2080 – which we designated as time steps "a" and "b," respectively. Under RCP2.6, the IPCC forecast for Asia indicates a temperature increase of less than 2 °C above baseline for both mid- and late 21st century, while precipitation for lower latitude areas, *e.g.* the Philippines, is projected to have no substantial change in natural variability. Under RCP8.5, a local analysis by PAGASA (2018) predicts an increase in temperature of 1.2–2.3 °C by
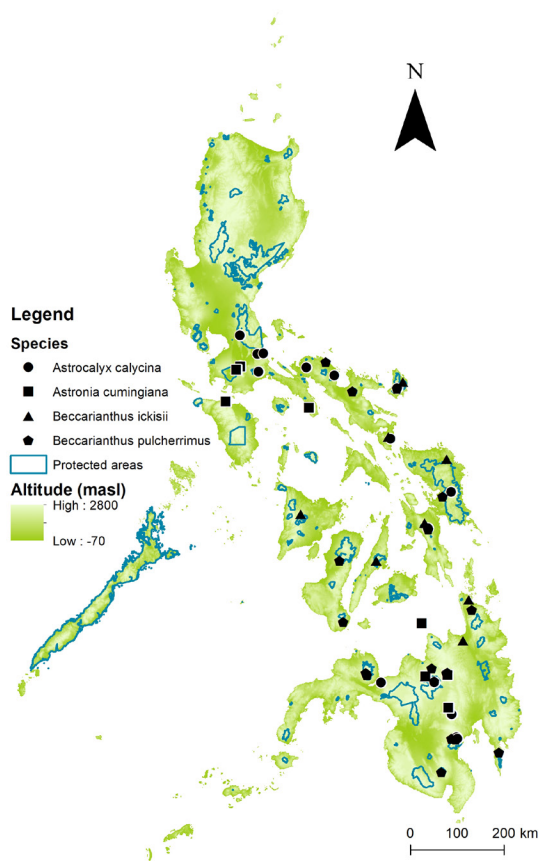
Table 1. Spearman's correlation coefficients between bioclimatic variables for the Philippines.

Variables	MAT	MDR	ISO	TS	MaxTWM	MinTCM	TAR	MeanTwetQ	MeanTDQ	MeanTwarmQ	MeanTCQ	AP	PWM	PDM	PS	PwetQ	PDQ	PwarmQ	PCQ	Altitude
MAT	1																			
MDR	-0.32	1																		
ISO	-0.23	0.55	1																	
TS	**-0.02**	**0.14**	-0.66	1																
MaxTWM	0.77	0.19	-0.10	0.26	1															
MinTCM	0.85	-0.65	-0.20	-0.31	0.42	1														
TAR	-0.27	0.86	0.10	0.58	0.30	-0.69	1													
MeanTwetQ	0.93	-0.23	-0.22	0.01	0.79	0.75	-0.15	1												
MeanTDQ	0.87	-0.43	-0.12	-0.19	0.59	0.90	-0.47	0.74	1											
MeanTwarmQ	0.94	-0.25	-0.40	0.24	0.85	0.69	-0.07	0.90	0.75	1										
MeanTCQ	0.92	-0.37	0.00	-0.34	0.62	0.93	-0.46	0.85	0.90	0.76	1									
AP	**-0.22**	**-0.03**	-0.16	0.29	-0.21	-0.19	0.06	-0.34	-0.10	-0.20	-0.28	1								
PWM	-0.10	0.02	-0.40	0.60	0.01	-0.24	0.29	-0.15	-0.16	0.03	-0.28	0.79	1							
PDM	-0.11	-0.10	0.32	-0.35	-0.23	0.09	-0.32	-0.27	0.21	-0.25	0.01	0.38	-0.12	1						
PS	**0.06**	**0.03**	-0.51	0.60	0.19	-0.16	0.36	0.13	-0.21	0.24	-0.15	0.13	0.64	-0.78	1					
PwetQ	-0.10	0.01	-0.41	0.60	0.01	-0.23	0.29	-0.15	-0.16	0.03	-0.28	0.79	1.00	-0.12	0.64	1				
PDQ	-0.12	-0.11	0.32	-0.35	-0.23	0.09	-0.33	-0.28	0.21	-0.25	0.01	0.38	-0.12	1.00	-0.79	-0.13	1			
PwarmQ	-0.39	0.30	0.06	0.30	-0.23	-0.45	0.35	-0.38	-0.40	-0.34	-0.46	0.64	0.50	0.24	0.06	0.50	0.24	1		
PCQ	**-0.06**	**-0.19**	0.16	-0.18	-0.16	0.13	-0.31	-0.25	0.28	-0.15	0.02	0.44	0.01	0.90	-0.62	0.01	0.90	0.12	1	
Altitude	-0.97	0.26	0.23	-0.07	-0.82	-0.77	0.17	-0.90	-0.84	-0.95	-0.85	0.22	0.09	0.09	-0.05	0.09	0.09	0.34	0.01	1

Predictors used in the ENMs of Astronieae species are in bold. These bioclimatic variables were downloaded from CHELSA v. 1.2 (http://chelsa-climate.org/). Altitude data was downloaded from CGIAR-CSI SRTM 90m Database (http://srtm.csi.cgiar.org).

