What explains the high island endemicity of Philippine *Rafflesia*? A species distribution modeling analysis of three threatened parasitic plant species and their hosts.

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Manuscript received _____; revision accepted _____.

Running head: Distribution modeling of three Philippine *Rafflesia* species

ABSTRACT

Premise: *Rafflesia* are rare holoparasitic plants. In the Philippines, all but one species are found only on single islands. This study aimed to better understand the factors contributing to this distribution pattern. Specifically, we sought to determine whether narrow environmental tolerances of host and/or parasite species might explain their island endemicity, or, instead or in addition, the limited distribution of *Rafflesia* species is the result of a narrow overlap between the environmental requirements of host and parasite.

Methods: We used Maxent species distribution modeling to identify areas with suitable habitat for *R. lagascae*, *R. lobata*, and *R. speciosa* and their *Tetrastigma* host species. These analyses were carried out for current climate conditions as well as two future climate change scenarios.

Key results: Whereas species distribution models indicated suitable environmental conditions for the *Tetrastigma* host species in many parts of the Philippines, considerably fewer areas have suitable conditions for the three *Rafflesia* species. Some of these areas are found on islands from which they have not been reported. All three species will face significant threats as a result of climate change. For *R. lagascae* and *R. lobata*, these may include a loss of suitable area as a result of changes to the distribution of their host species.

Conclusions: Our results suggest that limited inter-island dispersal abilities and/or specific environmental requirements are likely responsible for the current pattern of island endemicity of the three *Rafflesia* species, rather than the environmental requirements of their *Tetrastigma* host species.

Keywords

Climate change; conservation; Maxent; parasitic plant; Philippines; *Rafflesia*; Rafflesiaceae; species distribution modeling; *Tetrastigma*, Vitaceae.

Parasitic plants are considered particularly vulnerable to the effects of habitat destruction and climate change due to their obligate dependence on their host plants (Mkala et al., 2022). Yet, little attention has thus far been given to examining how their distribution ranges and those of their hosts might change under different climate change scenarios (Zamora and Mellado, 2019; Cai et al., 2022; Mkala et al., 2022; Renjana et al., 2022). This might be a result of the negative stereotype associated with parasitism, especially for species that are, correctly or incorrectly, considered noxious weeds (Costea and Stefanović, 2009), but there are also other reasons. Accurately predicting distribution ranges is challenging for parasitic species for which host specificity information is sparse, because the distribution of parasites is limited by the geographic distribution and ecosystem requirements of their hosts (Costea and Stefanović, 2009; Cai et al., 2022). These same factors complicate effective conservation management of parasitic plants.

The Philippines is one of the centers of biodiversity of *Rafflesia* R.Br. (Brown, 1821; Rafflesiaceae), a Southeast Asian genus of obligate endo-holoparasitic plants growing in primary and secondary rain forests (Meijer, 1997; Nais, 2001; Barcelona et al., 2009). The Philippine archipelago is home to at least 13 of the 31 to 39 *Rafflesia* species currently recognized (Nickrent, 1997 onwards; Pelser et al. 2011 onwards; Galindon et al., 2016; Pelser et al., 2019; Siti-Munirah et al., 2021). Twelve of these are each only found on a single island. The only exception is *R. speciosa* Barcelona and Fernando (2002), which grows on Panay as well as on the nearby island of Negros (Pelser et al., 2019). Although *Rafflesia* are found in various parts of the Philippines, they are notably absent from many islands, including the sizable islands of Bohol, Cebu, Leyte, Mindoro, and Palawan (Fig. 1; Pelser et al., 2011 onwards). It is presently unclear why *Rafflesia* is not known from these islands. Perhaps they are present but remain to be discovered? Because they are endoparasites,

67 *Rafflesia* plants can easily remain undetected when they are not in a reproductive state (e.g.,
68 Barcelona et al., 2007; Pelser et al., 2016; Renjana et al., 2022). However, it is also possible
69 that their absence is a result of local extinction. This is plausible, because most Philippine
70 *Rafflesia* species are only known from very few populations (Pelser et al., 2016, 2018) and
71 even populations of species that are relatively common and widespread are often small and
72 geographically and genetically isolated from each other (Pelser et al., 2017, 2018). Such
73 populations may therefore be particularly vulnerable to habitat loss, degradation and
74 fragmentation, which have impacted much of the natural forest ecosystems to which *Rafflesia*
75 are confined (Mittermeier et al., 1998; Ong et al., 2002; Chokkalingam et al., 2006; Laurance,
76 2007; Barcelona et al., 2009).
77
78 Pelser et al. (2019) suggested that if the high island endemism of *Rafflesia* is not a
79 result of island-level extinction or a gap in our knowledge of their current distribution, it
80 might be a result of poor inter-island dispersal ability, because the results of their molecular
81 phylogenetic and biogeographic analyses indicate that dispersal of Philippine *Rafflesia*
82 between islands has been relatively uncommon in their evolutionary history. Ants might be
83 the primary seed dispersers of *Rafflesia* (Pelser et al., 2013, 2018). Because ants typically do
84 not transport seeds further than 10–80 m (Gómez and Espadaler, 1998; Vittoz and Engler,
85 2008) and it can be assumed that large bodies of water are a significant barrier for
86 myrmecochory, *Rafflesia* seeds might only be very rarely dispersed between islands.
87
88 It has been considered less likely that the absence of *Rafflesia* on some islands in the
89 Philippines is due to the absence of suitable host species. Although *Rafflesia* species have
90 only been observed to parasitize *Tetrastigma* (Miq.) Planch. (Planchon, 1887; Vitaceae)
91 (Meijer, 1997; Nais, 2001; Pelser et al., 2016) and previous research suggests that Philippine

92 *Rafflesia* might even display some level of host specificity or host preference at the species
93 level, their reported hosts appear to be common and widespread in the Philippines (Pelser et
94 al., 2016). Detailed information about the distribution and environmental requirements of
95 these host species is however not currently available, because *Tetrastigma* are difficult to
96 identify to species level due to their morphological plasticity and dioecious life history
97 strategy (Pelser et al., 2016). Furthermore, specimens with reproductive parts (which can
98 greatly assist species identification) can be difficult to detect in dense forest canopies and are
99 therefore seldom collected (Obico et al., 2021; Renjana et al., 2022).
100
101 *Rafflesia* species are not only strikingly absent from several large islands in the
102 Philippines, but also from some areas within islands from which they have been reported
103 (Pelser et al., 2018). These include areas that still have primary or relatively intact secondary
104 forests and are within the elevational range throughout which *Rafflesia* have been found (i.e.,
105 c. 50–1380 m.a.s.l.; Barcelona et al., 2011; Pelser et al., 2018). For example, *Rafflesia* grow
106 throughout the Central Panay Mountain Range (CPMR; Galang, 2009; Pelser et al., 2018),
107 but they have never been reported from the forests of the nearby Northwest Panay Peninsula
108 Natural Park (Fig. 1). Such observations and the disjunct distribution of populations of other
109 Philippine *Rafflesia* species (e.g., Pelser et al., 2017) perhaps indicate that they have
110 environmental requirements that are more specific than currently assumed (e.g., Pelser et al.,
111 2018) or understood. Alternatively, or in addition to this, *Rafflesia* might not only disperse
112 poorly between islands but also within islands, as could be inferred from studies that
113 demonstrate strong genetic substructure within populations (Barkman et al., 2017) and poor
114 genetic connectivity among populations that are more than c. 20 km away from each other
115 (Pelser et al., 2018).
116

117 Here, we explore the hypothesis that Philippine *Rafflesia* species are range-restricted
118 because of narrow environmental tolerances; either their innate tolerances or those of their
119 *Tetrastigma* host species, or as a consequence of a narrow overlap between the environmental
120 amplitudes of parasite and host. We tested this hypothesis for three species of *Rafflesia* (*R.*
121 *lagascae* Blanco (1845), *R. lobata* Galang and Madulid (2006), *R. speciosa*; Fig. 2) and their
122 *Tetrastigma* hosts using a species distribution modeling approach. A better understanding of
123 differences between the observed and potential distribution patterns of *Rafflesia* species can
124 inform their conservation management by identifying areas that have environmental
125 conditions suitable for both parasite and host and that should therefore be prioritized when
126 developing protected area networks (Ancheta et al., 2021; Renjana et al., 2022). Because of
127 the potential negative impact of climate change on plant life (Kelly and Goulden, 2008), we
128 further aim to contribute to the conservation of these three *Rafflesia* species by investigating
129 projected future distribution patterns under two different climate change scenarios.

130 **MATERIALS AND METHODS**

131

132 ***Study species and distribution data—***

133

134 *Rafflesia lagascae* is the most common *Rafflesia* species in the Philippines. It has the
135 largest distribution area as well as the largest number of populations. *Rafflesia lagascae* is
136 endemic to Luzon and grows from its northernmost provinces to the Bicol Peninsula in the
137 south of the island (Fig. 1). It has a highly disjunct distribution pattern and most of the 11
138 populations that were included in a previous conservation genetic study showed poor genetic
139 connectivity with other populations (Pelser et al., 2017). *Rafflesia lagascae* has been
140 observed as a parasite of three *Tetrastigma* species: *T. ellipticum* Merr. (Merrill, 1916) s.l., *T.*

141 *loheri* Gagnep. (Gagnepain, 1910), and *Tetrastigma* sp. A (sensu Pelser et al., 2016). All
142 three are assumed to have a wide distribution area in the Philippines, because they have been
143 reported from all three regions of the Philippines: Luzon, Mindanao, and Visayas (Fig. 1). In
144 addition to the *R. lagascae* populations referred to above, one other population (Mt. Labo in
145 the Bicol Peninsula) has been identified as belonging to *R. lagascae*. Although the plants are
146 morphologically similar to those of other populations and were resolved as closely related to
147 them in a molecular phylogenetic study (Pelser et al., 2019), they are genetically distinct and
148 may represent a cryptic species (Pelser et al., 2017). We therefore excluded locality records
149 from the Mt. Labo population from the analyses included in the present study.
150
151 *Rafflesia speciosa* has a much smaller distribution area than *R. lagascae*, but is locally
152 common in the two areas from which it is known: the CPMR of the island of Panay and Mt.
153 Kanlaon on Negros (Fig. 1). Pelser et al. (2018) observed little genetic structure among
154 CPMR populations but substantial genetic differentiation between CPMR and the single
155 population known from Negros. *Tetrastigma harmandii* Planch. (Planchon 1887) and *T.* cf.
156 *magnum* Merr. (Merrill, 1916; sensu Pelser et al., 2016) are the only known host species of *R.*
157 *speciosa*. Like the aforementioned *Tetrastigma* hosts of *R. lagascae*, these two species have
158 been found in Luzon, Mindanao and the Visayas.
159
160 *Rafflesia lobata* is much rarer than *R. lagascae* and *R. speciosa*. It is restricted to the
161 CPMR (Fig. 1) where it is only known from five populations, of which the southernmost
162 three are possibly very small because we only observed one or two host plants for each.
163 However, the two northernmost populations are comparatively large. Unpublished estimates
164 of genetic connectivity among these populations using microsatellite data suggest limited
165 gene flow between these two northern populations and the others (J. F. Barcelona and P. B.

