Global Ecology and Conservation 34 (2022) e02063

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: www.elsevier.com/locate/gecco

Assessing potential habitat suitability of parasitic plant: A case study of *Rafflesia arnoldii* and its host plants

Elga Renjana [a,*], Inggit Puji Astuti [a], Esti Munawaroh [a], Sofi Mursidawati [a], Joko Ridho Witono [a], Yuzammi [a], Izu Andry Fijridiyanto [a], Puguh Dwi Raharjo [b], Saniyatun Mar'atus Solihah [d], Iyan Robiansyah [a], Wendell P. Cropper Jr. [c], Angga Yudaputra [a]

[a] *Research Center for Plant Conservation and Botanic Gardens, National Research and Innovation Agency, Jalan Ir. H. Juanda 13, Bogor 16122, West Java, Indonesia*
[b] *Research Center for Geotechnology, National Research and Innovation Agency, Jalan Sangkuriang, Bandung 40135, West Java, Indonesia*
[c] *School of Forest, Fisheries and Geomatics Sciences, University of Florida, Gainesville, FL 32611-0410, USA*
[d] *Bogor Botanic Garden, Mitra Natura Raya, Jalan Ir. H. Juanda 13, Bogor 16122, West Java, Indonesia*

A R T I C L E I N F O

Keywords:
Habitat suitability
Host plants
Maximum Entropy
Rafflesia arnoldii
Tetrastigma spp.

A B S T R A C T

Rafflesia are obligate endo-holoparasitic plants with the genus *Tetrastigma* playing an important role as their host plants. *Rafflesia arnoldii* is one of Indonesian endemic plants that grows in Sumatra island. This island is also known to have eleven species of *Tetrastigma*. Three of them are known as host plants of *R. arnoldii*, namely *Tetrastigma curtisii, T. pedunculare* and *T. leucostaphylum*. Unfortunately, it is not possible to survey the entire native distribution range of *R. arnoldii* and its host plants due to practical constraints. Species Distribution Modeling using Maximum Entropy (MaxEnt) is considered to be an alternative way to understand the potential regions that are suitable for a species. Predicting habitat suitability of a parasitic plant through predicting its host plant distribution may be a useful approach. The model prediction from MaxEnt for all host species has an AUC value more than 0.70, indicating the model adequately classified the occurrence records of *R. arnoldii* and its host plants. Suitable habitats for *R. arnoldii* were predicted to occur along the Bukit Barisan Mountain range from Lampung to Aceh, mostly in Lampung, Bengkulu, West Sumatra and Aceh. However, the suitable habitats of *R. arnoldii* estimated from host plants were predicted to occur predominately in Lampung, Bengkulu, West Sumatra, North Sumatra and Aceh. The important environmental variables affecting the occurrence of *R. arnoldii* and its host plants are mean temperature, slope, elevation, soil organic carbon and soil type. *Rafflesia* species can be found in various soil types, but mostly in Humic Andosols, Humic Acrisols, Orthic Acrosols, Dystric Fluvisols, Dystric Cambisols and Eutric Fluvisols based on the actual data points and predicted habitats. The suitable habitats of *R. arnoldii* based on its host plants were predicted to be mostly outside conservation areas, but suitable habitats were predicted inside approximately 46 conservation areas. The findings of this study may be used by the Government of Republic Indonesia, c.q. Ministry of Environment and Foresty for establishing

* Corresponding author.
E-mail addresses: elga.renjana@brin.go.id, prkt-iph@brin.go.id (E. Renjana), ingg001@brin.go.id (I.P. Astuti), esti001@brin.go.id (E. Munawaroh), sofi001@brin.go.id (S. Mursidawati), joko017@brin.go.id (J.R. Witono), yuza001@brin.go.id (Yuzammi), izua002@brin.go.id (I.A. Fijridiyanto), pugu003@brin.go.id (P.D. Raharjo), sani_sms@rocketmail.com (S.M. Solihah), iyan.robiansyah@brin.go.id (I. Robiansyah), wcropper@ufl.edu (W.P. Cropper), angg022@brin.go.id (A. Yudaputra).

https://doi.org/10.1016/j.gecco.2022.e02063
Received 8 November 2021; Received in revised form 13 February 2022; Accepted 13 February 2022
Available online 15 February 2022

protected areas and conservation-based management improvement and could also help inform the *R. arnoldii* listing status in IUCN red list category in the future.

1. Introduction

Parasites exist in all types of life forms including plants (Combes, 2001). Parasitic plants obtain water and nutrients through the haustorium, which is attached to shoots or roots of their host plant. These parasitic plants consist of the plants that are able to photosynthesize (hemiparasites) and are unable to photosynthesize (holoparasites) (Kuijt, 1969). One of the plant taxa which its members are holoparasitic plants is the Rafflesiaceae family. The vegetative parts and chlorophyll are absent in this family. Rafflesiaceae grows only in the stem and root tissue of the genus *Tetrastigma* (Miq.) Planch. as their specific host. Its habitat is in tropical rainforests of Southeast Asia. Based on molecular data, this family includes three genera, namely *Rafflesia* R.Br. ex Gray*, Rhizanthes* Dumort. and *Sapria* Griff. (Bendiksby et al., 2010). Among these genera, *Rafflesia* has a species *Rafflesia arnoldii* R. Br. that produces one of the biggest flowers in the plant kingdom. Since its discovery by Joseph Arnold in 1818, surveys have greatly increased the number of known occurrence sites. In Sumatra, the species is widely distributed in Bukit Barisan Mountain range from Southeast Lampung to Aceh (Meijer, 1997; Zuhud et al., 1998), especially in five Provinces of Sumatra, namely Aceh, West Sumatra, Riau, Bengkulu and Lampung.

Rafflesia arnoldii is one of Indonesian endemic plants which grows in Sumatra island (Asiandu, 2021). This species is an obligate endo-holoparasitc plant, and host specific. Its total dependency on a host plant for growth, water and nutrition has made distribution range of this species limited to that of its host plant *Tetrastigma* (Hidayati and Walck, 2016; Susatya, 2011). At least, three species of *Tetrastigma* have been identified as host plants of *R. arnoldii*, namely *T. leucostaphylum* (Dennst.) Alston ex Mabb., *T. curtisii* (Ridl.) Suess and *T. pedunculare* (Wallich ex. Lawson) Planch (Meijer, 1997; Pranata et al., 2020; Susatya, 2011; Zuhud et al., 1998). The disappearance of those host plants will inevitably lead to the extinction of *Rafflesia*. *Tetrastigma*, with a climbing habit, also requires other plants, usually large trees, for support and access to sunlight. There are 95 validly named *Tetrastigma* species in Malesia region (Chen et al., 2011; Wen, 2007). Study of Sumatran *Tetrastigma* revealed that 11 species were recorded (Rahayu, 2017). Eight out of 11 species known as host of *Rafflesia* (*T. diepenhorstii, T. tuberculatum, T. leucostaphylum, T. rafflesiae, T. dubium, T. glabratum, T. pedunculare* and *T curtisii*). In this case, *T. pedunculare* become the host for seven *Rafflesia* species, namely *R. arnoldii, R. hasseltii, R. keithii, R. kerrii, R. patma, R. pricei* and *R. zollingeriana* (Susatya, 2011).

Previous studies of *R. arnoldii* ecology suggested that these obligate endo-holoparasitic plants are far more susceptible to extinction compared to non-parasitic plants in the same habitat. Both the host and parasite species are affected by environmental fluctuations and disturbances in the ecosystem. Thus, habitat is a critical factor affecting their survival (Ellen et al., 2019; Pranata et al., 2019; Ramadhani et al., 2017; Susatya, 2020). Even though the *Tetrastigma* population is widespread in a habitat and known to be the host, *Rafflesia* does not necessarily grow. The determining factor of *Rafflesia*-host is physiological compatibility so it is difficult to measure which is complex or not caused by single factor. Data of climbing plant is rarely covered because the leaves and flowers grow above the canopy. When it happens to be dangling, the identification is more feasible.