Heading acronyms are as follows: MAT – mean annual temperature; MDR – mean diurnal range; ISO – isothermality; TS – temperature seasonality; MaxTWM – maximum temperature of warmest month; MinTWM – minimum temperature of coldest month; TAR – temperature annual range; MeanTwetQ – mean temperature of wettest quarter; MeanTDQ – mean temperature of driest quarter; MeanTwarmQ – mean temperature of warmest quarter; MeanTCQ – mean temperature of coldest quarter; AP – annual precipitation; PWM – precipitation of wettest month; PDM – precipitation of driest month; PS – precipitation seasonality; PwetQ – precipitation of wettest quarter; PDQ – precipitation of driest quarter; PwarmQ – precipitation of warmest quarter; PCQ – precipitation of coldest quarter.

the middle of the 21st century and 2.5–4.1 °C by late 21st century. It also foresees a 40% reduction in precipitation over Mindanao, while Luzon and Western Visayas each gain a 40% increase in rainfall. In addition, there are predicted increases in the frequency of extremely severe tropical cyclones with wind strengths of over 170 kph that could make landfall. This phenomenon, coupled with the predicted 0.2 m increase in sea levels across the archipelago by the end of the 21st century, exacerbates the danger of storm surges. These phenomena could have drastic effects on plant life in both montane and coastal environments.

Environmental Niche Modeling

We used maximum entropy or Maxent ver. 3.4.1 (Phillips *et al.* 2006) to model the environmental niches of our Astronieae species. Maxent works by taking in species coordinates and environmental predictors, *e.g.* bioclimatic variables, as inputs, then generates a sample of pseudo-absence points from the background where the species is absent. It then analyzes similar locations across the user-defined space to detect other areas of potential occurrences. It is used quite frequently in modeling species distributions as it can be used with even only presence data, and normally outperforms other models (Merow *et al.* 2013). Maxent has been proven to be effective when modeling rare species, even with small sample sizes as few as five points (Pearson *et al.* 2006). In the Philippines, it has previously been used to project climate change effects on Philippine tree species (Garcia *et al.* 2013; Banag *et al.* 2015).

We ran Maxent with 15 replicates for each species under default settings, except for the following adjustments as recommended by Merow *et al.* (2013): regularization coefficient is set to 1, and product and threshold features deactivated. We also turned on clamping to avoid overprediction and activated the jackknife setting to check individual variable contributions within each model. We used all species points for training because some of our species have only as few as 9 points. To evaluate the models, we used two indicators: the training area under the curve (AUC) score given by Maxent, and the true skill statistic (TSS) score, computed from the sensitivity and specificity values (see Allouche *et al.* 2006 for details). If model scores were in the acceptable range (> 0.7 for AUC; > 0.4 for TSS), we proceeded to project the species onto the future climate spaces separately for each ESM. We then averaged the continuous suitability rasters of each ESM for each RCP scenario and time step *via* raster calculator. To clearly demarcate areas as "suitable" and "unsuitable" for each species, we reclassified the suitability maps from continuous to binary using the maximum sensitivity and specificity threshold score. We used the *dismo* (Hijmans

et al. 2017), *rJava* (Urbanek 2019), and *raster* packages in R to perform these steps.

Visualizing Species Niches under Climate Change Scenarios

The percentage of suitable areas for each species under each climate scenario and time step was computed as the number of suitable pixels in the binary maps divided by the total number of pixels in the Philippines. To visualize areas where suitable areas for Astronieae overlap under each climate scenario, we created an Astronieae species heat map by adding all binary rasters, scoring each pixel as highly suitable for the melastomes when the pixel value is "4" and "0" if otherwise.

Altitude Analysis

To investigate the relationship between altitude and suitable habitats under different climate scenarios, we conducted linear regression analysis between the suitable areas under each climate scenario and their respective altitudes. Altitude data was extracted at each of the suitable area pixels using the *extract()* function of the *raster* package. We then used the linear regression function *lm()* in R, with climate scenario as the predictor and altitude as the response variable, and with separate runs for each species. Significant differences between groups were tested first with ANOVA type II and, when significant, were followed up by Tukey's honestly significant difference (HSD) adjusted pairwise tests.

Protected Areas Assessment

To assess the extent of protection the Astronieae species currently receive, we counted how many species points are presently within protected area boundaries. We also calculated the percentage of current suitable areas within these conservation areas. For each species, we extracted the number of suitable habitat pixels inside the PAs and computed the percentage by dividing the area of suitable habitats inside over the total area of suitable habitats for that species. The polygon shapefiles of PA boundaries in the Philippines that we used were obtained from the World Database on Protected Areas (protectedplanet.net, accessed on 01 Feb 2019) (UNEP-WCMC and IUCN 2020).

RESULTS

Environmental Niche Modeling

The Maxent models revealed differing important bioclimatic variables in predicting the environmental niches of the four endemic melastomes (Table 2). Mean annual temperature is the bioclimatic variable with the highest percent model

Table 2. Number of presence records (n); AUC and TSS scores; maximum sensitivity and specificity threshold (MSSTh); and percentage of contribution, permutation importance, and training gain (with and without the variable) for the bioclimatic variables (MAT, AP, TS, PS, PCQ) used in each species model.