166 Pelser, unpublished data). *Rafflesia lobata* is sympatric with *R. speciosa* in a part of its
167 known distribution area, but has a non-overlapping host range. However, its host species are
168 the same as those of *R. lagascae*: *T. ellipticum* s.l., *T. loheri*, and *Tetrastigma* sp. A.
169
170 We recorded all occurrence points of these *Rafflesia* species and their *Tetrastigma*
171 host species using Garmin GPS units. Duplicates were removed and spatial thinning was
172 implemented to retain only one occurrence point in every 30 arcsecond grid cell (equivalent
173 to ~1 km^2 at the equator) to avoid spatial sampling bias. This resulted to 36 data points for *R.*
174 *lagascae*, 6 for *R. lobata*, 40 for *R. speciosa*, 12 for *T. ellipticum*, 24 for *T. harmandii*, 79 for
175 *T. loheri*, 47 for *T.* cf. *magnum*, and 14 for *Tetrastigma* sp. A.
176
177
178 **Rafflesia *distribution modeling approaches*—**
179
180 Two approaches were used to model the distribution of the three *Rafflesia* species. In
181 the first approach (A1), species distribution models (SDMs) were built for each *Rafflesia*
182 species using only their occurrence points. However, because *Rafflesia* plants cannot survive
183 without their host plants, we also used a second approach (A2) in which SDMs for each
184 *Rafflesia* species and its specific *Tetrastigma* hosts were built separately and only those grid
185 cells where each *Rafflesia* species and at least one of its respective *Tetrastigma* hosts were
186 projected to co-occur were considered suitable areas for the parasite. The predicted suitable
187 areas resulting from both approaches were compared to determine for each *Rafflesia* species
188 if the environmental niche of its hosts is a limiting factor for its distribution.
189

The areas of co-occurrence between parasite and host SDMs in A2 were determined by adding the two SDM rasters of the parasite and the host using a raster calculator in the *raster* package (Hijmans, 2021) in R (R Core Team, 2021). To compare the suitable areas predicted by the two approaches (i.e., A1 and A2), the following three niche overlap metrics in the *ENMTools* package (Warren and Dinnage, 2022) were computed: Geographic Range Overlap, which indicates the percentage of overlapping areas between the two approaches (Fitzpatrick and Turelli, 2006), and two niche overlap indices, Schoener's D and Hellinger's I, which indicate the probability of two species being present together in the same location (Warren et al., 2008). For this comparison, the resulting niche ranges from the approaches were analyzed as two different "species". For all three metrics, a score of 0 means no niche overlap, while a score of 1 means complete overlap.

Environmental variables—

Climate affects plant growth (Schimper, 1902), and the impacts of this become especially observable under the current accelerated climate change (Kelly and Goulden, 2008). However, edaphic factors also affect plant distribution (Witkamp, 1971) and should therefore also be included in SDMs to assess whether potential changes in distribution are constrained by soil properties (Corlett and Tomlinson, 2020). To model the current distribution of *Rafflesia* and their hosts, both bioclimatic and soil variables were thus obtained from the CHELSA version 1.2 (Karger et al., 2017, 2018; https://chelsa-climate.org/bioclim/) and SoilGrids (Poggio et al., 2021; https://soilgrids.org/) databases, respectively. Pearson's correlation analyses were separately performed on the bioclimatic and soil variables to identify and exclude highly correlated ($|r| > 0.7$) variables (Pang et al., 2021). The bioclimatic variables retained were mean annual air temperature (MAT; bio1),

temperature seasonality (TS; bio4), annual precipitation (AP; bio12), precipitation seasonality (PS; bio15), and precipitation of the coldest quarter (PCQ; bio19), while the soil variables included bulk density, cation exchange capacity, soil pH, %clay, %silt, and %sand.

To constrain species modeling to the Philippines, bioclimatic and soil variables were cropped from the available global extent rasters using a shapefile of the Philippine archipelago. Soil variables were also resampled from their original 250 m resolution to 30" using bilinear interpolation to make them compatible with the original resolution of the bioclimatic variables. All geoprocessing was implemented using the *raster* package in R.

Species distribution modeling—

Species distribution models were generated for each individual *Rafflesia* and *Tetrastigma* species using Maxent (Phillips et al., 2006) implemented via the *dismo* package in R (Hijmans et al., 2020). For each species, six bootstrap replicates were run, and the jackknife setting was activated to determine individual variable contributions. This number is the lowest number of occurrences for any of the species included in our study (i.e., *R. lobata*). This is similar to the approach used by Banag et al. (2015). Earlier test runs which had more than six replicates did not improve model results significantly. The feature classes (FC) and regularization multipliers (RM) for each species were determined using the ENMevaluate() function of the *ENMeval* package in R (Kass et al., 2021). *ENMeval* examines a series of models across a range of settings for the FC and RM, and provides evaluation metrics to characterize model performance (Kass et al., 2021). In this study, the *ENMeval* analyses followed cross-validating model approaches by Pang et al. (2021): if species occurrence

points were fewer or equal to 25, the 'jackknife' method was used; beyond 25, the 'block' method was applied. For each species, models with different combinations of FC (i.e., L, H, LQ, LQH, LQHP, and LQHPT; where L = linear, H = hinge, Q = quadratic, P = product, and T= threshold) and RMs (1 to 5, in increments of 0.5) were tested. A background of 10,000 points was used for all *Rafflesia* and *Tetrastigma* species. The model setting with the lowest *delta.AICc* value was ultimately selected as the most optimal.

Except for *T. harmandii* and *T. loheri*, the first set of SDMs generated contained some environmental variables with zero contribution. To further optimize the models, these variables were subsequently excluded, and Maxent analysis was repeated with only the remaining environmental variables and a different set of FC and RM. See Appendix S1in Supplemental Data with this article for the Maxent settings used for each species. For the final SDMs, all five bioclimatic and soil variables were used, except for *R. lobata,* where only MAT and AP were retained.

To assess the reliability of the models, each SDM was evaluated using the Area Under the Curve (AUC) (Bradley, 1997) and the True Skill Statistic (TSS) (Allouche, 2006). Models were considered acceptable if they had both an AUC > 0.7 (Mandrekar, 2010) and a TSS value > 0.4 (Landis and Koch, 1977). Acceptable models were used to project the current and future species distributions onto space using the predict() function in *dismo*. The resulting continuous habitat suitability maps were then converted into binary maps using the minimum presence threshold (MPT) to distinguish areas with 'suitable' from those with 'unsuitable' habitat. The MPT, which was derived on the assumption that the least suitable habitat at which a species is known to occur is the species occurrence point with the lowest

habitat suitability score (Pearson, 2007), ensures that all the *Rafflesia* and *Tetrastigma* species occurrence points are included in the projected suitable habitats for each species.

An unsuitability mask layer was created using a consensus land cover dataset generated by Tuanmu and Jetz (2014) to exclude areas without habitat that is assumed to be suitable for *Rafflesia*. The consensus land cover map that was used for this purpose is an integration of four land cover products (i.e., GlobCover, MODIS2005, GLC2000, DISCover) and was reported to have an improved ability to capture fine grain land cover data and accurately detect the presence of every class (Tuanmu and Jetz, 2014). Three land cover class layers that were considered unsuitable for *Rafflesia*, namely class 7 (cultivated and managed vegetation), class 9 (urban/built-up areas), and class 11 (barren land), were obtained from EarthEnv (https://www.earthenv.org/landcover; accessed on 14 June 2022) at 30" resolution (Tuanmu and Jetz, 2014). To ensure occurrence points of *Rafflesia* and *Tetrastigma* species are not found within the boundaries of the unsuitable mask layer, the consensus prevalence, which is a measure of the overall agreement of the integrated land products, was set to 100% for the three classes to completely exclude pixels classified under them. Furthermore, a raster file of the occurrence points of *Rafflesia* and *Tetrastigma* species was subtracted from the class 7 layer to exclude pixels that were classified as cultivated and managed vegetation, but were otherwise observed in the field as actual habitats for our species. The three land cover layers were then combined to generate the unsuitable mask layer, which was then applied onto the resulting species SDMs.

The percentages of suitable areas of each *Rafflesia* and *Tetrastigma* species in the Philippines were computed using the following formula: number of pixels classified as 'suitable' divided by the total number of pixels in the whole extent x 100. For the *Rafflesia*

species, we also calculated the percentage of suitable area for each island (*R. lagascae, R. lobata*) or islands (*R. speciosa*) on which their presence has been confirmed in previous studies (hereafter referred to as 'native island range'; Pelser et al., 2019).

To observe niche differences among *Rafflesia* species, bioclimatic and soil values at predicted suitable areas were extracted per species using the extract() function of the *raster* package and displayed in box-and-whisker plots for native island ranges and the entire country.

Future projections and change detection analyses—

To ascertain the potential impact of climate change on species distributions, the future projections of the bioclimatic variables under two representative concentration pathways (RCPs), RCP 4.5 and RCP 8.5 for the years 2061–2080, were also obtained from CHELSA. The two RCPs represent the moderate and highest greenhouse gas emissions scenarios, respectively, according to the CMIP5 projections (van Vuuren et al., 2011). Three CMIP5 Earth System Models (ESMs) from CHELSA were used: CNRM-CM5, GFDL-CM3, and MPI-ESM-LR. These ESMs were reported to satisfactorily estimate Southeast Asian climate (McSweeney et al., 2015; Kamworapan and Surussavadee, 2019). The resulting SDMs from each ESM were averaged for each RCP scenario. Gain-loss statistics between current and future projections were then computed for each species using the Semi-automated Classification Plugin Tool in QGIS (Congedo, 2021). Grid cells that changed from unsuitable to suitable were counted as 'gains', while those that switched from suitable to unsuitable

were recorded as ‘losses’. Cells that did not change were marked ‘stable’. Calculations were performed for both the native island ranges and the entire Philippines.

Suitable plant habitats have been found to shift to higher elevation as a result of global warming (e.g., Kelly and Goulden, 2008; Mancera and Lapuz, 2020). To detect such changes for our *Rafflesia* species under future climate scenarios, linear regression analyses were conducted between each species’ suitable habitat for each climate scenario and their respective elevations. We limited this analysis to the native island range since we are interested in potential changes to existing *Rafflesia* habitats. The projected suitable habitat rasters for each species were first converted from raster to occurrence point data using the as.data.frame() function in the *raster* package. These were then used to extract elevation data from the SRTM 90m Digital Elevation Data ver. 4.1 available from CGIAR-CSI (Jarvis et al., 2008; accessed on 5 Sep 2022) using the extract() function. The linear regression function lm() in the *stats* package in R was used separately for each *Rafflesia* species, with climate scenario and elevation (transformed to square root for normality) as the predictor and response variables, respectively. The p-values between groups were tested for significance using ANOVA type II, followed by Tukey’s HSD adjusted pairwise tests.

Protected area gap analysis—

Lastly, suitable habitat area measurements were performed for each *Rafflesia* species to assess the protection that they receive under existing conservation regimes within their native island ranges. Protected Area boundary polygons for the Philippines were downloaded from the World Database on Protected Areas (UNEP-WCMC and IUCN, 2023). The

polygons were clipped to restrict them to the native island range of each species, then overlaid on top of the suitable habitat rasters modeled under current conditions and future climate scenarios. The suitable habitat areas within and outside the polygons were measured for each climate scenario. The workflow utilized the *raster* and *tidyverse* (Wickham et al., 2019) packages in R.

RESULTS

Model accuracy and comparative analyses of modeling approaches—

All species models for *Tetrastigma* and *Rafflesia* obtained acceptable average training AUC and TSS scores (Appendix S2). For *Tetrastigma* species, average training AUC scores ranged from 0.876–0.979, and average TSS scores ranged from 0.477–0.713. For *Rafflesia*, AUC values ranged from 0.970–0.997, and TSS scores ranged from 0.840–0.966. All species models were therefore considered for further analyses.

The comparative analyses between two modeling approaches (A1 and A2) for the three *Rafflesia* species using three niche overlap metrics for current climate conditions showed index values from 0.88–1.00 suggesting high congruence between A1 and A2 for all three species (Table 1). Consequently, analyses using either of the two approaches produced similar results, and we therefore used A1 for all subsequent analyses, except where explicitly mentioned.