Deforestation in Sumatra has been rapid and potentially represents a serious risk to native species. Eyes on the Forest (EoF, 2018) reported that Sumatra had 25 million hectares of natural forest in 1985; after over 31 years of deforestation only 11 million remained in 2016. With an average annual forest loss rate of 0.46 million hectares per year it is likely a significant threat to the future of *R. arnoldii*. It has not been listed in the International Union for Conservation of Nature (IUCN) Red List Categories as more comprehensive studies are still required. Time and financial constraints have prevented a comprehensive population survey in Sumatra. To date, a more practical method to assess population status and risks in large areas is available through habitat suitability model prediction. This method supports continuing inventory research through identifying possible new subpopulations in unsurveyed regions of Sumatra. In order to understand the prediction of habitat suitability, Species Distribution Models (SDM) are commonly used by combining species occurrence data and environmental variables (Anderson and Martínez-Meyer, 2004; Elith and Leathwick, 2009; Franklin and Miller, 2009; Raxworthy et al., 2003; Thorn et al., 2009). Among many species distribution model methods, Maximum Entropy (MaxEnt) is powerful and outperformed other tools when predicting rare species with narrow habitat ranges (Elith et al., 2006; Pearson et al., 2007; Phillips et al., 2006; Wisz et al., 2008).

This study aims to predict the most suitable habitats of *R. arnoldii* by considering the potential habitats of its host plants and identify the protected areas in Sumatra that have high suitability for *R. arnoldii*. The findings of this study may be used by the Government of Republic Indonesia for establishing protected areas and conservation-based for *R. arnoldii* and would also provide information relevant to the listing status in the IUCN red list category.

2. Materials and methods

2.1. Research sites

The occurrence records of *R. arnoldii* and three host plant species, namely *T. curtisii*, *T. pedunculare* and *T. leucostaphylum* were obtained from direct field surveys, plant inventory records, plant expedition reports, the GBIF database and reliable scientific journals. There were 28 occurrence records of *R. arnoldii* (Ellen et al., 2019; GBIF.org, 2022a; Latifah et al., 2012; Meijer, 1997; Munawaroh et al., 2013; Pranata et al., 2019, 2020; Ramadhani et al., 2017; Susatya, 2020; Zuhud et al., 1998), 3 occurrence records of *T. curtisii*

(GBIF.org, 2022b), 24 occurrence records of *T. pedunculare* (GBIF.org, 2022c; Rahayu, 2017; Susatya et al., 2017), and 19 occurrence records of *T. leucostaphylum* (GBIF.org, 2022d; Pranata et al., 2019; Rahayu, 2017; Rahma et al., 2017; Ramadhani et al., 2017; Setyowati and Wardah, 2007). Those occurrence points were recorded on the western region of Sumatra from Lampung to Aceh along the Bukit Barisan Mountain range (Fig. 1).

2.2. Study species

Morphological characters of *R. arnoldii*, and three host plant species are as follows: *Rafflesia arnoldii* R. Br has unisexual and sessile flowers, developing outside the host. Flower buds are protruding as a corky swelling with hexagonal patches, up to 34.7 cm in diam., dark brown or sometimes white or pale brown at the top when immature and pale to strong sorrel when mature. The bracts are brown to dark brown and are usually released prior to blooming. When the flowers bloom, they emit a strong odor, similar to that of a rotting carcass, attracting pollinators. The flower is up to 81 cm in diameter, with a tube up to 15.5 cm high, perigone consisting of 5 lobes, 22–29 cm long and 23.3–33 cm wide.

Tetrasigma, the host plant of *Rafflesia*, is widely dispersed in tropical and subtropical Asia through Australia (Chen et al., 2011; Rahayu et al., 2018). Amongst Indonesian archipelago, Sumatra is recognized as major dispersal of *Tetrastigma* which 11 species found, i.e. *Tetrastigma curtisii* (Ridl.) Suess., *T. dichotomum* (Blume) Planch., *T. diepenhorstii* (Miq.) Latiff, *T. dubium* (Lawson) Planch., *T. hookeri* (Lawson) Planch., *T. leucostaphylum* (Dennst.) Alston ex Mabb., *T. papillosum* (Blume) Planch., *T. pedunculare* (Wall. ex Lawson) Planch., *T. pisicarpum* (Miq.) Planch., *T. pyriforme* Gagnep. and *T. rafflesiae* (Miq.) Planch (Rahayu, 2017; Rahayu et al., 2018). Three species are commonly host of *R. arnoldii*, i.e. *T. curtisii, T. leucostapylum, T. pedunculare.* Taxonomical confusion occurred in view of (Veldkamp, 2008) where he proposed *T. rafflesiae* is a correct name instead of *T. leucostapylum* (stated the latter misapplied in Sumatera). In the following year, he sank *T. rafflesiae* together with *T. lanceolarium* (Roxb.) Planch. and *T. leucostaphylum* as synonym of *T. coriaceum* (DC.) Gagnep. (Veldkamp, 2009). However, this dispute has now been resolved after research conducted by (Rahayu et al., 2018) which designated *T. leucostapylum* and *T. rafflesiae* as two different species and sank *T. lanceolarium* as synonym of *T. leucostaphylum*. The following Table 1 showed morphological diagnosis characters of three *Tetrastigma* species (*Tetrasigma curtisii, T. leucostaphylum* and *T. pedunculare*).

This current study is focussed on *R. arnoldii* and its host plants, since distribution and habitat data of those species is available from herbarium records, scientific publications and our experience during field works. It will be a starting point to do a further study for

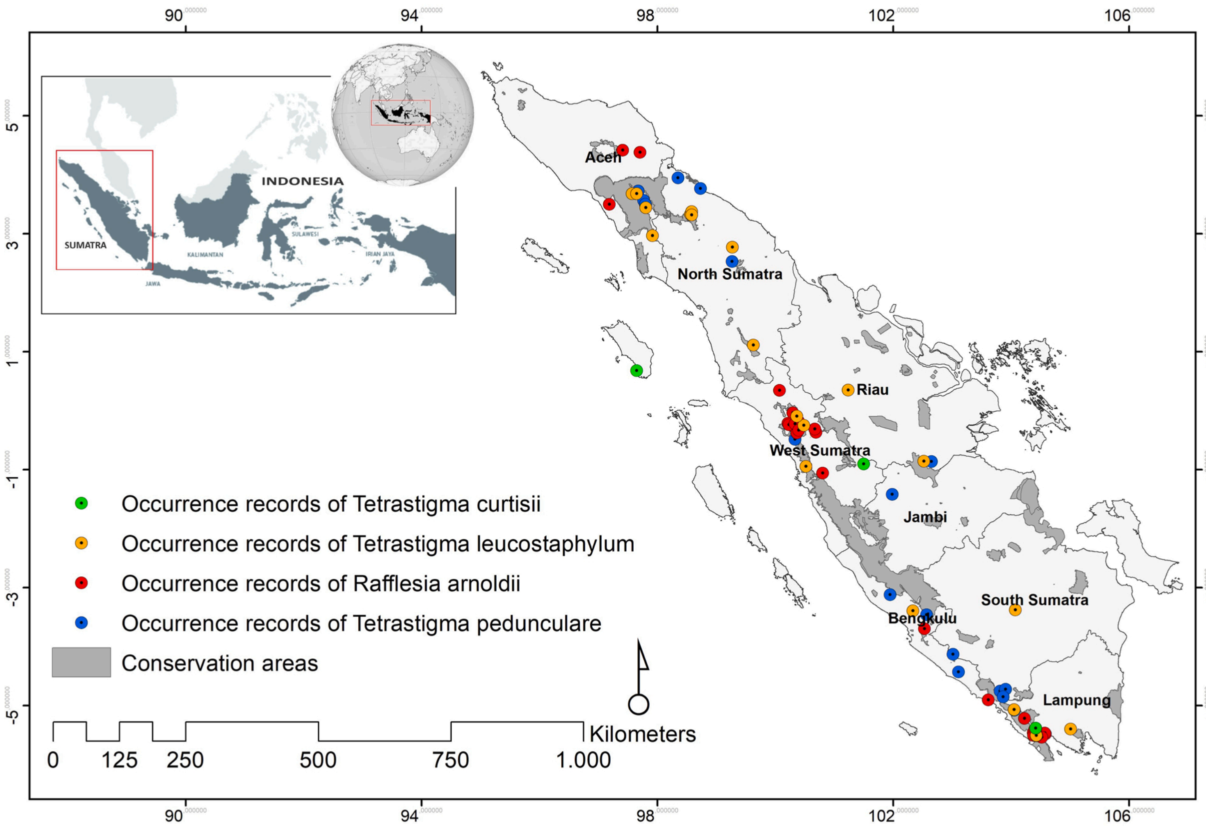

Fig. 1. The occurrence records of *Rafflesia arnoldii*, and three host plant species, namely *Tetrastigma curtisii*, *T. leucostaphylum* and *T. pedunculare* in Sumatra.