Species	Variable	n	AUC	TSS	MSSTh	MAT	AP	TS	PS	PCQ
Astrocalyx calycina		18	0.937	0.714	0.623					
	Contribution					54.583	15.202	12.000	0.163	18.052
	Perm. Importance					64.678	6.420	16.502	0.213	12.187
	Training gain without					0.473	0.909	0.839	0.948	0.932
	Training gain with only					0.500	0.300	0.059	0.073	0.246
Astronia cumingiana		12	0.857	0.666	0.538					
	Contribution					57.336	24.797	10.129	7.739	0.000
	Perm. Importance					59.926	18.748	7.944	13.381	0.000
	Training gain without					0.288	0.497	0.573	0.583	0.616
	Training gain with only					0.349	0.177	0.044	0.056	0.067
Beccarianthus ickisii		9	0.823	0.464	0.556					
	Contribution					0.000	37.809	3.379	9.787	49.026
	Perm. Importance					0.000	73.488	0.000	26.512	0.000
	Training gain without					0.241	0.176	0.231	0.212	0.241
	Training gain with only					0.000	0.174	0.013	0.033	0.166
Beccarianthus pulcherrimus		18	0.949	0.760	0.211					
	Contribution					66.628	11.961	8.626	0.729	12.056
	Perm. Importance					46.776	7.322	35.130	0.888	9.884
	Training gain without					0.769	1.598	1.669	1.790	1.734
	Training gain with only					1.156	0.329	0.227	0.120	0.238

contribution in three out of four species (*Astrocalyx calycina*, *Astronia cumingiana*, and *Beccarianthus pulcherrimus*). Precipitation of coldest quarter contributed the highest for *B. ickisii* and second highest for *Astrocalyx calycina* and *B. pulcherrimus*. Annual precipitation had the second highest percent contribution for *Astronia cumingiana* and *B. ickisii*, and ranked third highest in *Astrocalyx calycina* and *B. pulcherrimus*. The seasonality variables did not contribute as much. Temperature seasonality ranked fourth in most of the species (*Astrocalyx calycina*, *B. ickisii*, and *B. pulcherrimus*), while precipitation seasonality scored low in all four species.

Model performance for all four species were in the acceptable training AUC range (values > 0.7), and have fairly good scores (values > 0.4) for TSS; therefore, all species were projected onto the climate spaces. The environmental niches of all the Astronieae species under the current climate were mostly following a southern trail down the eastern track of the Philippines, starting from the eastern Luzon coast and Greater Samar-Leyte, down to eastern Mindanao, then spreading to the Mindanao highlands (Figures 3 and 4). Suitable habitats were also seen at the mountains of Panay, Negros, and Mindoro. This is an expansion of the known areas of occurrence of

the Astronieae (Mancera 2017). *B. ickisii* was observed to have the widest distribution, and *Astronia cumingiana* had the narrowest.

The suitable habitat areas for three out of four species (*Astrocalyx calycina*, *Astronia cumingiana*, and *B. pulcherrimus*) were observed to shrink under climate change, with reductions reaching –8% in suitable areas observed under RCP8.5 scenario by 2061–2080 (Table 3; Figure 5). It is worth noting that even under RCP2.6, the optimistic scenario, there is still an estimated substantial decrease in suitable habitat for these three species, with as much as –5.3% loss observed for *Astrocalyx calycina* by 2061–2080. Conversely, *B. ickisii* saw its suitable areas increasing under climate change, with gains reaching +5.3% under RCP2.6 and +7.2% under RCP8.5. While this is promising for this threatened species, we should note that *B. ickisii* has the fewest number of occurrences among the four melastomes (and, therefore, less robust model results), and advise that this prediction be regarded with caution.

Altitude Analysis
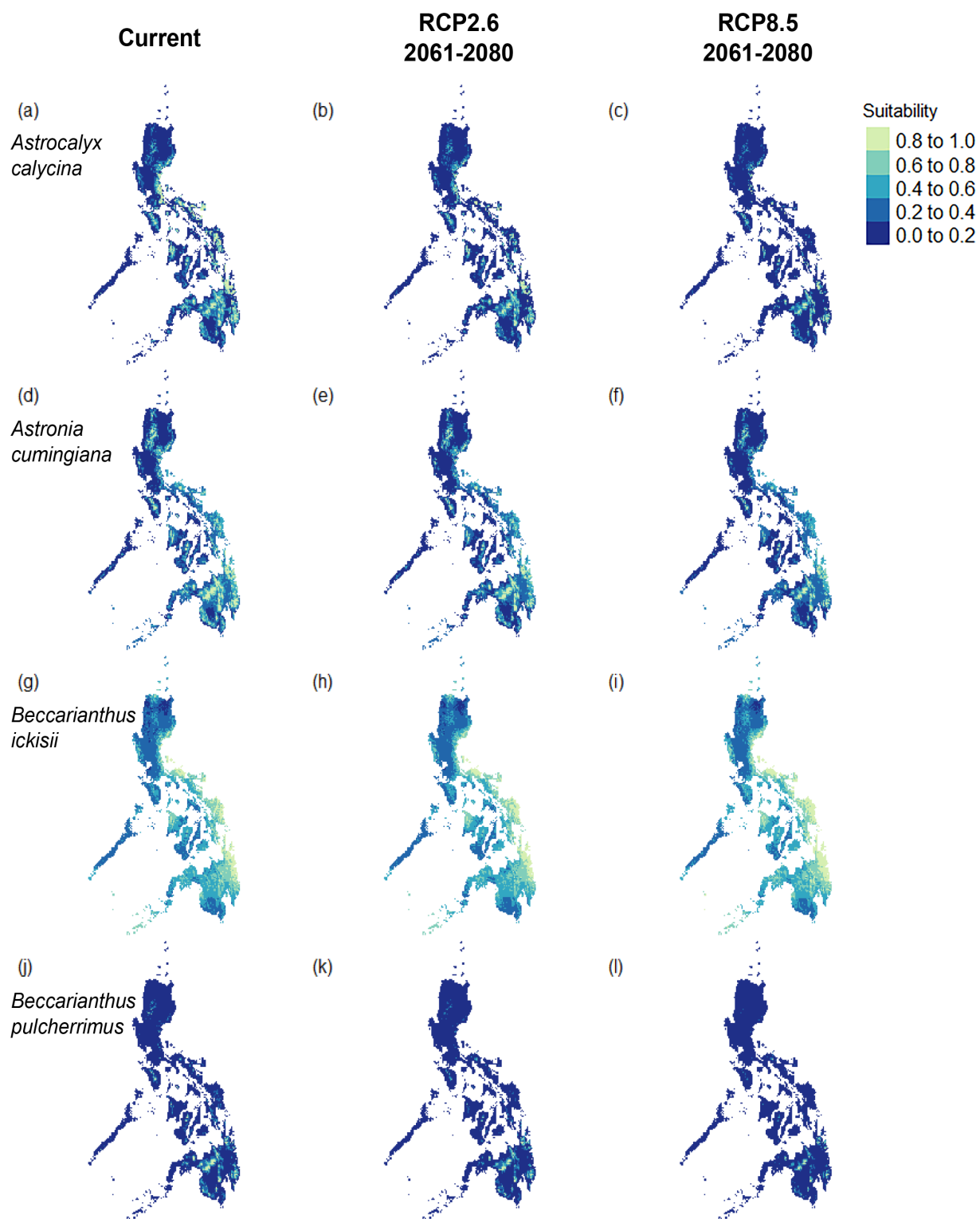There is a clear pattern of migration to higher areas