361 ***Species distributions under current climate—***

362

363 Tetrastigma *hosts*—

364

365 Because *Tetrastigma ellipticum, T. loheri*, and *Tetrastigma* sp. A are parasitized by *R.*
366 *lobata* and *R. lagascae*, while *T. harmandii* and *T. magnum* are parasitized by *R. speciosa*,
367 the combined predicted suitable areas of each of these two host groups are presented
368 separately. For both groups of *Tetrastigma* hosts, a large number of grid cells all over the
369 Philippines were predicted to have suitable habitat (Fig. 3).

370

371 Rafflesia *species*—

372

373 Areas that are predicted to have suitable habitat for *R. lagascae* were found on several
374 small and large islands in the Philippines, but mostly in the Luzon and central Visayas
375 regions (Figs. 1 and 4). They cover 12.9% of the Philippine land area (Table 2). The largest
376 portions of suitable habitat were found on mainland Luzon where its known populations are
377 found. These represent 32.1% of the Luzon mainland area, and are concentrated in the
378 island's main mountain regions. Suitable habitat for *R. speciosa* was found in Negros and
379 Panay, and in small areas in Calamianes and Mindoro (Figs. 1 and 5). The largest area with
380 suitable habitat is on Panay Island. The suitable area covers 8.1% of Panay and Negros,
381 which are the two islands from which *R. speciosa* has been reported. In total, only 0.7% of
382 the Philippines provides suitable habitat for this species (Table 2). Areas with suitable habitat
383 for *R. lobata* can be found on large and small islands across the Luzon, Visayas, and
384 Mindanao regions (Figs. 1 and 6), and these cover 5.9% of the Philippines. On Panay Island

where *R. lobata* is an endemic species, the suitable habitat covers 7.7% of the island and is mostly located in the CPMR.

***Environmental requirements of* Rafflesia *species*—**

The most important contributing variables to the SDM of *R. lagascae* were climate variables, of which mean annual temperature contributed most to the model (45.5%) (Appendix S3). Soil pH had a contribution of 11%. The climate variables were also the top contributors to the model for *R. speciosa* and had a total contribution of 87% with precipitation seasonality as the highest contributor (23%). The soil variables had a relatively low contribution of only 13% (Appendix S3). The prediction of the suitable habitat for *R. lobata* was only based on the contribution of two climate variables: annual precipitation (70.1%) and mean annual temperature (29.9%), and no soil variables were included (Appendix S3).

Figure 7 summarizes the relative differences in environmental requirements among the three *Rafflesia* species. These results indicate that *R. speciosa* occupies the warmest niches and *R. lobata* the coolest. *Rafflesia lobata* grows in the wettest environments and *R. lagascae* prefers the least precipitation. *Rafflesia lagascae* habitats show considerably more temperature seasonality than those of the two other species, whereas *R. speciosa* populations experience the highest precipitation seasonality. The three species are also different in their soil requirements. *Rafflesia speciosa* prefers soils that are more basic. Of the three species, it grows on the sandiest soils that have the least clay. On the other hand, *R. lagascae* prefers soils with higher silt and clay content.

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411

412 ***Future projected distribution changes in* Rafflesia—**

413

414 All modeled *Rafflesia* species are generally predicted to lose suitable habitat under
415 both future climate scenarios, with higher losses observed under RCP 8.5 (Table 2 and
416 Appendix S4; Figs. 4–6). When using models that only take *Rafflesia* occurrence points into
417 account (i.e., approach A1), *R. lagascae* will suffer the greatest losses within the currently
418 known distribution areas among the three: its total percentage of area in Luzon with suitable
419 habitat might be reduced by 9.3% (RCP 4.5) or 14.3% (RCP 8.5) (Table 2). Most of the
420 losses are observed along the fringes of the current area of suitable habitat, and are more
421 pronounced along the southern portions of the Sierra Madre Mountain Range and Bicol
422 peninsula (Figs. 1 and 4). When areas with suitable environmental conditions are considered
423 that are also elsewhere in the Philippines, the total area declines by 3.9% under RCP 4.5 and
424 5.5% under RCP 8.5 (Table 2), which signifies predicted losses of suitable habitat outside the
425 present range of *R. lagascae*. Minor gains (<1% of suitable habitat) are observed in the
426 central portions of the Cordillera mountain range in Luzon, and also in central portions of the
427 mountain ranges of Mindoro, Panay, and Northern Mindanao (Figs. 1 and 4).

428

429 The total area with suitable habitat for *R. speciosa* in Negros and Panay is projected to
430 decline by 0.9% under RCP 4.5 and 3.5% under RCP 8.5 (Table 2: A1). Most of these losses
431 are predicted for Panay Island (Fig. 5). When considering the whole of the Philippines, there
432 are negligible gains predicted under RCP 4.5. Losses are observed under RCP 8.5 (-0.2%;
433 Table 2), despite a potential gain of new suitable areas in northern Mindanao (Fig. 5).

434

Among the three species, *R. lobata* might be the least affected by climate change. The area with suitable habitat in Panay is only predicted to decline by 0.9% (RCP 4.5) and 1.5% (RCP 8.5; Table 2). The losses are all predicted to occur along the margins of its suitable areas in Panay (Fig. 6).

When changes to host distributions under RCP 4.5 and 8.5 are considered in addition to changes to the amount and location of suitable habitat for the parasite (i.e., approach A2), the amount of suitable area for *R. lagascae* and *R. lobata* is lower than when only occurrence points of these two species are used in the SDMs (i.e., approach A1; Table 2). In contrast, no differences between approach A1 and A2 were observed for *R. speciosa* (Table 2).

Not only is the amount of suitable habitat predicted to decrease for all three species, areas with such habitat are also predicted to shift to higher elevations on the islands where the three *Rafflesia* species are found (Fig. 8). For each species, a significant (*R. lagascae*: $F(2.92) = 5154.76$, $p<0.001$; *R. speciosa*: $F(2.56) = 641.85$, $p<0.001$; *R. lobata*: $F(2.28) =12.08$, $p<0.001$) increase in elevation is expected in approach A1 under both climate change scenarios (RCP 4.5: 180 m, RCP 8.5: 291 m for *R. lagascae*; RCP 4.5: 35 m, RCP 8.5: 57 m for *R. lobata*; RCP 4.5: 153 m, RCP 8.5: 349 m for *R. speciosa*; Appendix S5).

Protected area gaps—

The suitable habitat within protected areas under current climate for *Rafflesia lagascae,* which has the largest percentage at 68.0% (8369 km²), is projected to decrease to 50.8% under RCP 4.5 and 40.6% under RCP 8.5 (Table 3). *Rafflesia lobata* is likewise projected to lose suitable habitat within its native island range: from 31.4% under current

460 climate to 27.4% (RCP 4.5) and 24.5% (RCP8.5). For *R. speciosa* which has the smallest
461 protected suitable area (440 km²), a slight increase is projected under RCP 4.5 (to 17.0% to
462 20.4%), but a decrease under RCP 8.5 (to 15.6%).

463 **DISCUSSION**

464

465 ***What underlies the restricted distribution of Philippine Rafflesia?—***

466

467 This study sought to better understand the current distribution patterns of three
468 *Rafflesia* species endemic to the Philippines using species distribution models for these
469 parasitic plants and their *Tetrastigma* host species. Its main aim was to determine if narrow
470 environmental tolerances of host and/or parasite species might be contributing factors to the
471 limited distribution of the latter, with *R. lagascae* and *R. lobata* confined to one island and *R.*
472 *speciosa* to two. These analyses also allowed us to explore if, instead or in addition, a narrow
473 overlap between the environmental requirements of host and parasite provides an explanation
474 for these distribution patterns. Addressing these questions will improve our understanding of
475 the impact of climate change on parasitic plants. This is important because this is presently
476 very poorly known, despite the importance of parasitic plants to community-level ecological
477 interactions (Zamora and Mellado, 2019; Mkala et al., 2022).

478

479 The SDM results indicate that suitable environmental conditions for all five
480 *Tetrastigma* species included in this study are present on all or most large islands of the
481 Philippines (Fig. 3). SDM maps produced for both *Rafflesia* host groups (i.e., *T. ellipticum*
482 s.l., *T. loheri*, and *T.* sp. A. for *R. lagascae* and *R. lobata*; *T. harmandii* and *T.* cf. *magnum* for
483 *R. speciosa*) further suggest that five large islands from which *Rafflesia* species have never

484 been recorded (i.e., Bohol, Cebu, Leyte, Mindoro, Palawan) provide considerable areas of
485 suitable habitat for at least one of the observed host species for each of the three *Rafflesia*
486 species (Fig. 3). This suggests that it is unlikely that *R. lagascae, R. lobata* and *R. speciosa*
487 are absent from these islands because they do not provide a suitable environment for their
488 hosts. To further determine if environmental requirements of host species are limiting factors
489 to the current distribution of the three *Rafflesia* species, we produced SDM maps for *Rafflesia*
490 in which the results of SDM analyses of their host groups were used to identify grid cells that
491 contain suitable habitat for *Rafflesia*, but not for their host species (A2 approach; Table 1).
492 These maps (Appendix S6–S8) were identical or nearly identical to those for which this
493 limitation was not considered (A1 approach; Table 1). Therefore, our results provide support
494 for the hypothesis that the environmental requirements of *Tetrastigma* species are not a
495 limiting factor to the current distribution of the *Rafflesia* species included in our study (Pelser
496 et al., 2018). This pattern supports the 'parasite niche hypothesis' (Lira-Noriega and
497 Peterson, 2014): the distribution of parasites is mediated by their autecology instead of the
498 distribution of their hosts. Evidence in support of this hypothesis has been found for mistletoe
499 species in families Loranthaceae and Viscaceae (Lira-Noriega and Peterson, 2014; Ramírez-
500 Barahona et al., 2017; Ornelas et al., 2018). However, under future climate scenarios, the
501 amount of suitable area for *R. lagascae* and *R. lobata* is lower when a mask layer is used that
502 excludes grid cells without suitable habitat for their *Tetrastigma* host species than when this
503 mask is not applied (i.e., A2 vs. A1; Table 2). This could indicate that host distribution might
504 become a limiting factor to the distribution of these two parasite species (the 'host niche
505 hypothesis'; Lira-Noriega and Peterson, 2014) as a result of climate change.
506
507 If host distribution is not a limiting factor to the distribution of *R. lagascae*, *R. lobata*
508 and *R. speciosa* under current climate conditions, it is possible that these species have

509 relatively few populations and small observed distribution areas because they have quite
510 specific environmental requirements. If this is the primary reason for this distribution pattern,
511 then we expect that their recorded range would closely correspond to the areas with suitable
512 habitat as identified in the SDM analyses. However, this is not the case for all three *Rafflesia*
513 species.
514
515 *Rafflesia speciosa* seems to have the most restrictive habitat requirements of the three
516 species. The SDM results indicate that only 0.7% of the terrestrial area of the Philippines
517 provides suitable habitat for this species (Table 2). A total of 91.2% of this area is found
518 within the two islands that compose its known distribution area (i.e., Panay and Negros; Fig.
519 5), where 8.1% of their land mass was identified as having suitable conditions for *R. speciosa*
520 (Table 2). Suitable habitat was also predicted for other islands (i.e., Calamianes and
521 Mindoro), but only in relatively small and disjunct areas (Fig. 5). Even within Panay and
522 Negros, the most contiguous areas with suitable habitat are those from which this species is
523 currently known (Fig. 5). Although an area in Northern Negros Natural Park north of the Mt.
524 Kanlaon population of *R. speciosa* seems to be the exception to this pattern, anecdotal reports
525 suggests that the area might in fact be home to a second Negros population of this species (S.
526 Olimpos, personal communication). Therefore, *R. speciosa* might primarily be confined to its
527 currently known distribution area because of narrow environmental tolerances.
528
529 *Rafflesia speciosa* shares Panay with *R. lobata*, which is endemic to the CPMR. In
530 contrast to *R. speciosa*, sizable areas with suitable habitat for *R. lobata* might be present on
531 several islands from which this species has never been reported, including the mountain
532 ranges of Luzon, northern and eastern Mindanao, Mindoro, and Samar (Fig. 6). In addition,
533 whereas suitable habitat for *R. speciosa* does not appear to be present in the Northwest Panay

