Projecting expansion range of *Selaginella zollingeriana* in the Indonesian archipelago under future climate condition

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Abstract. *Setyawan AD, Supriatna J, Nisyawati, Nursamsi I, Sutarno, Sugiyarto, Sunarto, Pradan P, Budiharta S, Pitoyo A, Suhardono S, Setyono P, Indrawan M. 2021. Projecting expansion range of* Selaginella zollingeriana *in the Indonesian archipelago under future climate conditions. Biodiversitas 22: 2088-2103.* The expansion of plant species to outside areas of its original localities has attracted great interest in theoretical ecology. The scientific curiosity of such phenomenon is even deeper when the geographical expansion is confined by natural boundaries and affected by environmental changes, including climates. This study aimed to predict the current suitable habitat niche of *Selaginella zollingeriana* Spring, a species with original distribution in Java Island, and to project its potential suitable niche in the Indonesian archipelago accounting for future climate conditions. In doing so, we applied the Ecological Niche Modelings (ENMs) using MaxEnt algorithm by employing 30 presence data of *S. zollingeriana* and twelve enviro-climatic variables. The model predicted around 17.22% (22,095 km^2) of the Java Island area is potentially suitable for current habitat niche of *S. zollingeriana*, consisting of 10.93% (14,028 km^2), 4.75% (6,097 km^2), and 1.54% (1,970 km^2) of low, medium, and high suitability areas, respectively. Under future scenarios, the model predicted the possibility of species expansion into the other four big islands (i.e., Sumatera, Borneo, Sulawesi, and Papua). Nonetheless, the model also predicted a declining trend of the availability of suitable niches wherein from 2030 to 2080 the modeled niche declined about 58% and 59% under the most optimistic and most pessimistic climate change projections, respectively. While this study provides a primary example in predicting species expansion in tropical archipelago, similar studies in a range of contexts (e.g., species, region) are recommended to add more evidence to strengthen the theoretical ground of expansion ecology under climate changes.

Keywords: Climate change, endemic plant, Indonesia, *Selaginella zollingeriana*

INTRODUCTION

Plant species expansion is an ecological phenomenon that represents the proliferation, spread, and persistence of species transported by various means (e.g., human activities, animals, wind) to new and potentially distant ranges. Classic diffusion theory of species expansion typically considers scenarios of symmetrical, radial expansion from a central point, the speed of which is determined by the dispersal ability and reproductive rate of the population (Skellam 1951). The radial expansion of species theoretically occurs either at a constant rate that increases linearly along time, or at an accelerating rate wherein the distances gained increase each year (Shigesada et al. 1995). Theoretical and empirical approaches to analyzing range expansion have highlighted the importance of intra-species interactions, evolution, long-range dispersal events, temporal variability, and spatial heterogeneity as factors that significantly influence the

expansion process (reviewed in Hastings et al. 2005). Furthermore, landscape structure and configuration are also particularly crucial since few expanded landscapes are homogenous and geographical boundaries can restrict the extent of the expanded range (With 2002; LaMorgia et al. 2011). While model study typically focuses on range expansion from a single point of introduction, multiple introduction points are more coherent since it can enhance the likelihood of establishment and can ensure expansion range increase in heterogeneous landscape bounded by coastline, such as Indonesia (e.g. Kolbe et al. 2004; Miller et al. 2005; Urban et al. 2008; Zalewski et al. 2010; Sakai et al. 2001).