Figure 3. Niche suitabilities of the Astronieae species in the Philippines modeled using Maxent under current (a, d, g, j) and future (2061–2080) climate scenarios – RCP2.6 (b, e, h, k) and RCP8.5 (c, f, i, l).
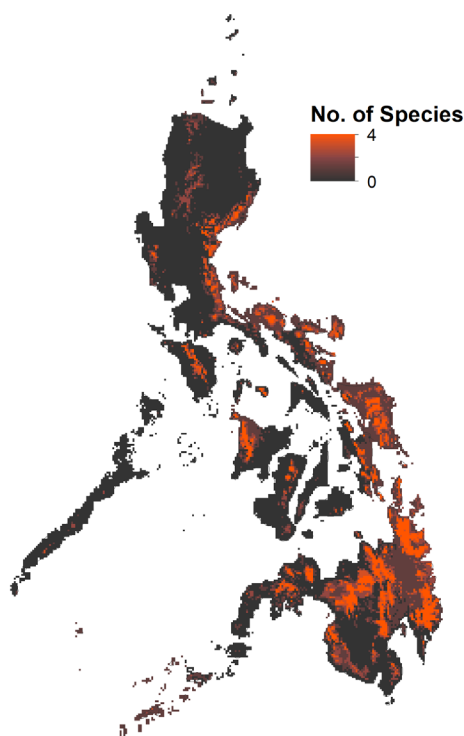
Figure 4. Astronieae species niche heat map showing areas in the Philippines where overlaps of the species suitabilities are highest.

observed in three out of four Astronieae species (Figure 6). This is supported by the regression analysis, which revealed significant differences between the climate scenarios with respect to altitude (Table 4). For *Astrocalyx calycina*, *Astronia cumingiana*, and *B. pulcherrimus*, altitude is significantly higher for suitable areas under the two future climate change scenarios *versus* suitable habitats during the current climate. Despite being the optimistic climate change scenario, mean altitude values for RCP2.6 were still observed to be significantly greater than current climate values, suggesting that the species are still likely to migrate to higher and, thus, cooler areas. However, the values across the two time steps are not significantly different, which could imply habitat stability. Suitable habitats for RCP8.5 are located at the highest elevations and are significantly higher than suitable habitats for current and RCP2.6 climates even as early as 2041–2060, and going even higher at 2061–2080. For *B. ickisii*, there was no observed significant difference between the mean altitude values of its suitable habitats across the climate scenarios.

Protected Areas Assessment
The protected areas assessment showed limited protected area coverage for all the Astronieae species (Table 5). Only 22 out of 57 species occurrences are within protected area boundaries, with *B. pulcherrimus* having the most points

inside PAs at 10 out of 18 points. Their current suitable habitats are also mostly outside conservation areas. The species with the highest percentage of suitable habitats protected is *Astrocalyx calycina* at 27.1%, followed by *B. pulcherrimus* at 24.8%, and *Astronia cumingiana* at 23.5%. *B. ickisii* lags behind at 12.1%. These numbers are alarming since three of these species are considered threatened.

DISCUSSION

General Insights into the Ecology and Biogeography of the Astronieae
Climatic factors are very significant predictors of plant distribution, especially in central Wallacea, which comprises Java, the Lesser Sunda Islands, Maluku, Sulawesi, and the Philippines (van Steenis 1979; van Welzen *et al.* 2011). The region is marked by relatively more distinct seasons due to monsoons and extreme drops in precipitation or pronounced dry periods during specific times of the year than the rest of Malesia. Even within the Philippines, different climatic variations are observed from north to south and west to east. The archipelago exhibits a mosaic of climatic types, with highly seasonal and drier northern and western regions and everwet southern and eastern tracks (Heaney 1991). Our resulting distribution maps of potentially suitable habitats for the Astronieae species confirm our hypothesis that their distribution would be nationwide but concentrated in those everwet tracks.