534 Peninsula, it may have suitable habitat for *R. lobata*, although this species has not been
535 reported from this area despite its proximity to the CPMR. *Rafflesia lobata* is the only one of
536 the three *Rafflesia* species for which the largest proportion of its suitable habitat is found
537 outside of the islands to which it is restricted (94.9%, vs. 8.9% for *R. speciosa* and 9.5% for
538 *R. lagascae*). These SDM patterns indicate that narrow environmental tolerances do not
539 adequately explain the island endemicity of *R. lobata* and that this may instead be a result of
540 poor inter-island dispersal abilities, as has been previously suggested (Pelser et al., 2019).
541
542 Suitable habitat for *R. lagascae* seems to be present throughout the Cordillera, Sierra
543 Madre and Zambales mountain ranges of Luzon, as well as in the mountains of the Bicol
544 peninsula (Figs. 1 and 4). These are all areas from which this species has previously been
545 reported. However, although these areas comprise most of the areas with suitable habitat for
546 *R. lagascae* in the Philippines (90.5%), the results of the SDM analyses indicate that sizable
547 areas that provide appropriate environmental conditions for this species can also be found on
548 islands in the central part of the Philippines, most notably Catanduanes, Marinduque,
549 Mindoro, Negros, Panay and Sibuyan (Figs. 1 and 4). Thus, *R. lagascae* displays SDM
550 patterns that are somewhat intermediate between those of *R. lobata* and *R. speciosa* and its
551 endemicity to Luzon might be explained by a combination of limited inter-island dispersal
552 ability and environmental conditions that are not present on some major islands in the
553 Philippines.
554
555 Climate, soil, and elevation data in the observed *Rafflesia* populations and modeled
556 with Maxent provided details about the different habitat requirements of the three species.
557 These show differences in temperature, precipitation, temperature and precipitation
558 seasonality, and soil composition requirements among the species (Fig. 7). *Rafflesia speciosa*

559 and *R. lobata* both grow in the CPMR, but are only found in sympatry at two locations. This
560 might be explained by their quite different environmental needs. *Rafflesia speciosa* grows in
561 the parts of the mountain range that are warmer and drier and that experience more
562 precipitation seasonality than the areas where *R. lobata* can be found (Fig. 7). It prefers soils
563 that are more basic and have a lower clay content. These sites are commonly found at a lower
564 elevation than those of *R. lobata* (Fig. 8). These different environmental requirements, their
565 non-overlapping host preferences (Pelser et al. 2016) and their different flower sizes (11–21
566 cm diameter for *R. lobata* vs. 45–56 cm diameter for *R. speciosa*; Barcelona et al., 2011)
567 might indicate the importance of divergent selection in the evolutionary history of *Rafflesia*
568 (Pelser et al., 2019). SDM and other studies that provide information about the environmental
569 needs of other *Rafflesia* species (e.g., Manuel and Hermocilla, 2021) that live in the same
570 areas but that are not or only partially sympatric could provide additional insights into the
571 role of divergent selection through habitat specialization. *Rafflesia lagascae* could be a useful
572 focal species for such studies in the Philippines because it is partially sympatric with *R.*
573 *consueloae* Galindon, Ong and Fernando, *R. leonardi* Barcelona and Pelser, and *R.*
574 *philippensis* Blanco (Blanco, 1845; Barcelona et al., 2008; Pelser et al., 2013, 2019; Galindon
575 et al., 2016).
576
577 In summary, the results of our SDM analyses support the hypothesis that the small
578 distribution ranges and high island endemicity of *R. lagascae*, *R. lobata* and *R. speciosa*
579 cannot be explained by narrow environmental requirements of their host species (Pelser et al.,
580 2018). Instead, these *Rafflesia* species might be confined to their current distribution areas by
581 their own environmental requirements and/or by having limited inter-island dispersal
582 abilities. The former hypothesis was previously considered unlikely (Pelser et al., 2018),
583 because *Rafflesia* species have been observed in both primary forests and those in various

stages of regeneration, across wide elevational ranges, and on different substrates (Nais, 2001; Barcelona et al., 2009). Yet, here we show that the environmental needs of some *Rafflesia* (e.g., *R. speciosa*) may be an important limiting factor, although others may have less specific habitat requirements (e.g., *R. lobata*). Ancheta (2021) concluded in a previous SDM study of two other Philippine *Rafflesia* species (*R. consueloae* and *R. schadenbergiana*) that suitable habitat for these island endemics is found throughout the Philippines. It is thus possible that poor inter-island dispersal ability is the more common reason for the island endemicity of Philippine *Rafflesia*.

Conservation of Philippine Rafflesia, now and into the future—

A better understanding of the distribution, habitat requirements, and dispersal abilities of species can result in more effective conservation management plans (Bellard et al., 2012; Guisan et al., 2013; Driscoll et al., 2014; Cai et al., 2022). This includes identifying areas that should be prioritized for formal protection (e.g., Spiers et al., 2018). Climate change may impact the size and location of suitable habitat in the future (e.g., Wilkening et al., 2019; Mancera and Lapuz, 2020). Understanding changes under different climate change scenarios can therefore inform management plans aimed at mitigating the impacts of climate change. This could consist of changing the boundaries of protected areas and establishing new protected areas to accommodate changes to distribution areas of threatened species and to ensure or enhance connectivity among protected areas. Parks et al. (2023) showed that the Philippines is one of the countries that has some of the highest climate connectivity failures in Asia. This emphasizes the urgency to review its protected area network and the need for studies like ours to inform this work.

All Philippine *Rafflesia* species are of conservation concern (Pelser et al., 2011 onwards; Galindon et al., 2016; DENR, 2017). Many of them are only known from one or a handful disjunct populations and these sometimes appear to be composed of a single *Tetrastigma* host plant. Previous population genetic studies show strong genetic structure among populations of *R. lagascae* and *R. speciosa*, indicating low genetic connectivity among populations more than c. 20 km away from each other (Pelser et al., 2017, 2018). The Philippine tropical rainforest has been reduced to an estimated 3–6% of its original cover (Mittermeier et al., 1998; Ong et al., 2002) and the ongoing destruction and degradation of natural forest ecosystems in the Philippines are likely to increase distances between populations in this already fragmented landscape, lower their numbers, and reduce their sizes. Ultimately, this can result in a loss of genetic diversity through genetic drift and inbreeding (Ellstrand and Elam, 1993) and, consequently, populations that are less resilient and therefore more prone to extinction (Frankham, 2005). Species with patchy distributions and poor dispersal abilities, such as *Rafflesia*, are particularly vulnerable to this (Wang et al., 2015). SDM models under RCP 4.5 and RCP 8.5 indicate that climate change will exacerbate this threat for Philippine *Rafflesia*. All three *Rafflesia* species included in this study are predicted to lose suitable habitat on the islands on which they are currently found (Tables 2 and 3; Figs. 4–6), but *R. lagascae* might be most severely impacted, potentially losing as much as 15.4% of the area in which suitable habitat is currently found (Table 2). Our results suggest that *Rafflesia* populations at lower elevations might be particularly impacted, as climate change will see suitable habitat shifting to higher elevations (Table 7). These are also the populations that are likely to be the most prone to habitat destruction as a result of land conversion by expanding human population centers for residential and agricultural use. Other *Rafflesia*

species, both in the Philippines as in other countries, face similar challenges (e.g., Kusuma et al., 2022; Renjana et al., 2022).

Climate change can cause changes in the availability and location of suitable habitat for host species, which in turn can lead to a decline in populations of parasitic plants (Liu et al., 2019). This is because a reduction in host availability can occur in locations with suitable habitat for parasitic species, potentially reducing the areas where parasitic plants can grow (Zamora and Mellado, 2019). Some evidence of this was found in this study for *R. lagascae* and *R. lobata*, because the total area that provides suitable habitat for these two species as well as their hosts under RCP 4.5 and 8.5 (A2) was predicted to be smaller than the total suitable area for these parasites (A1; Table 2) under these climate change scenarios. Reduced host availability might therefore be an additional threat to the conservation of some Philippine *Rafflesia*.

Rafflesia populations outside of protected areas are particularly vulnerable, now and in the future. For all three species and under each climate change scenario except for one (*R. speciosa* for RCP 4.5), the percentage of suitable area within the boundaries of present-day protected areas will reduce (Table 3). Although *R. lobata* is the species that is predicted to lose the least amount of suitable habitat in its native island range as a result of climate change (Table 2, Fig. 6a), none of its populations are located in protected areas (Appendix S9). Forest destruction, degradation and fragmentation as a result of logging, mining, farming, roading, new or expanding settlements, and other forms of encroachment thus appear to pose a greater risk to the survival of this species than climate change. About a third of the populations of *R. speciosa* are located in protected areas (Appendix S9). Most of these are at locations close to their boundaries and therefore more exposed to habitat degradation (Pelser

et al., 2018). In addition, many *R. speciosa* populations are at sites that are at risk of losing suitable habitat in the future (Fig. 5a). One of the recommendations resulting from a conservation genetic study of *R. speciosa* (Pelser et al., 2018) was that the entire CPMR should be given protective status. The results of the present study provide further support for this recommendation and indicate that this would also be the best course of action to protect *R. lobata*. In Luzon, many *R. lagascae* populations are at the fringes of areas with suitable habitat and at or close to locations that are predicted to lose this habitat in the future (Fig. 4a). In addition, populations in the northern part of Luzon are all located outside of the few protected areas in this part of the country (Fig. 1). Because of this and the disjunct distribution of *R. lagascae* populations (Pelser et al., 2017), strategically-located new protected areas should be considered to expand the protected area network in Luzon and improve its connectivity.

CONCLUSIONS

Rafflesia species have been referred to as the 'giant pandas of the plant world', given their rarity, bizarre endo-holoparasitic lifestyle, and large and foul-smelling flowers (Josephson, 2000). Recent studies of these flagships of plant conservation improved our understanding of their species diversity, reproductive biology, propagation, environmental preferences, patterns of genetic diversity and connectivity, evolutionary relatedness, biogeographic history, and host preference and specificity in the Philippines (e.g., Barcelona et al., 2014; Galindon et al., 2016; Pelser et al., 2016, 2017, 2018, 2019; Molina et al., 2017; Lit, 2019; Tolod et al., 2020; Ancheta, 2021; Manuel and Hermocilla, 2021). This SDM

study of *R. lagascae, R. lobata* and *R. speciosa* built on these insights. Its results suggest that they are not rare because their *Tetrastigma* host species are rare. Instead, their island endemicity, small number of populations and disjunct distribution are most likely a result of poor inter-island dispersal abilities and/or specific environmental requirements, which appear to vary among the three species. Furthermore, all three species are projected to lose suitable habitat as a result of climate change, both within and outside protected areas on their native islands. However, some species are predicted to be more vulnerable than others. Additionally, the effectiveness of the current protected area network in the Philippines in meeting the conservation needs of these species varies among the three species, both presently and in the future. By understanding the similarities and differences among these three *Rafflesia* species, conservation strategies can be developed to protect each species as well as Philippine *Rafflesia* as a whole.