The 21st century experienced the most robust global warming of the last millennium, and future temperature rises are likely to exceed this trend with a predicted increase of between 1.7°C and 4°C until the end of the century (Solomon et al. 2007). The potential impact of these rapid changes of climate on the conservation and

distribution of biodiversity is something that must become an object of great concern. One of the major effects is that animal and plant species worldwide might move to higher latitudes and elevations in response to deviate off the enviro-climatic conditions to which they are adapting (Parmesan 2006). Several model-based projections suggested that the expected future climate conditions would allow many species to expand their current distribution range several hundred kilometers towards higher latitudes and/or elevations within a few decades (Skov and Svenning 2004; Struebig et al. 2015). Much ambiguity exists, however, to which extent species will be capable of achieving such large-scale expansions in pace with rapid changes of climate. The answer to this question might include wide-ranging ecological and evolutionary consequences spanning from the population to the biome level. Therefore, the expansion process might strongly affect the wider-range genetic structure of species and the potential adaptability of their populations (Excoffier et al. 2009). The discrepancies in migration capacity of species should result in considerable reshufflings of local and regional communities of species (Ackerly 2003; Jackson et al. 2009), and the expansion of biomes with its components will directly influence future climate, be it as a mitigating (e.g., by cloistering CO2) or an exacerbating force (Bonan 2008).

There are two processes that are necessarily involved in plant range expansion: i) the dispersal of propagules beyond the current range limit, and ii) the establishment and growth of pioneer populations (Nathan et al. 2003). Both processes contain a strong hypothetical component which usually undetected by direct observation and hence is extremely difficult to measure in nature (Nathan et al. 2003; Nathan 2006; Simberloff 2009). Nevertheless, methods for differentiating the current and potential expanded distribution of species had received little consideration. Since the current distribution of many plant species that has the potential to expand their ranges may be much smaller than their maximum distributions (e.g., studies by Ward et al. 2009), robust methods are required for discriminating suitable habitat that is occupied and habitat that could potentially be occupied. The first necessary step is to distinguish "suitable" from "unsuitable" habitat in its current range limit, and recently two general approaches have been used for this purpose. Presence-only data and enviro-climatic variables can be used to fit predictive "niche-based models" of distribution by various methods (Elith et al. 2006). Nevertheless, presence-only modeling requires careful attention on how the data collected so that major spatial and detection biases may be reduced or even eliminated (Gu and Swihart 2004; Wintle et al. 2005; Araujo and Guisan 2006). The second step is to project the potentially "suitable" habitat outside of current range limit in its vicinity regardless of how the process of its dispersal.

Recently, Ecological Niche Modelings (ENMs) with its set of enviro-climatic variables are being used for the purposes, for instance, in the prediction of expansion biology, particularly to predict invasion risks (in the case of invasive species) and optimize control strategies (e.g.,

Bradley et al. 2010; Jimenez-valvarde 2011; Giljohann et al. 2011; Tulloch et al. 2014; Lecocq et al. 2016; Kramer et al. 2017). However, there are two key assumptions of ENMs that are often violated in expansion biology. Firstly, niche conservatism in ENMs is an assumption required for model transferability, whereby climate niches of the species being modeled from the native area are to be projected onto new geographical spaces to estimate the likelihood of successful expansions there (Barbet-Massin et al. 2018). In the context of expansion biology, niche conservatism differs remarkably from evolutionary niche conservatism (fundamental niche conserved over evolutionary time), since the question is to understand whether the species' realized niche is preserved over space, Nonetheless, the assumption of niche conservatism over space is not always conjoint, since the naturalized climatic niches of expansive species can differ from their native climatic niches (Medley et al. 2010; Early and Sax 2014; Parravicini et al. 2015). Secondly, up till the latest stage of expansion, the species is not yet at equilibrium with its environment (Gallien et al. 2012); therefore its climatic niche is likely underestimated. Despite the criticisms, the pivotal need for predictive models is such that ENMs are still often used in species range expansion studies.

Using the theoretical frameworks explained above, here we demonstrate the application of Ecological Niche Modelings (ENMs) to predict the distribution of current "suitable" niche for *Selaginella zollingeriana* Spring in Java Island and its potential "suitable" niche across the Indonesian archipelago based on enviro-climatic variables. Since the potential expansion would occur for decades, we incorporate the potential changes in future climate conditions through the implementation of projected future climate conditions using various scenarios. Therefore, we could gather information on the distribution of areas/regions where the species could potentially be dispersed and survived outside of recent-known distribution.