Phylogenetic niche conservatism states that ecological niches are more conserved throughout lineages, emphasizing the importance of integrating the evolutionary history of taxa with any inference of their distribution, instead of focusing solely on environmental correlations (Donoghue 2008; Pyron *et al.* 2015). One of the model cases of this theory is the predominant distribution of species of Order Myrtales, which Melastomataceae is a member of, along the everwet southern and eastern regions of the Philippines (Vallejo 2011). Our findings corroborate the said pattern of distribution for the Astronieae, with increasing distribution as one goes from north to south and west to east, making central and eastern Mindanao island the center of distribution for the tribe (Mancera 2017). The tribe may be described then as low temperature- and/or precipitation seasonality-dependent, although wider sampling will improve its generalizability. Aside from the historically low sampling in the Palawan group of islands, the nearly complete absence of the Astronieae there (only *Astronia acuminatissima* var. *palawanensis* has been documented in the area) may be due to its extremely seasonal location, besides its complex tectonic history and long isolation from nearby landmasses (Esselstyn *et al.* 2010).
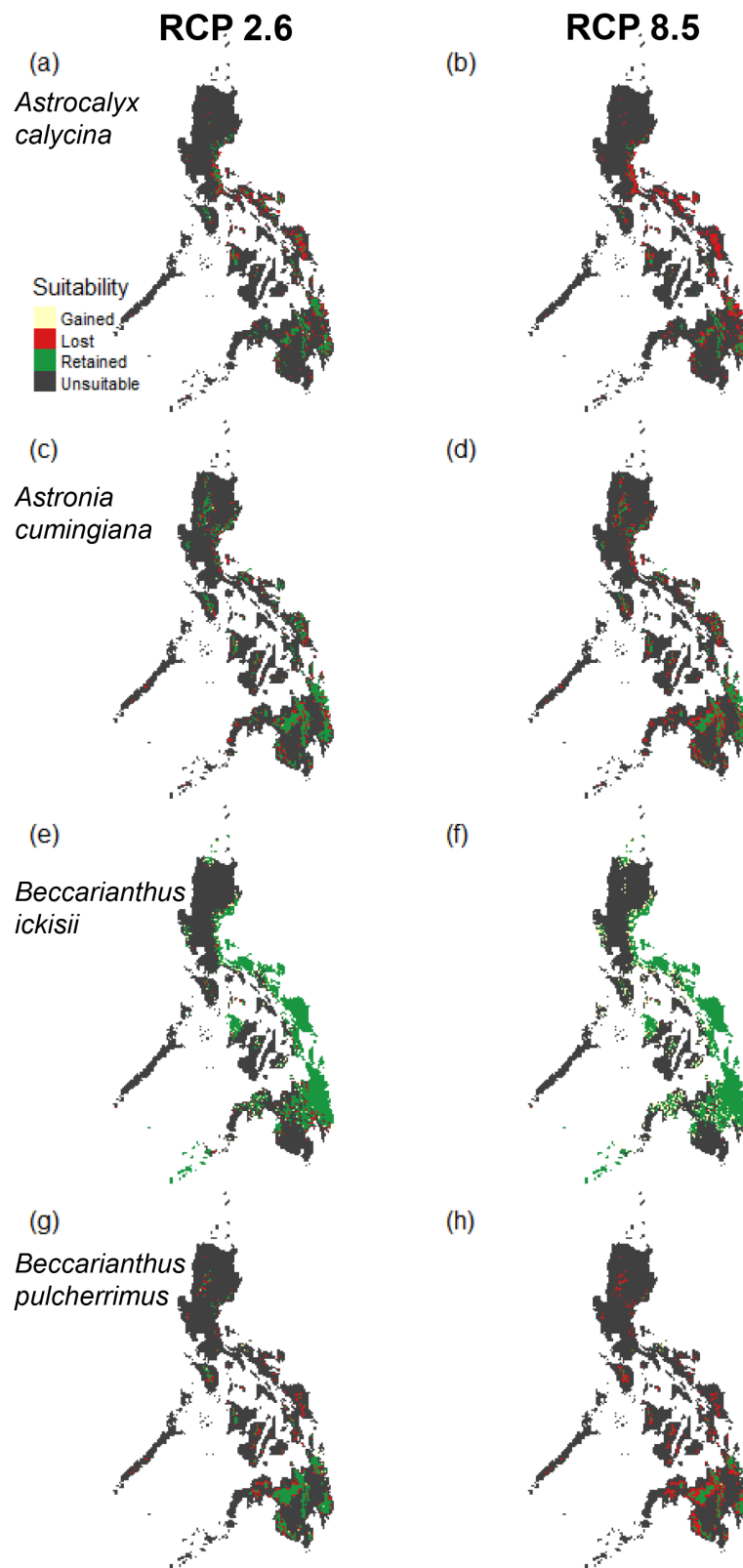
Figure 5. Niche gains and losses for each species under RCP2.6 (a, c, e, g) and RCP8.5 (b, d, f, h) scenarios during 2061–2080, derived from their current and future binary suitability maps.

Table 3. Land areas (x 10^4 sq.km) of suitable and unsuitable habitats, percentage of suitable habitats, and percentage of area gained or lost under different IPCC climate scenarios for each species in the Philippines.