Table 1
Morphological diagnosis characters of *T. curtisii, T. leucostaphylum* and *T. pedunculare*.

Characters	*T. curtisii*	*T. leucostaphylum*	*T. pedunculare*
Tendrils	forked	stout	two branched
Stem	cylindrical	rough, grooved	rounded
Petiole length (cm)	3.4–8.6	3–11.6	7–15
Leaflets	3-(5)	3-(4)-5–7	(2)-3-(4)
Leaf blade	coriaceous, glabrous	sub-coriaceous, glabrous	coriaceous, glabrous above, densely covered with glaucous fine indumentum beneath
Terminal leaflet	broadly obovate to elliptic	lanceolate to oblong	broadly elliptical to obovate
Terminal leaf base	acute	acute	acute
Lateral leaflet	oblong	lanceolate to oblong, oblique	asymetrically oblong
Lateral leaflet base	obtuse	acute to rounded	oblique
Margin	serrate	serrate	serrate
Venations	easily recognized by its diffuse venation between the secondary veins, notably conspicuous adaxially	inconspicuous/smooth	cone shape adaxially and nearly rectangular abaxially

Sources: (Arshad et al., 2020; Latiff, 1984; Rahayu et al., 2018; Yeo et al., 2012) and direct observation.

other species of *Rafflesia*, not only in Sumatra but throughout the world.

2.3. Species distribution modeling (SDMs)

Habitat suitability data for species distribution modeling (SDMs) were obtained from previous research and downloaded from available websites (see below). These data include annual mean temperature, annual precipitation, elevation, soil data and land cover. Annual mean temperature and annual precipitation were extracted from WorldClim version 2.1. These variables are the average for the years 1970–2000 with the spatial resolution 30 s (1 km^2) (Fick and Hijmans, 2017) (https://www.worldclim.org/). The elevation data with resolution 30 s (1 km^2) was derived from the Shuttle Radar Topography Mission (SRTM) Digital Elevation Model Data (Farr et al., 2007; NASA SRTM, 2013). Slope was calculated from elevation data. Soil pH, soil type, soil organic carbon and Cation Exchange Capacity (CEC) were derived from SoilGrids (global gridded soil information). These data were available at a spatial resolution of 250 m (Hengl et al., 2017) (https://soilgrids.org/). Land cover data were derived from Moderate Resolution Imaging Spectroradiometer (MODIS) Land Cover Type (MCD12Q1) Version 6 (ORNL DAAC, 2018) (https://earthexplorer.usgs.gov/). The land cover data were from 2018 and represents our best estimates of the current land cover.

Habitat suitability was modeled using Maxent software version 3.4.4 for *R. arnoldii* and its host plants by implementing a machine learning technique called Maximum Entropy (MaxEnt) (Phillips et al., 2021). We used default setting on MaxEnt java program. However, for model assessment with few localities, a jackknife (or 'leave-one-out') procedure was applied. A model built using the remaining n-1 localities. Hence, for a species with n observed localities, n separate models were built for testing (Pearson et al., 2007). For the MaxEnt setting: random test percentage 1, regularization multiplier 1, number of background points 10^4, replicate run type (cross validation), maximum iteration 500, convergence threshold 10^{-5} and default prevalence value of 0.5.

The predicted suitable habitats of *R. arnoldii* and three species of *Tetrastigma* were intersected between each other to create three intersection areas (*R. arnoldii* and *T. curtisii*), (*R. arnoldii* and *T. pedunculare*) and (*R. arnoldii* and *T. leucostaphylum*). The intersection areas of those species were then overlaid with conservation areas to identify the high suitable habitats inside conservation areas. Four classes of potential habitats were grouped as follows: unsuitable ($\leq$ 0.10), low potential (0.11–0.30), moderate potential (0.31–0.70) and high potential ($\geq$ 0.71) (Choudhury et al., 2016; Qin et al., 2017; Yang et al., 2013).

3. Results

The predicted Maximum Entropy habitat models of *Rafflesia arnoldii* and three host plant species, namely *Tetrastigma curtisii*, *T. leucostaphylum* and *T. pedunculare* can be evaluated using Area Under Curve (AUC) values, representing the predictive skill of the model on a 0–1 basis. The model prediction of *R. arnoldii* has AUC value of 0.855, *T. curtisii* has 0.853, *T. pedunculare* has 0.749 and *T. leucostaphylum* has 0.725 Model outputs were used to map habitat suitability throughout Sumatra (Fig. 2).

The predicted highly suitable habitats of *R. arnoldii* covers areas an area of 3,248,189 ha throughout the Sumatra. The predicted highly suitable habitats of *T. leucostaphylum* and *T. pedunculare* cover relatively large areas throughout Sumatra compared to *T. curtisii*. The high suitable habitats of *T. curtisii*, *T. pedunculare* and *T. leucostaphylum* are respectively of 1,934,865 ha, 3,378,917 ha and 9,180,691 ha. In order to better predict the highly suitable habitats of *R. arnoldii* in conjunction with its host plants the intersection areas between *R. arnoldii* and the host plants are determined. The intersection areas of highly suitable habitat between *R. arnoldii* and *T. curtisii* covers a 307,910 ha area, *R. arnoldi* and *T. pedunculare* covers 894,630 ha and *R. arnoldii* and *T. leucostaphylum* covers 1,896,781 ha (Fig. 3).

The predicted highly suitable habitat based on the intersection areas of those species is mostly located outside of conservation