ACKNOWLEDGMENTS

We are grateful to current and former staff of regional and local offices of the Department of Environment and Natural Resources (DENR), the Protected Area Management Board (PAMB) of Aurora Memorial National Park, Bataan Natural Park, Mt. Banahaw-San Cristobal Protected Landscape, Mt. Kanlaon Natural Park, Sibalom Natural Park, and Pantabangan-Carranglan Watershed Forest Reserve for facilitating the issuance of collecting and transport permits. We thank the local government units, communities, and field assistants and guides in Barbaza, Culasi, Pandan, San Remigio, Sibalom and Valderamma (Antique); Baler and Maria Aurora (Aurora); Mariveles (Bataan); Itogon (Benguet); Lal-o and Gattaran (Cagayan); Alcoy, Boljoon, Dalaguete, Cebu City, and Argao (Cebu); Leon, Igbaras, and Miag-ao (Iloilo); Bauang (La Union); Los Baños (Laguna); Dagami (Leyte); Dolores (Quezon); and Rodriguez (= Montalban) and Tanay (Rizal). For logistical support and

assistance in the field, we are grateful to H. Alburo (Cebu Technological University-Argao), V. Salares (University of San Carlos), V. L. Dacumos (Nueva Ecija University of Science and Technology or NEUST), J. R. Callado and D. N. Tandang (National Museum of the Philippines), Aurora State College of Technology (ASCOT), L. R. Heaney and D. S. Balete (Field Museum, Chicago, IL, USA), Makiling Center for Mountain Ecosystem (MCME), M. A. O. Cajano (Museum of Natural History, University of the Philippines, Los Baños (UPMNH)). Thanks to our NGO partners: The Antique Outdoors (TAO), Cagayan Valley Partners in People Development (CAVAPPED) through P. A. Visorro, Conservation International, Philippines, Foundation for Philippine Environment (FPE), Philippines Biodiversity Conservation Foundation (PBCFI) through Lisa Paguntalan, and Tanggol Kalikasan, Quezon through J. Lim. D. J. V. Laborada and S. M. A. Ong (University of the Philippines Manila) assisted with or performed the preliminary species distribution modeling analyses for *Tetrastigma* species. This work was supported by the Marsden Fund Council from Government funding administered by the Royal Society of New Zealand [grant number UOC1102] and the Rufford Small Grant Foundation [grant number 20207-1].

AUTHOR CONTRIBUTIONS

J. J. A. O., R. S. L., and P. B. P. conceptualized the research and methodology including data analysis and interpretation. P. B. P., J. F. B., and J. J. A. O. collected the data. P. B. P., J. J. A. O., R. S. L., and J. F. B. wrote and revised the manuscript. All authors gave their approval for the final version of the manuscript.

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TABLES

Table 1. Scores from comparison metrics between two *Rafflesia* distribution modeling approaches: SDM using only *Rafflesia* occurrence points (A1), and *Rafflesia* SDMs masked using *Tetrastigma* habitat SDMs (A2).

Metric	***R. lagascae***	***R. speciosa***	***R. lobata***
Geographic Range Overlap	1.00	1.00	1.00
Schoener's D	0.98	1.00	0.88
Hellinger's I	0.99	1.00	0.94

Table 2. Percentages of areas with suitable *Rafflesia* habitat for the native island ranges and the entire Philippines under current climate conditions and two future climate change scenarios (i.e., RCP 4.5, RCP 8.5) resulting from SDMs using *Rafflesia* occurrence points only (A1) and *Rafflesia* SDMs masked using *Tetrastigma* habitat SDMs (A2). Values in brackets indicate the amount of change for that climate scenario when compared against predictions under the current climate.

	Native island ranges			**Entire Philippines**		
Species	**Current (A1)**	**RCP 4.5 (A1/A2)**	**RCP 8.5 (A1/A2)**	**Current (A1)**	**RCP 4.5 (A1/A2)**	**RCP 8.5 (A1/A2)**
R. lagascae	32.1	22.8/22.0 (-9.3/-10.1)	17.8/16.7 (-14.3/-15.4)	12.9	9.0/8.7 (-3.9/-4.0)	7.4/7.0 (-5.5/-5.7)
R. speciosa	8.1	7.1/7.1 (-0.9/-0.9)	4.6/4.6 (-3.5/-3.5)	0.7	0.8/0.8 (+0.1/+0.1)	0.6/0.6 (-0.2/-0.2)
R. lobata	7.7	6.8/6.7 (-0.9/-1.0)	6.2/6.0 (-1.5/-1.8)	5.9	5.9/4.3 (+0.1/-0.9)	5.4/3.3 (-0.5/-1.9)

Table 3. Areas (km^2) and percentages of suitable habitats within protected area boundaries for *Rafflesia* species in their native islands. Calculated with SDMs using *Rafflesia* occurrence points only (A1).

Species	**Current**	**RCP 4.5**	**RCP 8.5**
R. lagascae	8369 / 68.0%	6253 / 50.8 %	5001 / 40.6%
R. speciosa	440 / 17.0%	530 / 20.4%	406 / 15.6%
R. lobata	273 / 31.4%	238 / 27.4%	213 / 24.5%

FIGURES

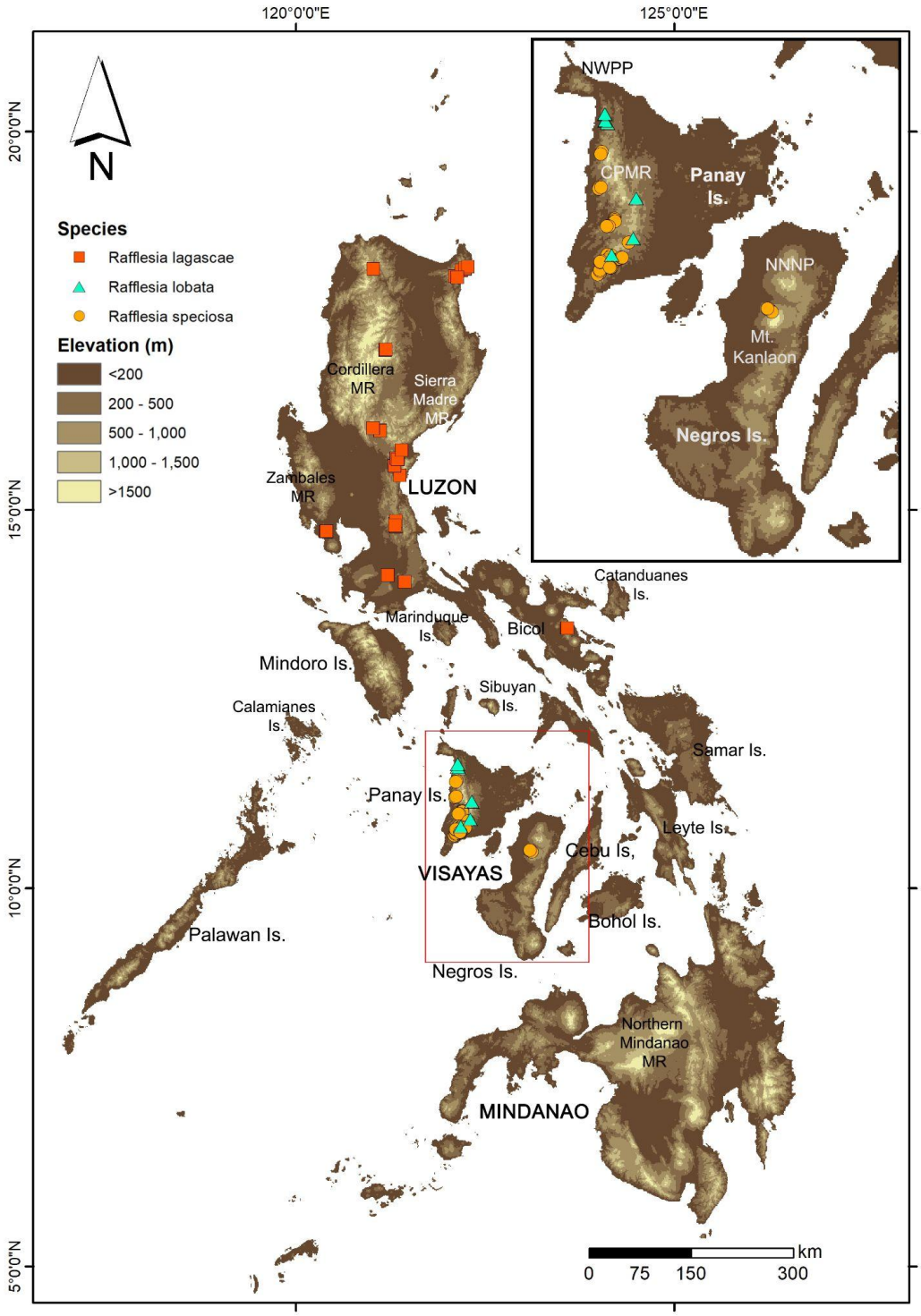


Figure 1. Map of the Philippines showing major island groups (in capital letters), islands (Is.), and mountain ranges (MR). Negros and Panay islands are highlighted within inset (boxed red in main map). Fill colors correspond to elevation in meters. *Rafflesia* occurrence points are

overlaid to show native ranges of each species. CPMR = Central Panay Mountain Range; NNNP = Northern Negros Natural Park; NWPP = Northwest Panay Peninsula.

Figure 2. Flowers of (A) *Rafflesia lagascae*, (B) *R. speciosa*, and (C) *R. lobata*.

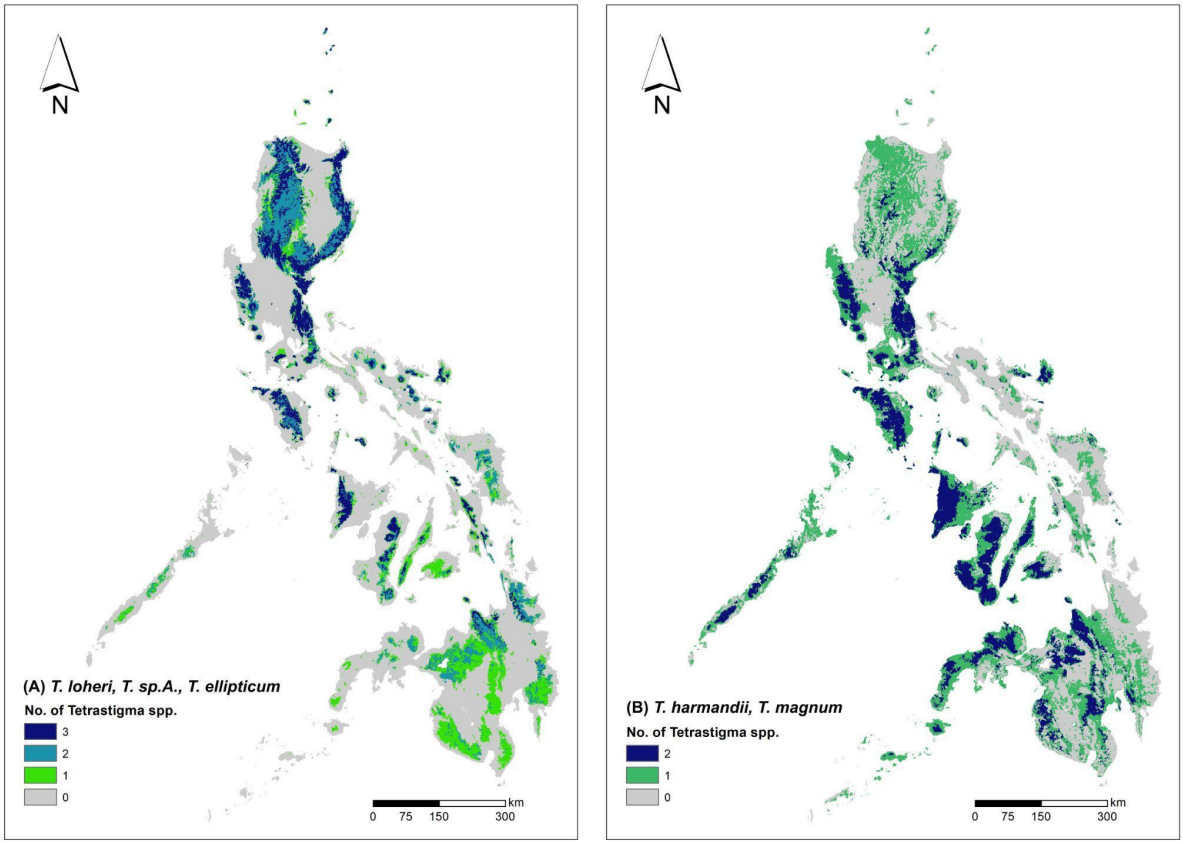


Figure 3. Distribution of suitable habitat of two *Tetrastigma* host groups: (A) the hosts of *R. lobata* and *R. lagascae* and (B) the hosts of *R. speciosa*. Colors show the number of *Tetrastigma* species that are predicted to occur in each grid cell.