Species	Climate scenario	Suitable areas (x 10^4 km²)	Unsuitable Areas (x 10^4 km²)	% suitable habitat in PHL	Gain/loss percentage
Astrocalyx calycina	Current	3.9	28.8	11.90	
	RCP2.6a	2.6	30.2	7.80	–4.1
	RCP2.6b	2.2	30.6	6.57	–5.3
	RCP8.5a	1.7	31.0	5.22	–6.7
	RCP8.5b	1.1	31.6	3.49	–8.4
Astronia cumingiana	Current	5.5	27.3	16.7	
	RCP2.6a	4.5	28.2	13.9	–2.8
	RCP2.6b	3.9	28.8	12.0	–4.7
	RCP8.5a	3.4	29.3	10.5	–6.1
	RCP8.5b	2.9	29.9	8.7	–8.0
Beccarianthus ickisii	Current	10.4	22.3	31.8	
	RCP2.6a	12.1	20.6	37.1	5.3
	RCP2.6b	10.7	22.0	32.7	0.9
	RCP8.5a	11.7	21.0	35.7	3.8
	RCP8.5b	12.8	20.0	39.0	7.2
Beccarianthus pulcherrimus	Current	4.2	28.5	12.9	
	RCP2.6a	3.1	29.6	9.4	–3.5
	RCP2.6b	3.0	29.7	9.2	–3.8
	RCP8.5a	2.2	30.5	6.8	–6.1
	RCP8.5b	1.5	31.2	4.7	–8.2

Table 4. ANOVA results for ordinary linear regression analysis testing whether mean altitude differs between climate scenarios across Astronieae species.

Species	n	Transformation	F-statistic	*p*-value	Adjusted R²
Astrocalyx calycina	5637	Square root	186.2	< 0.001	0.12
Astronia cumingiana	9944	Square root	17.19	< 0.001	0.01
Beccarianthus ickisii	27299	Cube root	0.62	0.64	0
Beccarianthus pulcherrimus	6924	Square root	46.04	< 0.001	0.03

Aside from providing potential explanations to observed distributions of species, environmental niche models also inform us of areas that may have been inadequately sampled or remain unexplored but actually have a high probability of finding populations of the rare species or their closest relatives (Bentlage *et al.* 2009). For instance, ancestral species may have established themselves a long time ago in shared, more extensive environments, which were more identical in the past, after which the subsequently radiating species evolved new characteristics and underwent niche differentiation to occupy new habitats (Swenson 2008). In the case of the Astronieae, in which *Astrocalyx calycina* is being proposed to be basally diverging, a cooler and wet ancestral niche could have probably been extensive in the country and conducive for the radiation of the tribe in the

past. Niche differentiation then occurred in crown groups that allowed *Astronia* and *Beccarianthus* to colonize warmer but still wet regions, as supported by the wider bioclimatic niche of *Astronia cumingiana* and *B. ickisii* depicted in the models. *B. pulcherrimus* – with its high-elevation range, as opposed to that of the congeneric *B. ickisii* – may very well be distinct from it not only morphologically (to the point that it was once named a different genus, *Everettia* Merr.) but also ecologically. In the case of *B. ickisii*, another proof of the high affinity of closest relatives to occupy the same niche is the resulting "overprediction areas" (Raxworthy *et al.* 2003) that may coincide with the habitat of its closest relatives from Borneo and New Guinea, which are *B. pulcher* Cogn. and *B. robustus* Nayar, respectively – both low-elevation species. Similarly, the consistent appearance
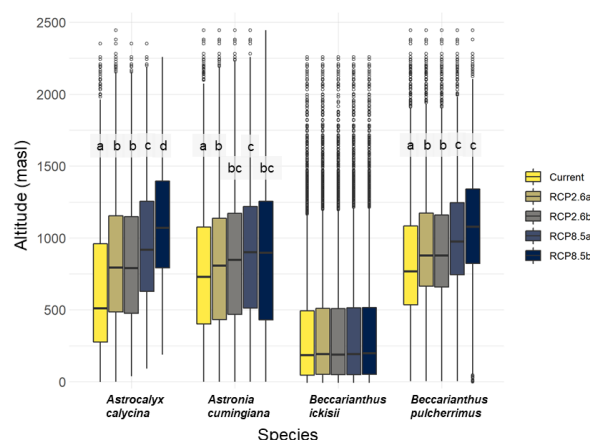
Figure 6. Differences in mean altitude between different climate scenarios across the four Astronieae species. Letters indicate non-significant differences between groups based on Tukey HSD pairwise tests ran separately for each species. Panels without letters indicate groups for which significant variation between groups was not detected (see Table 4 for ANOVA tests and adjusted R^2 values for models). Note that for each RCP, "a" refers to time step 2041–2060, and "b" refers to time step 2061–2080.

of suitable habitats for *Astrocalyx calycina*, *B. ickisii*, or *B. pulcherrimus* in northern Luzon, Mindoro, or Palawan islands – despite the non-occurrence of the species there – may be explained by the actual occurrence of a few species of *Astronia* in the northern Sierra Madre and Mindoro island and a lone species (a subspecies at that) in Palawan island. These all suggest that it will not be impossible to find more closely related but undescribed species from the suitable habitats that the niche models present despite the apparent lack of records there.

Contraction and Upward Migration of Melastome Tree Habitats are Chiefly Linked to Extreme Warming
Consistent with our hypothesis, the projections of suitable bioclimatic niches generally revealed narrowing and increasingly higher habitats for the Astronieae under the warmer climate scenarios, as temperature proved

to be essential in modeling their niches. Temperature is important in the development of flowering plants, especially in crucial reproductive processes and phenology. It affects events as intrinsic as floral anthesis and maturation, pollen germination, stigmatic receptivity, and seed germination to as extrinsic as availability of pollinators and dispersers, which then affect plant survival and distribution (Corlett and Lafrankie 1998; Hedhly *et al.* 2008; Chuine 2010). Temperature may also indirectly affect plant distribution by shaping the surrounding vegetation that may thrive and dominate, which themselves may serve as dispersal barriers for plants unadapted to such assemblages (Slik *et al.* 2011).