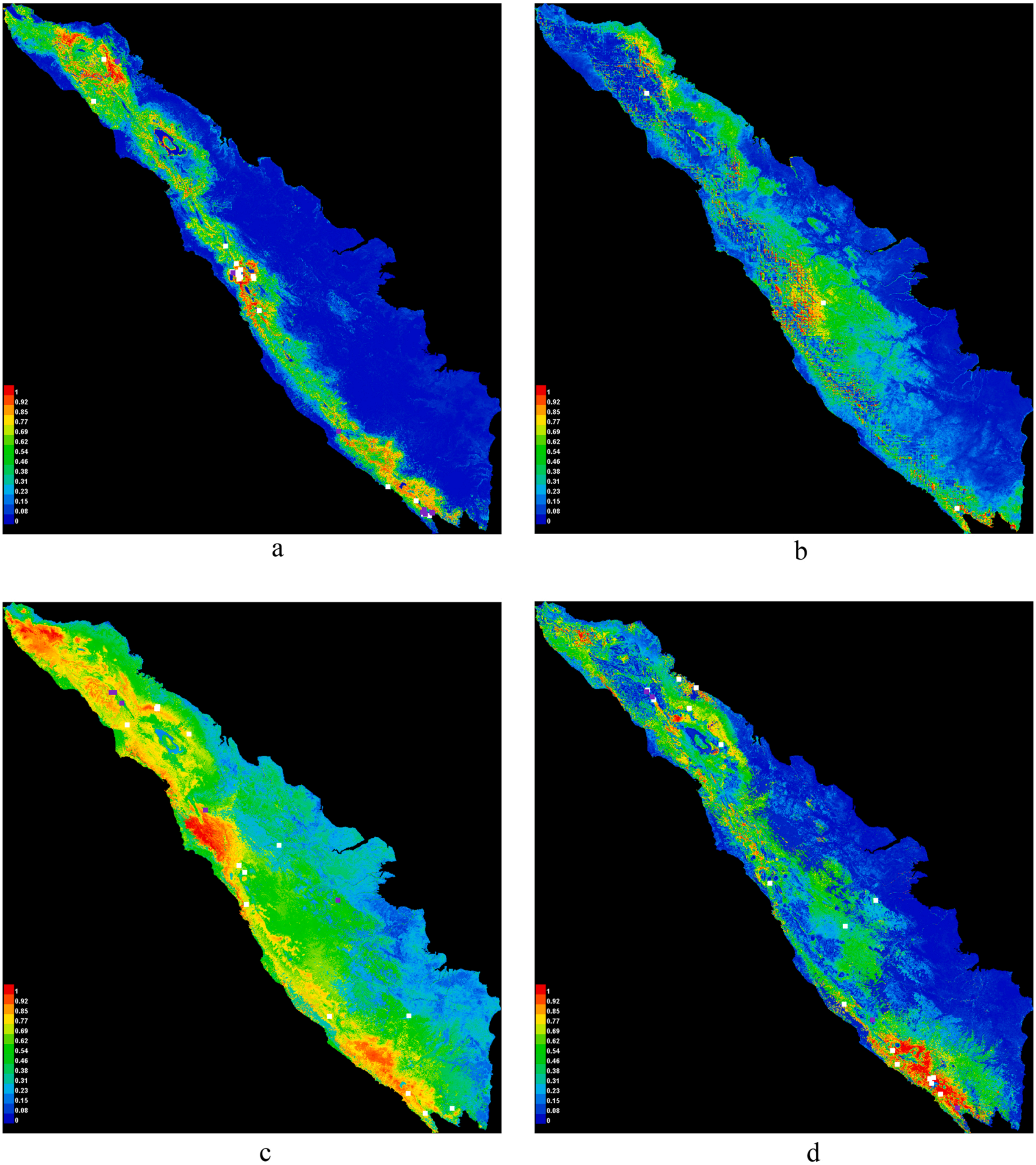

Fig. 2. The predicted suitable habitats provided by MaxEnt Models. (**a**) *Rafflesia arnoldii*; (**b**) *Tetrastigma curtisii*; (**c**) *T. leucostaphylum*; (**d**) *T. pedunculare*. The regions with the grid cells that have value > 0.5 indicating more suitable, while the regions with the value of grid cells < 0.5 indicating less suitable.

areas. The total highly suitable predicted outside conservation area includes 2,239,122.161 ha (72.33%), while the total suitable habitats inside conservation areas covers around 856,625.327 ha (27.67%). The intersection areas between *R. arnoldii* and *T. curtisii* includes 86,228.956 ha (28.11%) inside conservation areas throughout Sumatra, the intersection between *R. arnoldii* and *T. pedunculare* includes 204,565.783 ha (22.87%), and the intersection between *R. arnoldii* and *T. leucostaphylum* includes 565,830.588 ha (29.86%) (Fig. 4).

There are 34 conservation areas in Sumatra that identified as high suitable habitats between *R. arnoldii* and *T. curtisii*, 26 conservation areas for *R. arnoldi* and *T. pedunculare,* and 37 conservation areas for *R. arnoldii* and *T. leucostaphylum* (Table 2).

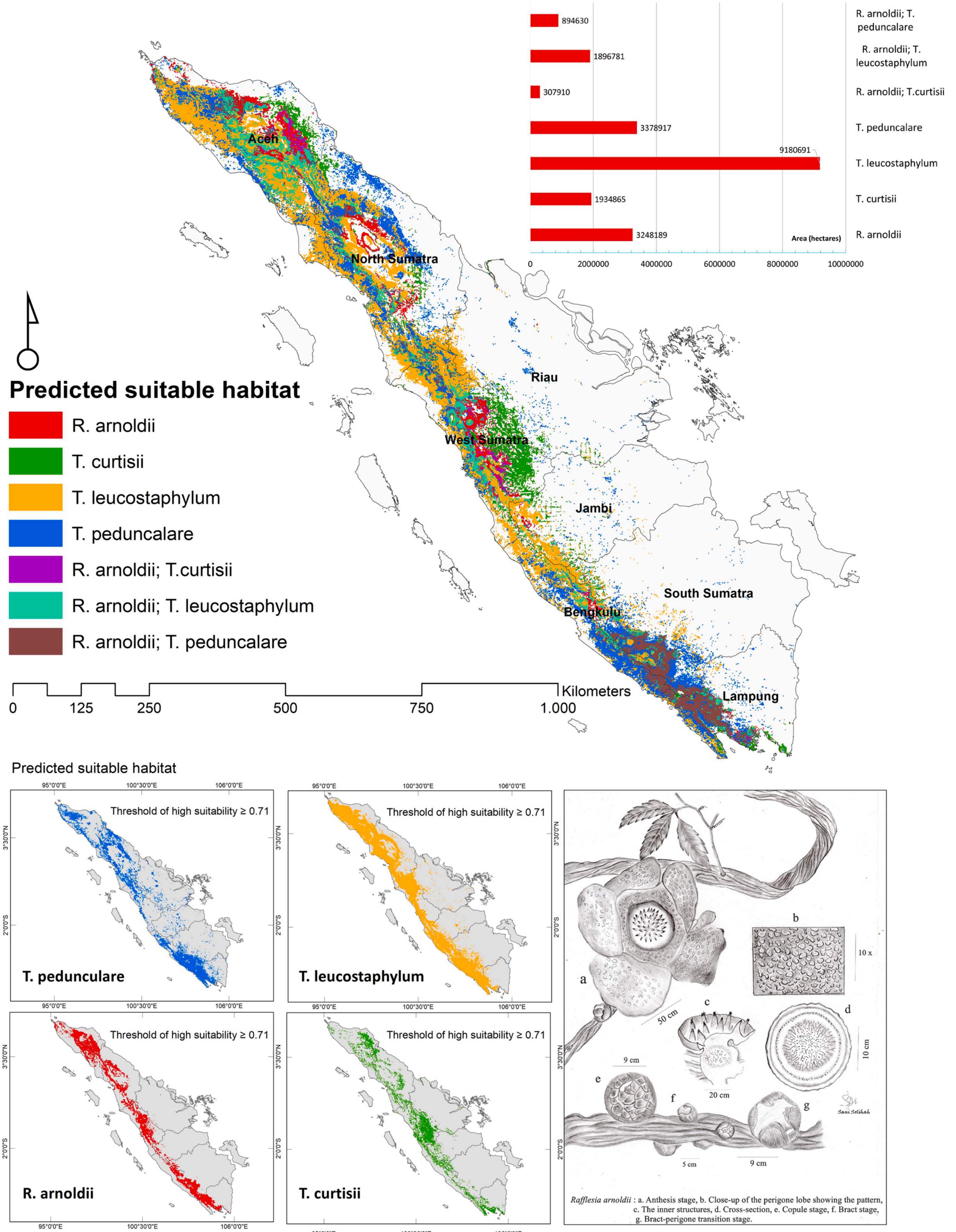

Fig. 3. The predicted intersection areas of *Rafflesia arnoldii* and three species of *Tetrastigma* as its host plants.