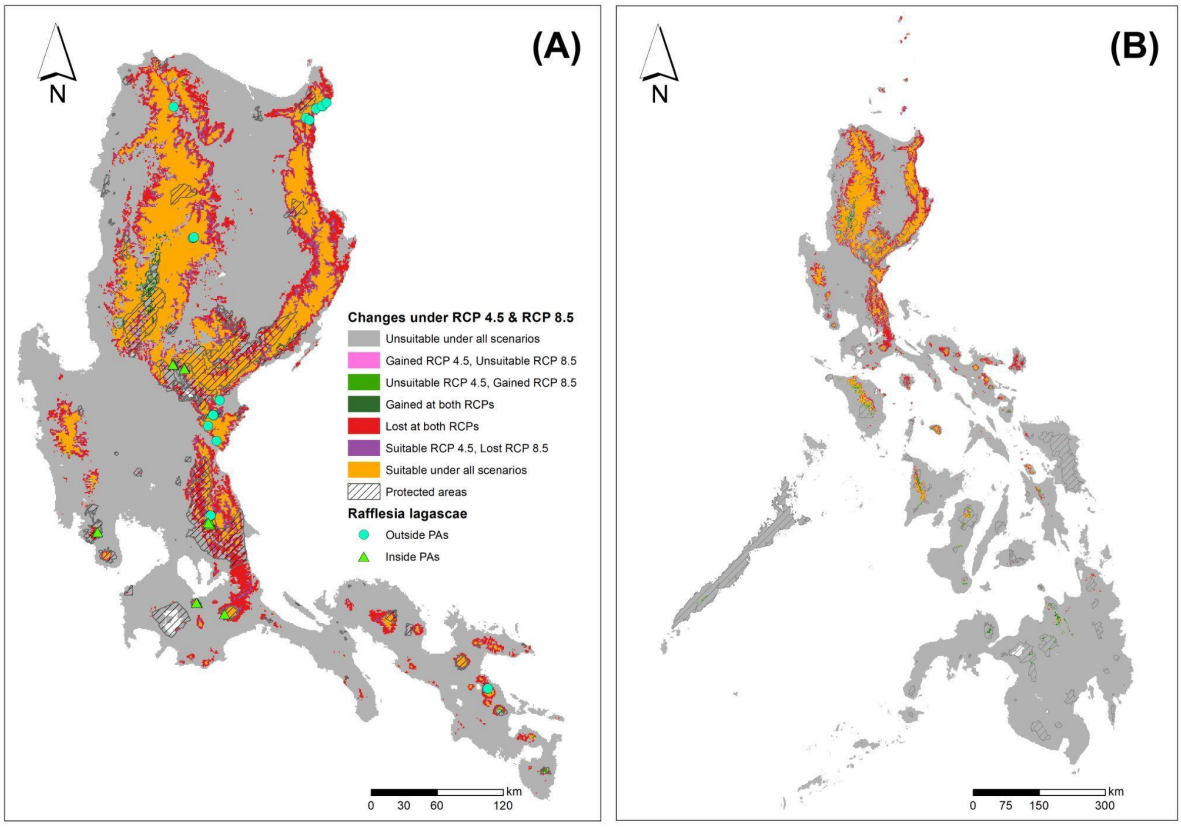


Figure 4. Distribution of suitable habitat of *Rafflesia lagascae* for (A) Luzon, the only island from which it is known and (B) the entire Philippines and combined changes to this under RCP 4.5 and RCP 8.5 from current climate. 'Suitable under all scenarios' refers to consistently suitable habitats from current to future climate scenarios. 'Unsuitable under all scenarios' refers to consistently unsuitable habitats from current to future climate scenarios. 'Gained' refers to habitats that became suitable under future climate, while 'Lost' refers to habitats that became unsuitable under future climate. Hatched areas are protected areas. Species points are labeled based on their inclusion within protected area boundaries. Calculated with SDMs using *Rafflesia* occurrence points only (A1).

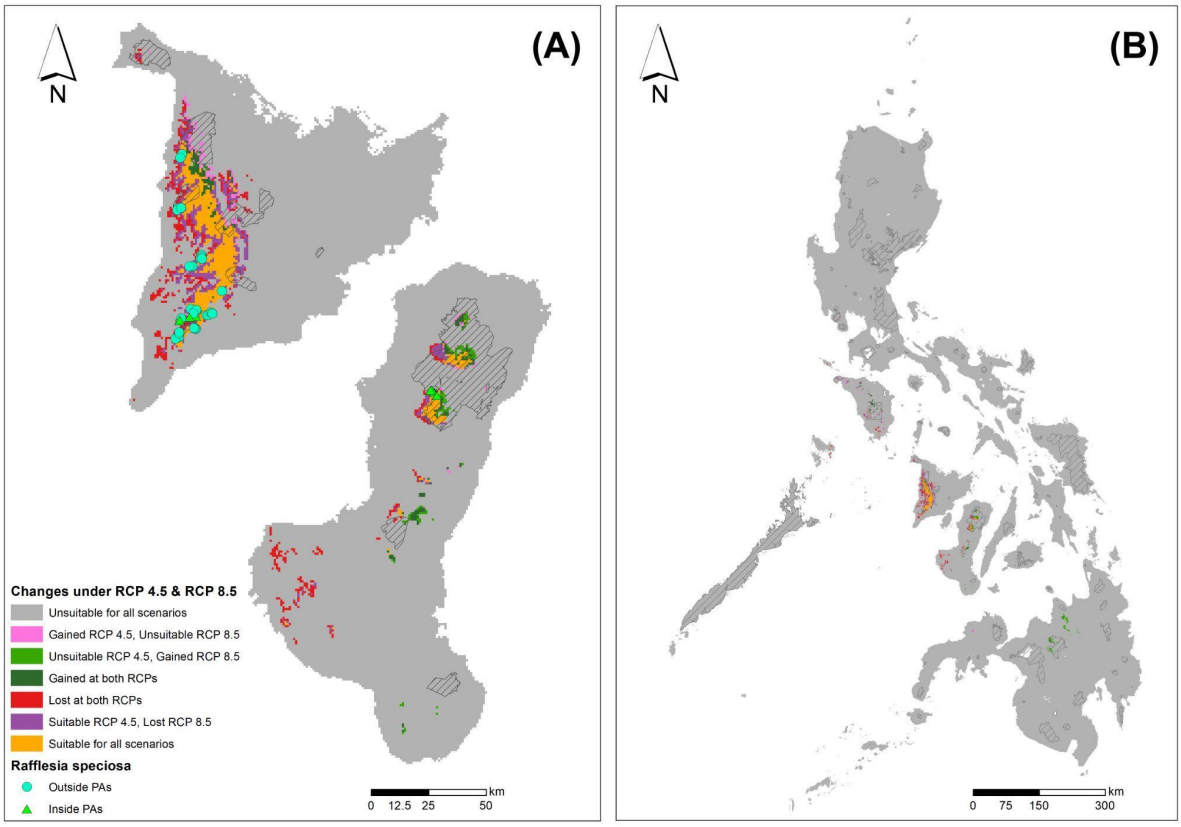


Figure 5. Distribution of suitable habitat of *Rafflesia speciosa* on (A) Panay and Negros, the only islands from which it is known and (B) the entire Philippines and combined changes to this under RCP 4.5 and RCP 8.5 from current climate. 'Suitable under all scenarios' refers to consistently suitable habitats from current to future climate scenarios. 'Unsuitable under all scenarios' refers to consistently unsuitable habitats from current to future climate scenarios 'Gained' refers to habitats that became suitable under future climate, while 'Lost' refers to habitats that became unsuitable under future climate. Hatched areas are protected areas. Species points are labeled based on their inclusion within protected area boundaries. Calculated with SDMs using *Rafflesia* occurrence points only (A1).

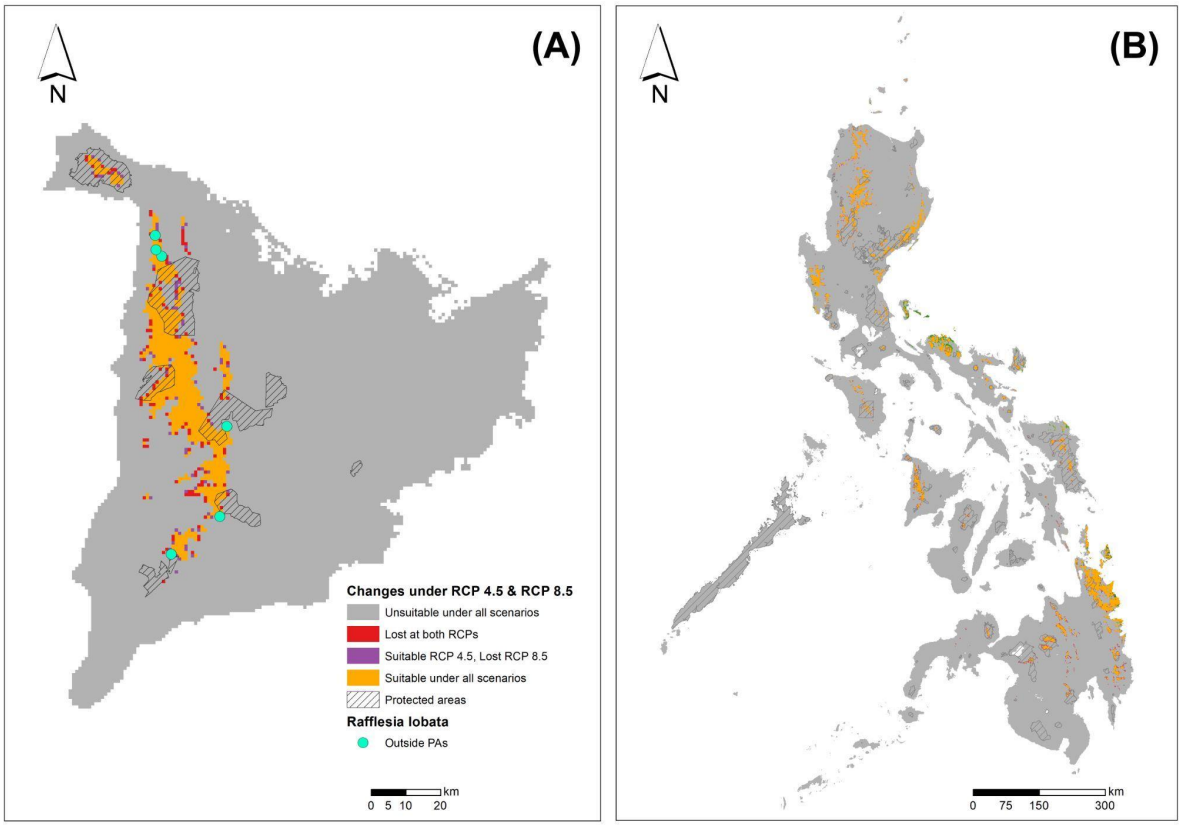


Figure 6. Distribution of suitable habitat of *Rafflesia lobata* on (A) Panay, the only island from which it is known and (B) the entire Philippines and combined changes to this under RCP 4.5 and RCP 8.5 from current climate. 'Suitable under all scenarios' refers to consistently suitable habitats from current to future climate scenarios. 'Unsuitable under all scenarios' refers to consistently unsuitable habitats from current to future climate scenarios. 'Gained' refers to habitats that became suitable under future climate, while 'Lost' refers to habitats that became unsuitable under future climate. Hatched areas are protected areas. Species points are labeled based on their inclusion within protected area boundaries. Calculated with SDMs using *Rafflesia* occurrence points only (A1).