Astrocalyx calycina, *Astronia cumingiana*, and *B. pulcherrimus* have very narrow projected suitable areas due to their strong requirement of cooler temperature, which in the tropics is a function of altitude. The projected recession of their refugia under both RCP scenarios across time would then entail migration of the species to much higher elevations (van Zonneveld *et al.* 2009; Feeley 2011; Hsu *et al.* 2011; Snelder *et al.* 2013), a potential adaptation that is supported by our altitude analysis. However, besides low temperature, *Astronia cumingiana* also has a relatively high consideration for precipitation which may explain its relatively wider bioclimatic niche than *Astrocalyx calycina* and *B. pulcherrimus*. Nevertheless, all three species are anticipated to adapt to climate change by migrating upward, a direct response to extreme warming.

It must be noted, however, that the success of species migration depends largely on habitat connectivity and dispersal ability as much as on bioclimatic factors. Habitat fragmentation and weak dispersal capacity both decrease genetic diversity by impeding gene flow between isolated populations and prevent adaptive evolution by promoting inbreeding (Engler *et al.* 2009; Leimu *et al.* 2010). The establishment of biodiversity corridors will then be essential in connecting fragmented habitats and in aiding pollen and seed dispersal, thereby enhancing the flow of genes, especially climate-adaptive ones (Christmas *et al.* 2016). While wider sampling and comprehensive assessment of the status of populations of

Table 5. Protected area assessment results showing number of points within PA boundaries, area of suitable habitats under current climate (x 10^4 km^2) and the percentage of suitable habitats protected under present protected area boundaries.

Species	No. of species points inside PA / total no. of points	Suitable habitat inside PA (x 10^4 km^2)	Total area of suitable habitat (x 10^4 km^2)	Suitable habitat protected (%)
Astrocalyx calycina	8/18	1.06	3.89	27.1
Astronia cumingiana	2/12	1.28	5.46	23.5
Beccarianthus ickisii	2/9	1.26	10.42	12.1
Beccarianthus pulcherrimus	10/18	1.05	4.22	24.8

the Astronieae have yet to be conducted, their absence in many collections from expeditions within the past decade – coupled by the unchecked land use changes in many of its historical localities – decreases the chance that this upward migration will be realized. This is where *in situ* conservation, seed banking, and subsequently, assisted migration, may become vital to ensure the successful adaptation of climate-vulnerable species.

For the endangered *Astrocalyx calycina*, upward migration means the reduction of actual observed habitats in the Bicol peninsula and Samar island and total extirpation of potentially suitable habitats in northern Luzon, Zambales mountain range, and Marinduque province. For the vulnerable *B. pulcherrimus*, massive habitat declines in the original localities in the Bicol peninsula and the islands of Catanduanes, Negros, and Leyte await, coupled with the drastic reduction of potentially suitable habitats in virtually all islands, especially in Luzon and the Visayan group. For *Astronia cumingiana*, while contraction is the most severe effect projected in both observed occurrence and potentially suitable areas, it is still massive at 50% decline, an alarming area reduction for the most common yet sparsely distributed species in the tribe.

Finally, Mindanao island – with its widest suitable habitat area for all three species regardless of severe climate scenarios and time steps – is reinforced as the last frontier in the country that needs a more comprehensive and aggressive conservation plan. Observations from nationwide botanical expeditions in the past decade by the first author already show the decline in abundance of *B. pulcherrimus* and virtual loss of *Astrocalyx calycina* in their historical occurrence sites in Luzon and Visayan islands.

Expansion of Suitable Habitat May Not Guarantee Survival and Proliferation
However, we also saw that precipitation could potentially counter habitat shrinkage if a species is more reliant on this parameter. *Beccarianthus ickisii*, whose habitat suitability model depends more on annual precipitation and precipitation of the coldest quarter, was projected to possess the widest probability occurrence, notably in the everwet eastern track of the country. Moreover, the least contributing bioclimatic variable to its distribution appears to be mean annual temperature, opposite to that of the other species. This could be attributed to the fact that the realized elevation range for the species is 150–927 masl, one of the lowest typical species ranges in the tribe (Mancera 2017). Closest relatives of *B. ickisii* in Borneo (*B. pulcher*, *Purseglove 5108*, L!) and West Papua (*B. robustus* Nayar, *Kalkman BW 6260*, L!) were recorded at even lower elevations, with 92 and 10 masl, respectively. Since the climate scenarios predict extreme increases in

rainfall, *B. ickisii* is anticipated to largely retain its suitable habitat, regardless of any increase in warming.

Few gains in the projected suitable areas for *B. ickisii* based on the bioclimatic niche – however, while optimistic – may be difficult to attain in reality, especially for such species with limited dispersal capacity and specialized flowers (Struebig *et al.* 2008; Reginato *et al.* 2020). The Astronieae, with capsular fruits, are abiotically dispersed, which means open and consistently, sufficiently, or at least seasonally dry habitats are essential for propagation (Renner 1989; Correa *et al.* 2015; Chen *et al.* 2017). *B. ickisii*, aside from bearing dry capsules that rely on wind for seed dispersal, has also been observed in the field as being visited by sunbirds, the curved beak of which may be correlated with the brightly colored, pseudocampanulate, erect corolla of the species, potentially representing one of the rare pollination syndromes in the family. Highly specialized pollination syndromes require that the pollinators co-exist with the plant for assured survival and proliferation. With increased warming coupled with anthropogenic pressure in the remaining lowland forests in the country, *B. ickisii* may not necessarily thrive as much as its distribution models show. Nevertheless, wider and more comprehensive sampling is necessary to improve the projection for very rarely collected species such as *B. ickisii*.