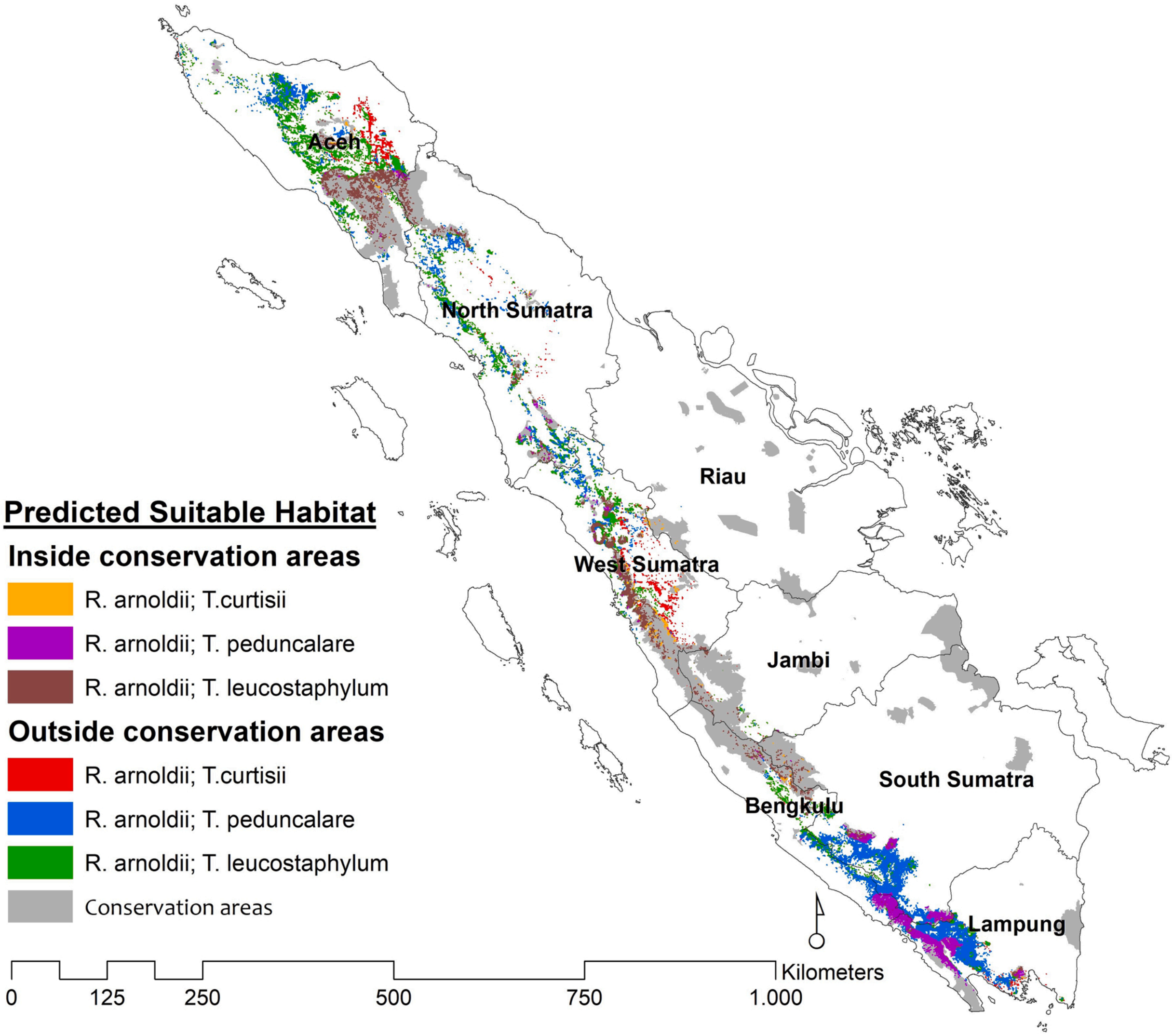

Fig. 4. The predicted intersection areas between *Rafflesia arnoldii* and three species of *Tetrastigma* that located inside and outside conservation areas.

MaxEnt modeling allows identification of the relative influence of the environmental variables on habitat suitability. The three most important variables affecting the habitat suitability of *R. arnoldii* are mean annual temperature, slope and elevation. Whereas soil organic carbon, soil type, land cover and precipitation of driest month were found to be biophysical variables moist important for predicting host plant habitat suitability (Fig. 5).

4. Discussion

According to the observed occurrence records, *R. arnoldii* is evenly distributed throughout the western side of Sumatra along the Bukit Barisan Mountain range from Lampung to Aceh. While only few occurrence records of its host plants are available due difficulty in identification in the wild. The occurrence records of *R. arnoldii* and its host plants are used to model the habitat suitability for those species. There are three criteria to choose the actual data points: 1). Using the actual data coordinate points of targeted species locations, 2) Choosing the data points with detailed location information on the targeted species, and 3). Excluding data points located in the built-up areas and human-cultivated lands. The presence data may be biased depending on accuracy of the data, sampling methods and the species detection possibility (Barbet-Massin et al., 2010).

Another inputs that are very important in the modeling process are environmental variables. Environmental variables selection process that are meaningful in determining the occurrence records of the parasitic plant and its host plants remains a challenge (Araújo et al., 2019). The choice to select the correct predictors is a crucial in determining the habitat suitability of the species (Petitpierre et al., 2017; Porfirio et al., 2014). To build this model predictions, there are four predictors (topography, soil, climate and land cover)

Table 2
Identified conservation areas that suitable habitats of the *Rafflesia arnoldii* and three species of *Tetrastigma* as its host plants.

Conservation areas	Areas status	Intersection areas		
		RA and *TC*	*RA* and *TP*	*RA* and *TL*
Air Putih	Nature Recreation Park	x		
Arau Hilir dan Air Terusan	Wildlife Reserve	x	x	x
Baringin Sati	Nature Reserve	x		
Barisan	Wildlife Reserve	x	x	x
Barumun	Wildlife Reserve	x	x	x
Batang Gadis	National Park	x	x	x
Batang Palupuh	Nature Reserve	x		
Batang Pangean I	Nature Reserve	x		
Batang Pangean II	Nature Reserve	x		
Bukit Barisan	Grand Forest Park	x		x
Bukit Barisan Selatan	National Park	x	x	x
Bukit Kaba	Nature Recreation Park	x		x
Bukit Rabang - Gluguran	Grand Forest Park		x	x
Bukit Rimbang Bukit Baling	Wildlife Reserve	x		
Cut Nyak Dien	Grand Forest Park			x
D. Sicikeh-cikeh	Nature Recreation Park			x
Danau TES	Nature Recreation Park	x	x	
Dolok Sibual-buali	Nature Reserve	x		x
Dolok Sipirok	Nature Reserve			x
Dolok Surungan	Wildlife Reserve	x	x	x
Dr. Muhammad Hatta	Grand Forest Park			x
Gumai Pasemah	Wildlife Reserve	x	x	x
Gunung Leuser	National Park	x	x	x
Gunung Leuser National Park	UNESCO-MAB Biosphere Reserve	x	x	x
Gunung Marapi	Nature Recreation Park	x		x
Gunung Raya	Wildlife Reserve	x	x	x
Gunung Sago Malintang	Nature Recreation Park	x		x
Hutan Pinus/Janthoi	Nature Reserve		x	x
Isau-isau Pasemah	Wildlife Reserve	x	x	x
Janthoi	Nature Recreation Park		x	
Kerinci Seblat	National Park	x	x	x
Kuta Malaka	Nature Recreation Park		x	x
Lembah Anai	Nature Reserve	x		x
Lembah Harau	Nature Recreation Park	x		
Lingga Isaq	Hunting Park	x	x	x
Lubuk Raya	Nature Reserve	x		x
Malampah Alahan Panjang	Wildlife Reserve	x	x	x
Maninjau	Nature Reserve	x	x	x
Mega Mendung	Nature Recreation Park			x
Pocut Meurah Intan	Grand Forest Park			x
Rimbo Panti	Nature Recreation Park		x	x
Semidang Bukit Kabu	Hunting Park		x	x
Singgalang Tandikat	Nature Recreation Park	x	x	x
Siranggas	Wildlife Reserve	x	x	x
Tropical Rainforest Heritage of Sumatra	World Heritage Site (natural or mixed)	x	x	x
Wan Abdul Rahman	Grand Forest Park	x	x	x

Note: RA = *R. arnoldii*, TC = *T. curtisii*, TP = *T. pedunculare*, TL = *T. leucostaphylum*, the mark (x) indicates the suitable areas of *R. arnoldii*.

that used as inputs. We considered those variables are meaningful for determining the habitat suitability of those species. The inclusion of land cover as input of the model was considered to be important. The inclusion of land cover improved significantly the explanatory power of bioclimatic models and the most relevant variables across groups were those not explained or poorly explained by climate (Thuiller et al., 2004).

The predictive habitat suitability model for *R. arnoldii* and *T. curtisii* have the AUC value > 0.80 indicating that those models have good performance, whereas *T. pedunculare* and *T. leucostaphylum* have the AUC value > 0.70 indicating that those models have fair performance. The value of AUC represents the categories of predictive model performance, model with AUC in range 0.9–1 (excellent), 0.8–0.9 (good), 0.7–0.8 (fair), 0.6–0.7 (poor), and 0.5–0.6 (fail) (Krzanowski and Hand, 2009). In addition, the predictive model that has the value of AUC in range 0.7–0.8 is considered acceptable, and 0.8–0.9 is considered excellent (Hosmer and Lemeshow, 2000). Although only few records of the host plants of *R. arnoldii* in which three records for *T. curtisii*, the evaluation of model performance was acceptable with the AUC value > 0.80.