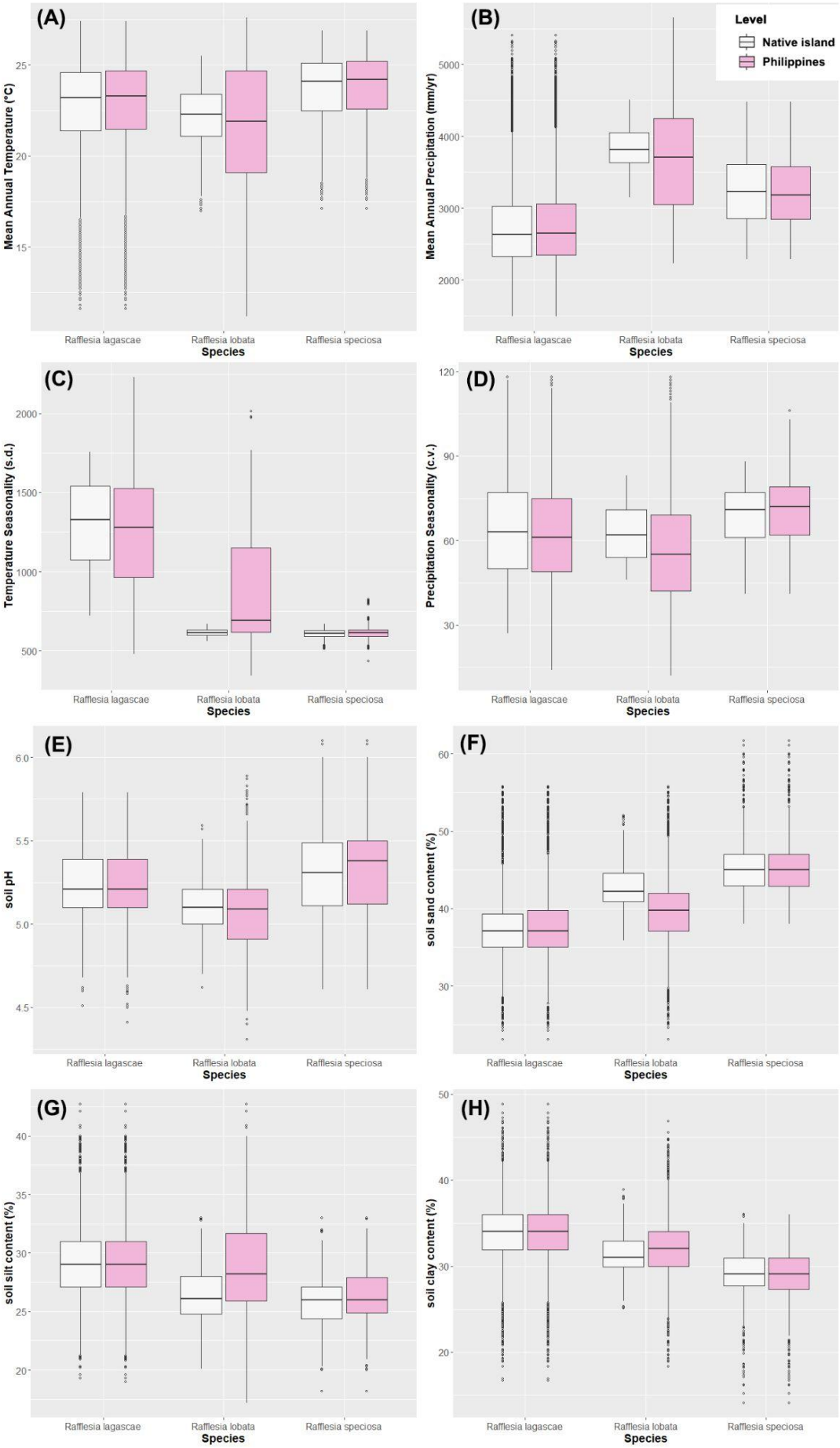

(A)
Mean Annual Temperature (°C)
25
20
15
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(B)
Level
Native island
Philippines
Mean Annual Precipitation (mm/yr)
5000
4000
3000
2000
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(C)
Temperature Seasonality (s.d.)
2000
1500
1000
500
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(D)
Precipitation Seasonality (c.v.)
120
90
60
30
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(E)
soil pH
6.0
5.5
5.0
4.5
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(F)
soil sand content (%)
60
50
40
30
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(G)
soil silt content (%)
40
35
30
25
20
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species
(H)
soil clay content (%)
50
40
30
20
Rafflesia lagascae
Rafflesia lobata
Rafflesia speciosa
Species

Figure 7. Boxplots depicting the differences in environmental requirements among *Rafflesia* species (s.d.: standard deviation; c.v.: coefficient of variation) estimated for the islands on which each species has been found (native island, white boxes) and the entire Philippines (pink boxes). Calculated with SDMs using *Rafflesia* occurrence points only (A1).

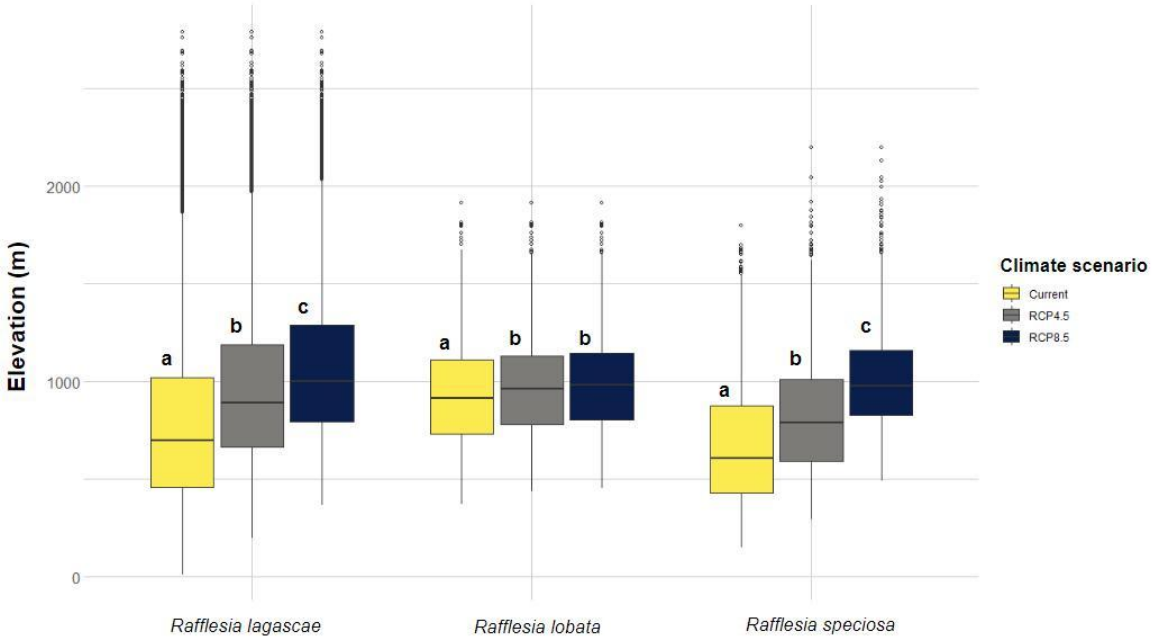


Figure 8. Boxplot showing elevational changes in suitable habitats of *Rafflesia* species under current and future climate scenarios (RCP 4.5 and RCP 8.5) on islands on which they are currently present. Letters indicate differences among climate scenarios that are statistically significant at $p < 0.05$ as tested using ANOVA type II, followed by Tukey's HSD adjusted pairwise tests. Calculated with SDMs using *Rafflesia* occurrence points only (A1).

Appendix S1. List of Maxent feature classes, regularization multipliers, and number of points used for modeling each species. L = Linear, Q = Quadratic; P = Product; H = Hinge; T = Threshold.

Species	**Maxent FC**	**Regularization Multiplier**	**No. of Points**
Rafflesia speciosa	LQHPT	1.5	40
Rafflesia lagascae	L	1.5	36
Rafflesia lobata	H	3	6
Tetrastigma cf. *magnum*	LQH	3	47
Tetrastigma harmandii	LQ	1	24
Tetrastigma loheri	LQHPT	1	79
Tetrastigma ellipticum	LQH	4.5	12
Tetrastigma sp.A	LQHPT	2.5	14

Appendix S2. Average training Area Under the Curve (AUC) and True Skill Statistic (TSS) scores for the distribution models of each species.

Species	**Average Training Area Under the Curve (AUC) Score**	**Average True Skill Statistic (TSS) Score**
Rafflesia speciosa	0.997	0.966
Rafflesia lobata	0.970	0.835
Rafflesia lagascae	0.972	0.840
Tetrastigma loheri	0.979	0.611
Tetrastigma sp. A	0.945	0.713
Tetrastigma ellipticum	0.876	0.477
Tetrastigma harmandii	0.930	0.515
Tetrastigma cf. magnum	0.963	0.661

Appendix S3. Percent contribution values of each environmental variable for each individual SDM. Variables marked with (–) were not used in modeling the final distribution of that species. Values in bold were the highest for that species.

Environmental variable	***R. lagascae***	***R. speciosa***	***R. lobata***	***T. loheri***	***T. cf. magnum***	***T. ellipticum***	***T. sp. A***	***T. harmandii***
Mean Annual Temperature	**45.5**	16.3	29.9	**31.2**	**38.4**	**68.4**	**49.4**	1.3
Temperature Seasonality	35.8	15.5	–	29.1	19.7	17.3	18.1	3.5
Annual Precipitation	0.1	19.7	**70.1**	7.9	5.6	3.5	13.8	24.3
Precipitation Seasonality	1.9	**23.2**	–	2.8	2.3	0.7	0	14.5
Precipitation of the Coldest Quarter	5.3	12.6	–	4.3	11.7	4.2	1.0	21.7
Sand %	0	10.8	–	3.0	7.4	–	4.7	**29.3**

Silt %	0.3	0.2	–	0.5	0	0	–	1.1
Clay %	–	0.9	–	1.4	13.6	–	0.7	2.8
Soil pH	11.0	1	–	11	0.8	5.7	0.8	0.2
Soil Cation-Exchange Capacity	0.1	–	–	4.0	0.5	–	–	1.0
Bulk Density	–	–	–	4.7	–	0.1	11.4	0.3