Many Melastome Trees are Outside Protected Areas, Especially in Mindanao
Our map showing the occurrences of the Astronieae species *vis-à-vis* current protected areas in the country validates our hypothesis that the current boundaries are insufficient to cover both their occurrences and projected suitable habitats, a finding that warrants a revisit of the country's protected area systems. In Luzon, the regions of southern Sierra Madre and northern Bicol peninsula – which are type localities for most of the species – need an expansion of their protected areas. In the Visayas, the islands of Panay, Negros, Leyte, and Samar need attention for the protection of all threatened species, *Astrocalyx calycina*, *B. ickisii*, and *B. pulcherrimus*. The same is true for Mindanao, with several occurrences just outside already established protected areas in Caraga, Mt. Kitanglad and Mt. Apo Natural Parks, and northwestern Mindanao. The central cordillera of the island, the Pantaron mountain range, serves as the home of *Astrocalyx calycina* and *B. ickisii*, yet no areas here have been declared as protected.

Expansion of protected areas is important not only to conserve observed distributions of rare species but also to promote ecological connectivity between increasingly fragmented habitats and establish buffer zones against climate change or social fence against anthropogenic pressures (Garcia *et al.* 2013; Snelder *et al.* 2013;

De Alban *et al.* 2015). The need for a climate-smart reformulation of protected areas and habitat restoration in the Philippines has already been suggested (De Alban *et al.* 2015) and our findings corroborate that. For instance, De Alban *et al.* (2015) also recommended for protected area expansion in the Pantaron mountain range, which they deem as a high conservation value area north of Mt. Apo. Finally, the expansion of protected areas should include lowland forests, which must be given equal priority (Slik *et al.* 2011), especially to ensure that the projected expansion of suitable habitat for the low-elevation *B. ickisii* is realized despite higher anthropogenic pressures. For instance, the protected area system in the Philippines remains to be elevation-dependent, with areas above 1000 masl typically making up the core zones that are governed by stricter rules, compared to buffer areas below that may very well be classified as key biodiversity areas but remain open access for human activities (Mallari *et al.* 2016). Expansion of protected areas will also entail broadening networks and strengthening programs with indigenous people and farmers who are the major stakeholders in these rare species-rich areas, as well as local government units and civil society organizations, for a more collective and sustainable conservation effort.

Our Response to Intensified Climate Change is More Vigorous Research and Action
As with other rare species, especially narrowly endemic and threatened ones, there is a need to increase occurrence points to further boost the training and predictive power of species distribution modeling. This can be done by more rigorous expeditions throughout the archipelago, which has mostly been stalled since the beginning of the 21st century. Simultaneously, despite our efforts in georeferencing old collections of the Astronieae species for occurrence data, over a hundred herbarium collections of other species in the tribe await similar geolocation efforts. This entails surveying old taxonomic accounts to trace actual historical collection sites, as well as integrating present observations on the ground. Ground-truthing then becomes important not only in proving the predictions presented in this study but also in obtaining more information about the specific habitat and general ecology of the members of the tribe. Not only will these improve future species distribution models for the tribe, it also allows seamless sharing of ecological and biogeographic information among researchers doing global studies (Ramos *et al.* 2012).

While bioclimatic factors are integral to understanding species distribution especially in climate-diverse regions like Malesia and the Philippines, other equally important factors such as soil, topographic, biotic, and anthropogenic data need to be incorporated in future species distribution models of the Astronieae. At a time when deforestation, land use conversion, extinction of pollinators and dispersers, and unchecked urbanization are simultaneously happening with climate change, multivariable niche modeling becomes a standard (Lasco *et al.* 2012; Snelder *et al.* 2013). This way, the extent to which other environmental factors drive diversity loss in the country may be measured and targeted for mitigation as early and accurately as possible.

Finally, our findings – coupled with the latest floristic surveys on the ground – show the dire need to reassess the conservation status of Philippine native trees, especially those that are endemic and threatened. Despite being reported as endangered in 2008, *B. ickisii* and *B. pulcherrimus* were later demoted to vulnerable (DENR 2017) despite the alarming results of ground-truthing. More importantly, despite the national red listing in 2017 – which has been recognized by the Botanic Gardens Conservation International – neither *Astrocalyx calycina*, *B. ickisii,* nor *B. pulcherrimus* has been listed yet by the International Union for Conservation of Nature in their Red List of Species. While a systematic global red list assessment for the species is underway, preliminary geographic data and analyses in this study may be used for more comprehensive ecological and conservation studies, which will – in turn – better inform future environmental niche modeling and actual conservation strategies for the species.

CONCLUSION

Environmental niche models showed reduction and upward movement of suitable habitats for the Philippine-endemic (*Astronia cumingiana*) and threatened (*Astrocalyx calycina* and *Beccarianthus pulcherrimus*) melastome trees for the next 60 years under both moderate and extreme climate change scenarios due to projected higher temperatures. Increasing rainfall, however, could potentially retain suitable habitats for one threatened species (*B. ickisii*). The intersection of current habitat niches of all species increases eastward and southward of the archipelago, pointing to Mindanao island as the center of suitability for the Astronieae. However, the protected area coverage in the region is presently insufficient, and we propose the expansion and adaptation of climate-smart strategies to ensure species conservation. Parallel environmental niche modeling that adds biophysical and anthropogenic parameters on the same set of species, as well as confirmation of habitat presence on the ground, is further recommended.

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STATEMENT ON CONFLICT OF INTEREST

The authors have no conflict of interest.

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