A jackknife (or 'leave-one-out') procedure was applied to model few presence localities of *T. curtisii*. Using the jackknife test applied to the MaxEnt model, high success rates and statistical significance were obtained with small sample size as low as five (Pearson et al., 2007). However, a model that includes less than four presence locations has a poor success rate (Pearson et al., 2007). A critical difficulty in the current study is small number of *T. curtisii* locations of from the few available studies. In order to have a more reliable

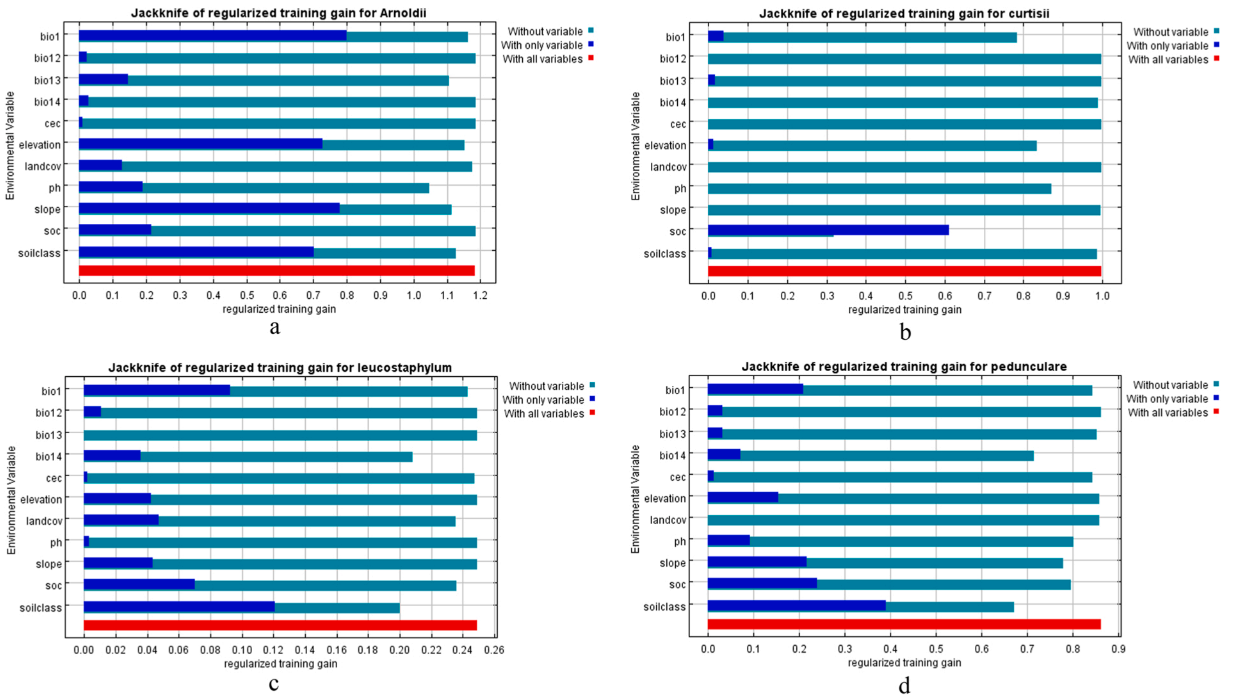

Fig. 5. The importance variables that affecting *R. arnoldii* and three species of *Tetrastigma* as its host plants. (**a**) *Rafflesia arnoldii*; (**b**) *Tetrastigma curtisii*; (**c**) *Tetrastigma leucostaphylum*; (**d**) *Tetrastigma pedunculare*.

model for *T. curtisii*, additional presence records should be obtained. Some previous studies used MaxEnt modeling to predict the potential distribution of endemic or rare species with small number of records, occurrence points of 23 (Kebede et al., 2012); occurrence points of 10 (Deb et al., 2017); occurrence points of 32 (Abdelaal et al., 2019).

The suitable habitats of the species represented by the value range from 0 to 1. The regions that have the value more than 0.5 indicating those regions are more suitable habitats of this species, while the value less than 0.5 indicating those regions are less suitable habitats of this species. The predicted suitable habitats of *R. arnoldii* are mostly in portions of southern, central and northern Sumatra. All those predicted suitable habitats are located along the Bukit Barisan Mountain range. It consists primarily of active and non-active volcanoes shrouded in dense jungle cover with higher slopes. This corresponds well with the observation records with almost all points found in western Sumatra. Eastern Sumatra is predicted as less suitable habitat represented by blue color (Fig. 2). The regions in eastern Sumatra are dominated by peat swamp forests that are not suitable for this species. The suitable habitats of *T. curtisii* are mostly predicted in West Sumatra, North Sumatra, Bengkulu and eastern Aceh. The regions in Lampung, Bengkulu, small part regions of West Sumatra, North Sumatra and some regions spread throughout Aceh are predicted as suitable habitat for *T. pedunculare*. Highly suitable habitats for *T. leucostaphylum* are predicted mostly in entire western part of Sumatra from Lampung to Aceh. The observed location data points are sometimes not predicted to be highly likely suitable habitat due to data limitations. In the evaluation of model performance there are two type of errors (commission errors and omission errors). A commission error an occurrence of absence wrongly predicted as presence (Krzanowski and Hand, 2009), while an omission error is a presence observation wrongly predicted an absence (Lobo et al., 2008). Those two type of errors may affect the accuracy of model in spatially predicting the habitat suitability of the targeted species in this study.

The most important biophysical variable contributing to the occurrence of this species is mean annual temperature, followed by slope. According to (Ramadhani et al., 2017), the habitat of *R. arnoldii* has the temperature range 25–29 °C in moderate slope hills (30–45%). This condition is likely associated with reliable water flow away from upper areas. The slope is a very complex environment for the plant community (Chiatante et al., 2002). Elevation was the third most important factor affecting the occurrence of *R. arnoldii*. This species has been found in lowland forests at an altitude from 35 to 600 m above sea level (Susatya, 2011), from 490 to 1024 m above sea level (Pranata et al., 2019) and from a 490 to 558 m above sea level (Ramadhani et al., 2017). The occurrence of *R. arnoldii* is determined by its host plants. Soil organic carbon was the most important modeled biophysical variable affecting the occurrence of the host plants of *R. arnoldii*. Those host plants tend to occupy the primary forest, secondary forest, and lowland dipterocarp-forest that have a relatively dense canopy cover (Latiff, 1984; Rahayu, 2017; Wan Zakaria et al., 2017; Yeo et al., 2012). The canopy cover of vegetation creates a warm and moist microclimate under the canopy which accelerates the decomposition of litter (Wang et al., 2010). This could affect accumulation of soil organic carbon. Soil type was also important variable that affect the presence of the host plants. According to the digital soil map of the world (Sanchez et al., 2009), the actual presence localities and predicted habitats of the host plants have various type of soils, including Humic Andosols, Humic Acrisols, Orthic Acrosols, Dystric Fluvisols, Dystric Cambisols and Eutric Fluvisols. Only few regions in eastern part of Sumatra are predicted as suitable habitats because Histosols are widely distributed there. Histosols is a soil primarily comprised of organic materials (peaty soils). Other important prediction variables include mean annual temperature, elevation, and slope. These variables are similar to the most important contributing factors affecting the occurrence of *R. arnoldii*.

The habitat suitability map of *R. arnoldii* and its host plants resulting from this study may not precisely predict the locations where those species currently occur because it depends only on biophysical variables including topography, soils, climate and land cover. Factors such as human management and site history could also be important. Although the predicted habitat suitability of a location might be high there are many reasons why the species might not be found at that location. It is possible that the species are not able to disperse to that location. Unidentified biotic interactions could inhibit the recruitment or survival in some locations. Possibly the species was once found in the predicted habitat but has since been extirpated from the area. A failure to find *R. arnoldii* even when present might be due to dormancy. In contrast, the model may predict that a certain region is unsuitable habitat, but the species may occur in that location. Some species are able to disperse to a location and adapt physiologically to the unsuitable habitats (Peterson et al., 2011). Given the difficulty in exhaustive sampling to determine the locations of rare, but important species, MaxEnt modeling is useful to assess potential habitat suitability of *R. arnoldii* and other species of *Rafflesia* throughout the world.

The findings of this study may be used by the Government of Republic Indonesia, c.q. Ministry of Environment and Forestry for establishing protected areas and conservation-based management improvement and could also help inform the *R. arnoldii* and its host plants listing status in IUCN red list category in the future. We believe that this study is the first report modeling potential habitat suitability of a parasitic plant and its host plants. Further studies on other species of parasitic plant by incorporated biophysical variables, dispersal aspect, human activities, and site habitat history could provide an important tool for management and conservation.