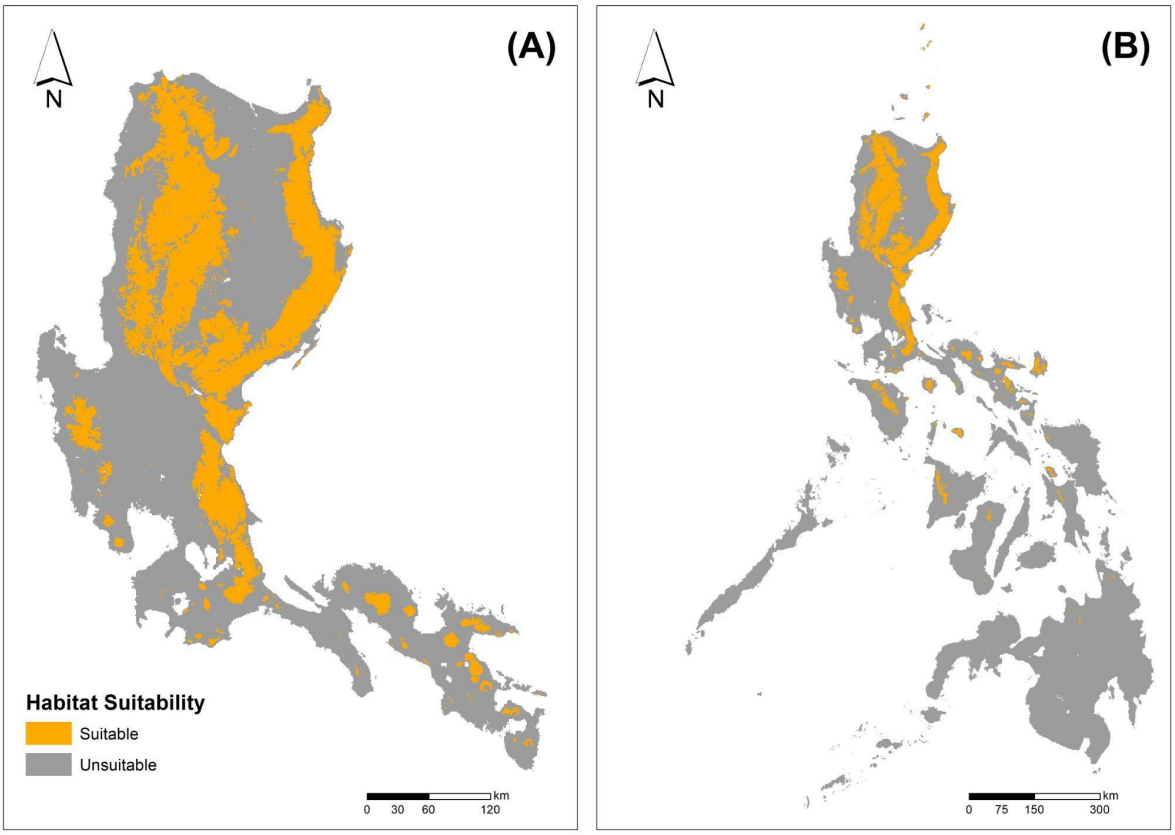
Appendix S4. Gain-loss statistics for *Rafflesia* species relative to that of the islands from which they have been recorded (native island ranges) and the entire Philippines indicating changes in their amount of suitable habitat under the RCP 4.5 and RCP 8.5 climate scenarios in SDMs using *Rafflesia* occurrence points only (A1).

		Native island ranges		**Entire Philippines**	
	%	**RCP 4.5**	**RCP 8.5**	**RCP 4.5**	**RCP 8.5**
Rafflesia lagascae	**Gains**	0.49	0.49	0.31	0.55
	Losses	9.78	14.82	4.18	6.05
	Stable: Suitable	22.30	17.26	8.70	6.83
	Stable: Unsuitable	67.43	67.43	86.81	86.57
R. speciosa	**Gains**	1.21	1.14	0.27	0.29
	Losses	2.15	4.65	0.21	0.44
	Stable: Suitable	5.92	3.42	0.51	0.28
	Stable: Unsuitable	90.73	90.80	99.00	98.99
R. lobata	**Gains**	0.00	0.00	0.33	0.40
	Losses	0.92	1.48	0.28	0.88

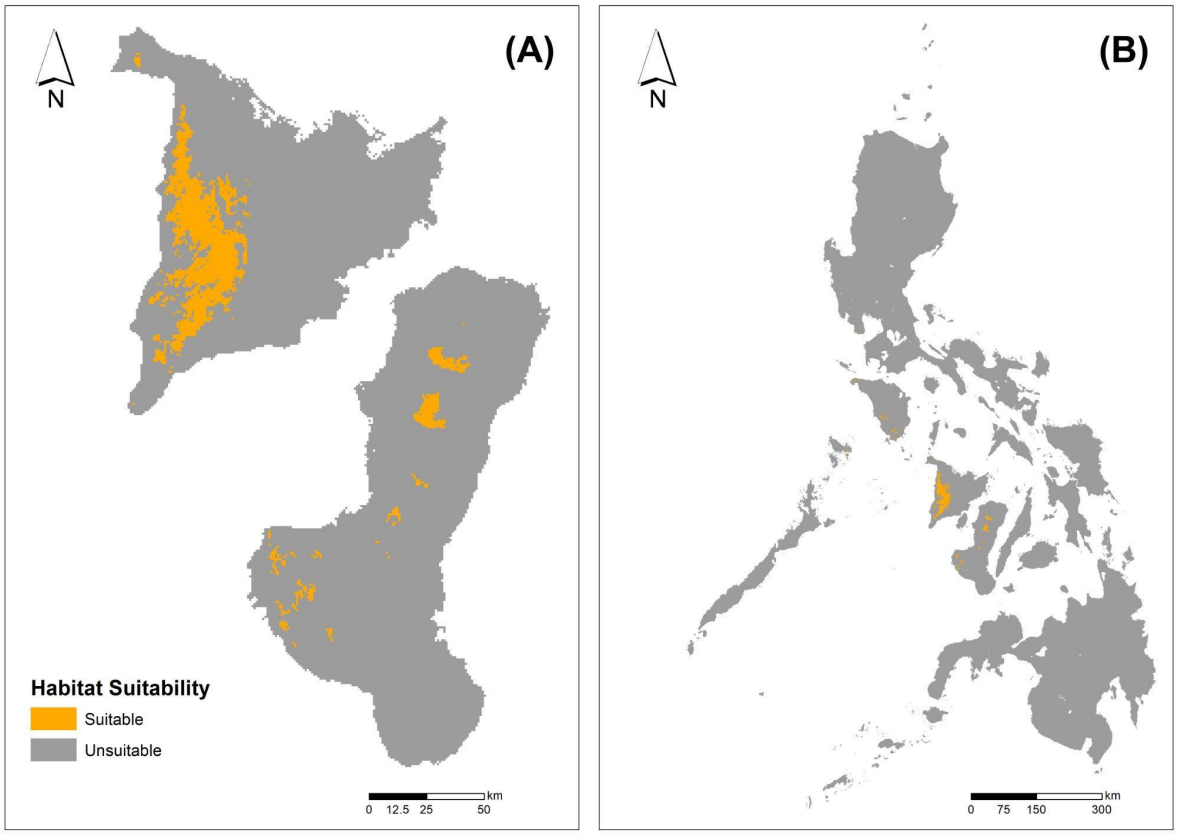
	Stable: Suitable	6.79	6.23	5.59	4.98
	Stable: Unsuitable	92.29	92.29	93.80	93.74

Appendix S5. Mean elevation (m) ± standard deviation (m) of *Rafflesia* species suitable habitat under different climate scenarios. Superscripts indicate significant differences between scenarios for each species.

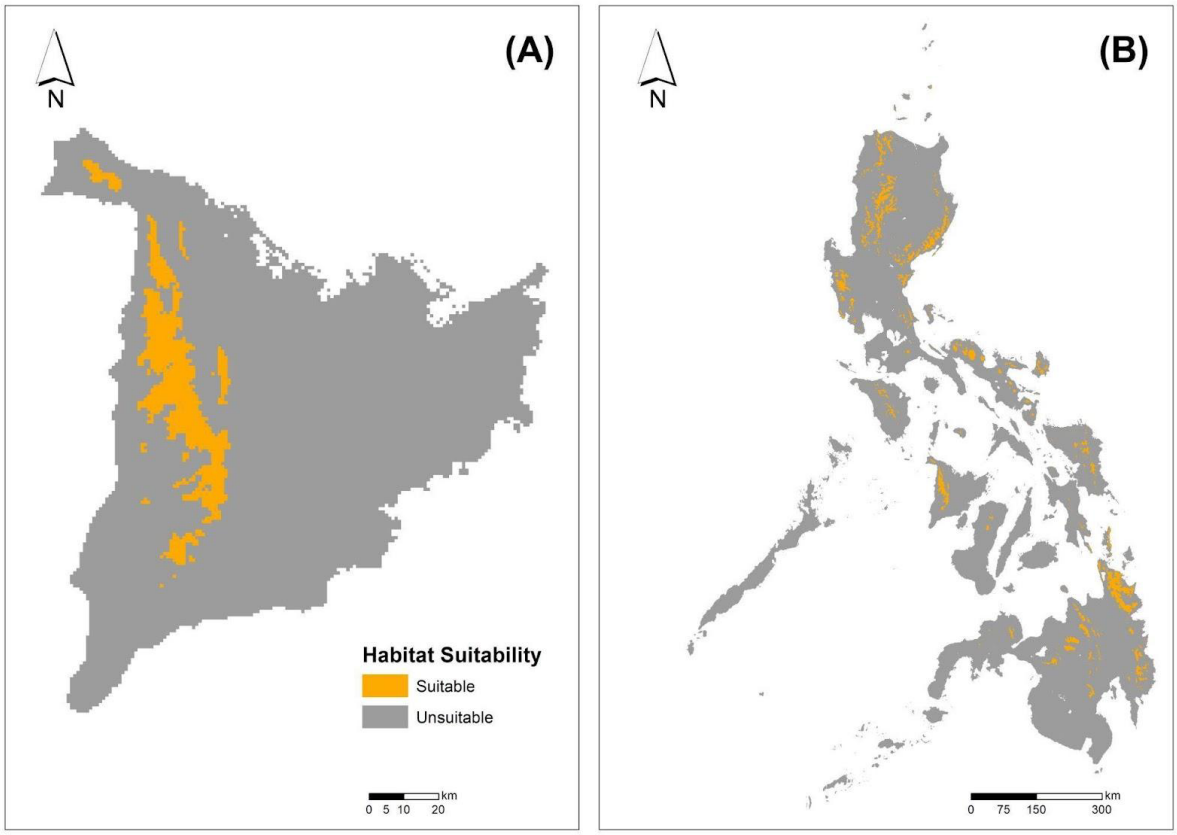
	Climate Scenarios		
Species	**Current**	**RCP 4.5**	**RCP 8.5**
Rafflesia lagascae	$785.46^{a} \pm 423.77$	$965.88^{a} \pm 397.75$	$1076.86^{a} \pm 381.00$
Rafflesia speciosa	$674.59^{b} \pm 310.26$	$827.60^{b} \pm 296.62$	$1023.23^{b} \pm 269.28$
Rafflesia lobata	$941.21^{c} \pm 274.48$	$976.60^{b} \pm 266.77$	$997.71^{c} \pm 263.14$



Appendix S6. Distribution of suitable habitat of *Rafflesia lagascae* on Luzon, the only island from which it is known (A) and the entire Philippines (B) under current climate conditions based on *R. lagascae* SDMs masked with *Tetrastigma* habitat SDMs (A2 approach).



Appendix S7. Distribution of suitable habitat of *Rafflesia speciosa* on Negros and Panay, the only islands from which it is known (A) and the entire Philippines (B) under current climate conditions based on *R. speciosa* SDMs masked with *Tetrastigma* habitat SDMs (A2 approach).



Appendix S8. Distribution of suitable habitat of *Rafflesia lobata* on Panay, the only island from which it is known (A) and the entire Philippines (B) under current climate conditions based on *R. lobata* SDMs masked with *Tetrastigma* habitat SDMs (A2 approach).

Appendix S9. Number of species points inside protected area (PA) boundaries.

Species	**Points inside PA**	**Total Points**	**% inside PAs**
Rafflesia lagascae	17	36	47.2
Rafflesia lobata	0	6	0
Rafflesia speciosa	13	40	32.5
Tetrastigma cf. magnum	13	47	27.7
Tetrastigma ellipticum s.l.	7	12	58.3
Tetrastigma harmandii	5	24	20.8
Tetrastigma loheri	22	79	27.8
Tetrastigma sp. A	7	14	50