5. Conclusions

The predicted best habitat suitability of *R. arnoldii* in Sumatra tends to be concentrated on the western side of Sumatra along the Bukit Barisan Mountain range. However, the suitable habitat assessed by also considering its host plants include a much smaller area. The highly suitable habitats of *R. arnoldii* and its host plants are mostly predicted to be outside conservation areas. There are 46 conservation areas that are predicted to be highly suitable habitats for *R. arnoldii* and its host plants.

CRediT authorship contribution statement

The following statements should be used "Conceptualization, E.R. and A.Y.; Methodology, A.Y., P.D.R.; Software, E.R., A.Y. and P.D.R.; Validation, J.R.W., Y. and S.M.; Formal analysis, E.R., A.Y. and P.D.R.; Investigation, E.M. and I.P.A.; Resources, E.M., I.P.A., I.A.F., I.R. and S.M.; Data curation, S.M., E.M. and S.M.S.; Writing – original draft, All authors.; Writing – review & editing, All. authors; Visualization, A.Y., P.D.R. and S.M.S.; Supervision, A.Y., S.M., J.R.W. and W.P.C.J. All authors have read and agreed to the published version of the manuscript.

Funding

This research received no external funding.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We thank the Director of Research Center for Plant Conservation and Botanic Gardens who allowing us to conduct this study. Our great appreciation delivered to our research coordinator that support all of our research activities.

References

Abdelaal, M., Fois, M., Fenu, G., Bacchetta, G., 2019. Using MaxEnt modeling to predict the potential distribution of the endemic plant Rosa arabica Crép. in Egypt. Ecol. Inform. 50 (January), 68–75. https://doi.org/10.1016/j.ecoinf.2019.01.003.

Anderson, R.P., Martínez-Meyer, E., 2004. Modeling species' geographic distributions for preliminary conservation assessments: an implementation with the spiny pocket mice (Heteromys) of Ecuador. Biol. Conserv. 116 (2), 167–179. https://doi.org/10.1016/S0006-3207(03)00187-3.

Araújo, M.B., Anderson, R.P., Márcia, B.A., Beale, C.M., Dormann, C.F., Early, R., Garcia, R.A., Guisan, A., Maiorano, L., Naimi, B., Al, E., 2019. Standards for distribution models in biodiversity assessments. Sci. Adv. 5 (1), eaat4858.

Arshad, S., Juhari, M.A.A., Talip, N., Wahab, N.A.A., Fadzilah, S., Adam, J., 2020. Perbandingan Ciri Anatomi Daun Tetrastigma rafflesiae (Miq.) Planchon dan Tetrastigma pedunculare (Wall. ex Laws.) Planch. di Semenanjung Malaysia. Sains Malays. 49 (4), 721–728.

Asiandu, A.P., 2021. Biological aspects and conservation of Rafflesia arnoldii: Indonesian endemic plant conservation. Konserv. Hayati 17 (2), 49–55.

Barbet-Massin, M., Thuiller, W., Jiguet, F., 2010. How much do we overestimate future local extinction rates when restricting the range of occurrence data in climate suitability models? Ecography 33 (5), 878–886. https://doi.org/10.1111/j.1600-0587.2010.06181.x.

Bendiksby, M., Schumacher, T., Gussarova, G., Jamili, N.J., Mat-Salleh, K., Sofiyanti, N., Madulid, D., Smith, S.A., Barkman, T., 2010. Elucidating the evolutionary history of the Southeast Asian, holoparasitic, giant-flowered Rafflesiaceae: pliocene vicariance, morphological convergence and character displacement. Mol. Phylogenet. Evol. 57, 620–633.
Chen, P.T., Chen, L.Q., Wen, J., 2011. The first phylogenetic analysis of Tetrastigma (Miq.) Planch., the host of Rafflesiaceae. Taxon 60, 499–512.
Chiatante, D., Scippa, S.G., Di Iorio, A., Sarnataro, M., 2002. The influence of steep slopes on root system development. J. Plant Growth Regul. 21 (4), 247–260. https://doi.org/10.1007/s00344-003-0012-0.
Choudhury, M.R., Deb, P., Singha, H., Chakdar, B., Medhi, M., 2016. Predicting the probable distribution and threat of invasive Mimosa diplotricha Suavalle and Mikania micrantha Kunth in a protected tropical grassland. Ecol. Eng. 97, 23–31. https://doi.org/10.1016/j.ecoleng.2016.07.018.
Combes, C., 2001. Parasitism. University of Chicago Press.
Deb, C.R., Jamir, N.S., Kikon, Z.P., 2017. Distribution prediction model of a rare orchid species (Vanda bicolor Griff.) using small sample size. Am. J. Plant Sci. 8, 1388–1398. https://doi.org/10.4236/ajps.2017.86094.
Elith, J., Graham, C.H., Anderson, R.P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R.J., Huettmann, F., Leathwick, J.R., Lehmann, A., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29, 129–151.
Elith, J., Leathwick, J.R., 2009. Species distribution models: ecological explanation and prediction across space and time. Annu. Rev. Ecol. Evol. Syst. 40, 677–697. https://doi.org/10.1146/annurev.ecolsys.110308.120159.
Ellen, A., Nasihin, I., Supartono, T., 2019. Pemetaan Kesesuaian Habitat Rafflesia (Rafflesia arnoldii R. Br) di Taman Nasional Bukit Barisan Selatan. Konserv. Untuk Kesejaht. Masy. I 174–183.
EoF, 2018. Sumatra. ⟨https://www.eyesontheforest.or.id/backgrounders/sumatra⟩.
Farr, T.G., Rosen, P.A., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., Alsdorf, D., 2007. The need for global topography. Rev. Geophys. 45 (2), 1–43. ⟨http://www2.jpl.nasa.gov/srtm/SRTM_paper.pdf⟩.
Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.
Franklin, J., Miller, J.A., 2009. Mapping Species Distributions-Inference and Predictions. Cambridge University Press.
GBIF.org, 2022a. GBIF Occurrence Download. ⟨https://doi.org/10.15468/dl.p7du5g⟩.
GBIF.org, 2022b. GBIF Occurrence Download. ⟨https://doi.org/10.15468/dl.8tuavs⟩.
GBIF.org, 2022c. GBIF Occurrence Download. ⟨https://doi.org/10.15468/dl.mcst4u⟩.
GBIF.org, 2022d. GBIF Occurrence Download. ⟨https://doi.org/10.15468/dl.2ncmte⟩.
Hengl, T., De Jesus, J.M., Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS One 12 (2), 1–40. https://doi.org/10.1371/journal.pone.0169748.
Hidayati, S.N., Walck, J.L., 2016. A review of the Biology of Rafflesia: what do we know and what's next? Bul. Kebun Raya 19 (2), 67–78.
Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression, 2nd ed. John Wiley and Sons. https://doi.org/10.1002/0471722146.
Kebede, F., Bekele, A., Moehlman, P., Evangelista, P., 2012. Endangered Grevy's zebra in the Alledeghi Wildlife Reserve, Ethiopia: species distribution modeling for the determination of optimum habitat. Endanger. Species Res. 17 (3), 237–244. https://doi.org/10.3354/esr00416.
Krzanowski, W.J., Hand, D.J., 2009. ROC Curves for Continuous Data, 1st ed. Chapman and Hall/CRC.
Kuijt, J., 1969. The Biology of Parasitic Flowering Plants. University of California Press.
Latifah, D., Munawaroh, E., Wijayanti, S., 2012. Eksplorasi Flora di Kawasan Taman Nasional Bukit Barisan Selatan Ka. Propinsi Lampung, Tanggamus.
Latiff, A., 1984. Studies in Malesian Vitaceae, VII. The genus Tetrastigma in the Malay Peninsula. Gardens' Bull. 36 (2), 213–228.
Lobo, J.M., Jiménez-valverde, A., Real, R., 2008. AUC: a misleading measure of the performance of predictive distribution models. Glob. Ecol. Biogeogr. 17 (2), 145–151. https://doi.org/10.1111/j.1466-8238.2007.00358.x.
Meijer, W., 1997. Rafflesiaceae. Flora Malesiana-Series 1. Spermatophyta 13 (1), 1–42.
Munawaroh, E., Suhendar, Wijayanti, S., 2013. Eksplorasi Flora di Kawasan Taman Nasional Bukit Barisan Selatan, Kabupaten Pesisir Barat, Lampung.
NASA SRTM, 2013. Shuttle Radar Topography Mission (SRTM) Global, Distributed by OpenTopography. ⟨https://doi.org/10.5069/G9445JDF⟩.
ORNL DAAC, 2018. MODIS and VIIRS Land Products Global Subsetting and Visualization Tool. ORNL DAAC, Oak Ridge, Tennessee, USA. ⟨https://daac.ornl.gov/cgi-bin/dsviewer.pl?ds_id=1379⟩.
Pearson, R.G., Raxworthy, C.J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. J. Biogeogr. 34 (1), 102–117. https://doi.org/10.1111/j.1365-2699.2006.01594.x.
Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martínez-Meyer, E., Nakamura, M., Araújo, M.B., 2011. Ecological Niches and Geographic Distributions. Princeton University Press.
Petitpierre, B., Broennimann, O., Kueffer, C., Daehler, C., Guisan, A., 2017. Selecting predictors to maximize the transferability of species distribution models: lessons from crosscontinental plant invasions. Glob. Ecol. Biogeogr. 26 (3), 275–287.
Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. Ecol. Model. 190, 231–259. https://doi.org/10.1016/j.ecolmodel.2005.03.026.
Phillips, S.J., Dudik, M., Schapire, R.E., 2021. Maxent Software for modelling species niches and distribution (3.4.1). ⟨http://biodiversityinformatics.amnh.org/open_source/maxent/⟩.
Porfirio, L.L., Harris, R.M.B., Lefroy, E.C., Hugh, S., Gould, S.F., Lee, G., Bindoff, N.L., Mackey, B., 2014. Improving the use of species distribution models in conservation planning and management under climate change. PLoS One 9 (11), 21.
Pranata, S., Sulistijorini, Chikmawati, T., 2019. Ecology of Rafflesia arnoldii (Rafflesiaceae) in Pandam Gadang West Sumatra. J. Trop. Life Sci. 9 (3), 243–251. https://doi.org/10.11594/jtls.09.03.05.
Pranata, S., Sulistijorini, Chikmawati, T., 2020. Habitat vegetation of Rafflesia arnoldii (Raffelsiaceae) in Panorama Baru Ngarai Sianok West Sumatra. J. Eng. Health Sci. 4, 135–148.
Qin, A., Liu, B., Guo, Q., Bussmann, R.W., Ma, F., Jian, Z., Xu, G., Pei, S., 2017. Maxent modeling for predicting impacts of climate change on the potential distribution of Thuja sutchuenensis Franch., an extremely endangered conifer from southwestern China. Glob. Ecol. Conserv. 10, 139–146. https://doi.org/10.1016/j.gecco.2017.02.004.
Rahayu, Y., 2017. Revision of Tetrastigma (Vitaceae) in Sumatra. IPB University, Bogor.
Rahayu, Y., Chikamawati, T., Widjaja, E.A., 2018. Nomenclatural study of Tetrastigma Leucostaphylum and Tetrastigma Rafflesiae (Vitaceae): two common hosts of Rafflesia in Sumatra. Reinwardtia 17 (1), 59. https://doi.org/10.14203/reinwardtia.v17i1.3552.
Rahma, Y., Arma, S.P., Syamsuardi, 2017. Analisis vegetasi habitat Rafflesia Gadutensis Meijer. di Taman Hutan Raya Dr. M. Hatta, Kota Padang. J. Biol. Sci. 4 (2), 196–201.
Ramadhani, D.N., Setiawan, A., Master, J., 2017. Populasi dan Kondisi Lingkungan Rafflesia arnoldii di Rhino-Camp Resort Sukaraja Atas Taman Nasional Bukit Barisan Selatan (TNBBS). J. Sylva Lestari 5 (2), 128. https://doi.org/10.23960/jsl25128-141.
Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426 (6968), 837–841. https://doi.org/10.1038/nature02205.
Sanchez, P.A., Ahamed, S., Carré, F., Hartemink, A.E., Hempel, J., Huising, J., Lagacherie, P., Mcbratney, A.B., Mckenzie, N.J., De, M., Mendonça-santos, L., Minasny, B., Montanarella, L., Okoth, P., Palm, C.A., Sachs, J.D., Shepherd, K.D., Vågen, T., Vanlauwe, B., Zhang, G., 2009. Digital soil map of the world. Science 325 (5941), 680–681. https://doi.org/10.1126/science.1175084.
Setyowati, F.M., Wardah, W., 2007. Diversity of medicinal plant by Talang Mamak tribe in surrounding of Bukit Tiga Puluh National Park, Riau. Biodivers. J. Biol. Divers. 8 (3), 228–232. https://doi.org/10.13057/biodiv/d080313.

Susatya, A., 2011. Rafflesia, Pesona Bunga Terbesar di Dunia. Pustaka Nasional.

Susatya, A., 2020. The growth of flower bud, life history, and population structure of rafflesia arnoldii (Rafflesiaceae) in Bengkulu, Sumatra, Indonesia. Biodiversitas 21 (2), 792–798. https://doi.org/10.13057/biodiv/d210247.

Susatya, A., Hidayati, S.N., Riki, S., 2017. Rafflesia kemumu (Rafflesiaceae), a new species from Northern Bengkulu, Sumatra, Indonesia. Phytotaxa 326 (3), 211–220. https://doi.org/10.11646/phytotaxa.326.3.5.

Thorn, J.S., Nijman, V., Smith, D., Nekaris, K.A.I., 2009. Ecological niche modelling as a technique for assessing threats and setting conservation priorities for Asian slow lorises (Primates: Nycticebus). Divers. Distrib. 15 (2), 289–298. https://doi.org/10.1111/j.1472-4642.2008.00535.x.

Thuiller, W., Araujo, M.B., Lavorel, S., 2004. Do we need land-cover data to model species distributions in Europe? J. Biogeogr. 31 (3), 353–361.

Veldkamp, J.F., 2008. The correct name for the Tetrastigma (Vitaceae) host of Rafflesia (Raffleciaceae) in Malesia and a (not so) new species. Reinwardtia 12 (4), 261–265.

Veldkamp, J.F., 2009. Notes on the Names of the Tetrastigma (Vitaceae) Hosts of Rafflesia (Rafflesiaceae). Reinwardtia 13 (1), 75–78.

Wan Zakaria, W.N.F., Puad, A.S.A., Zainudin, R., Latiff, A., 2017. A revision of Tetrastigma (Miq.) Planch. (Vitaceae) in Sarawak, Borneo. Malay. Nat. J. 69 (1), 71–90.

Wang, S., Ruan, H., Han, Y., 2010. Effects of microclimate, litter type, and mesh size on leaf litter decomposition along an elevation gradient in the Wuyi Mountains, China. Ecol. Res. 25 (6), 1113–1120. https://doi.org/10.1007/s11284-010-0736-9.

Wen, J., 2007. Vitaceae. In: Kubitzki, K. (Ed.), The Families and Genera of Vascular Plants. Springer.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J.R., Lehmann, A., Lohmann, L., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Zimmermann, N.E., 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14 (5), 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x.

Yang, X.Q., Kushwaha, S.P.S., Saran, S., Xu, J., Roy, P.S., 2013. Maxent modeling for predicting the potential distribution of medicinal plant, Justicia adhatoda L. in Lesser Himalayan foothills. Ecol. Eng. 51, 83–87. https://doi.org/10.1016/j.ecoleng.2012.12.004.

Yeo, C.K., Ang, W.F., Lok, A.F.S.L., 2012. Tetrastigma Planch. (Vitaceae) of Singapore: with a special note on Tetrastigma dichotomum (Bl.) Planch. Nat. Singap. 1920 (0019172), 263–270.

Zuhud, E.A.M., Hikmat, A., Jamil, N., 1998. Rafflesia Indonesia: Keanekaragaman, Ekologi dan Pelestariannya. Yayasan Suaka Alam dan Suaka Margasatwa Indonesia dan Laboratorium Konservasi Tumbuhan Jurusan Konservasi Sumberdaya Hutan, Fakultas Kehutanan, IPB University.