The choice of *S. zollingeriana* provides an excellent context of the study on modeling species expansion under future climate projection. According to Setyawan et al. (2013), this species is distributed mainly in the islands of Java and Bali, and found mostly on the cliff walls of headstone and tomb, or on the shaded cliff, or on the plastered roadside and dirt drainage ditch. The recorded altitude of species' presence is at 1150-1222 m asl. This species is capable of surviving and growing its colony among the biotic interactions between species in Java Island along with its climatic, physiographic, topographic, and edaphic conditions for the unrecorded periods of time. This has become a subject of interest for ecologist and botanist since the vast variety of enviro-climatic condition in Java Island more or less represents the enviro-climatic condition of Indonesia. Therefore, questions regarding whether there are other areas outside the island that are capable of supporting the survival of this species may arise. Then, an inquiry regarding how that suitability degree may change in conjunction with the possible changes in future climate conditions will also emerge.

MATERIALS AND METHODS

Study area

Indonesia is an archipelagic country located in the southeast region of Asia. This country consists of about 17,508 islands wherein only 16,056 of its island names have been verified by the United Nations Group of Experts on Geographical Names (UNGEGN) in July 2017 (https://unstats.un.org/unsd/ungegn/). The geographic scope of this study includes the region of approximately 6 °N to 11°S latitude and 95 °E to 141 °E longitudes (Figure 1), covering about 1.9 million km² of lands. The highest peak of Indonesia is Mt. Puncak Jaya at roughly 4,884 m asl located in Papua Island.

The climate in Indonesia is varied wherein it is mostly experiencing a tropical rainforest climate with some areas have tropical monsoon and tropical savanna. Nevertheless, oceanic climates and subtropical highland climates are also found in several high-altitude regions in this country, mostly between 1,500 and 3,500 meters above sea level. Regions that are above 3,500 m asl (mostly in Papua highlands) experiencing tundra climate and subpolar oceanic climates (Climate-data.org).

Procedures

Presence Records

For this study, authors collected the occurrence data of *S. zollingeriana* from two primary sources, i.e., field survey and the Global Biodiversity Information Facility (GBIF) database. Field survey aiming to obtain the primary presence records for the species was conducted in all provinces across Java Island between July 2007 and January 2014. The specimens found were identified using several references on Selaginella of the Malay Archipelago and adjacent regions (Alston 1934, 1935a,b, 1937, 1940; Wong 1982, 2010; Tsai and Shieh 1994; Li and Tan 2005; Chang et al. 2012; Zhang et al. 2013) to ensure the high-confidence level of species identification. The coordinate of each specimen was recorded using Garmin eTrax GPS series. Subsequent to confirming the species taxonomy, twenty-four coordinate records were used in this study. None of the error-correction methods were conducted since we ensured that the level of telemetry error of modern GPS has little effect on the accuracy of the model (Montgomery et al. 2011).

The second source of presence records was from the GBIF database (GBIF 2016). All of the records acquired from GBIF were carefully verified, and errors that may occur were corrected using Google Earth software (Google Earth Pro 2017). Records with no latitudinal and longitudinal information were geo-referenced using Biogeomancer Workbench (http: //www.biogeomancer.org) guided by locality descriptions on each datum, and then data records that do not have specific locality description and cannot be geo-referenced were removed (Guralnick et al. 2006). We comprehend the possibility of strong geographic biases that often contained in such open database wherein its data were collected from opportunistic observation and/or historical collection of records (Stolar and Nielsen 2015). Moreover, the biases mentioned above proved to have strong effects on modeling prediction ability and later interpretation (Kramer-Schadt et al. 2013; Fourcade et al. 2014). Therefore, we conducted two out of five sampling bias correction methods proposed by Fourcade et al. (2014). Subsequently, after we identified the type of sampling data bias contained in the sampling data used for this study, we conducted two out of five sampling bias correction methods, i.e., (i) Spatial filtering, performed by creating a grid of 2 km x 2 km cell size and randomly select only one point of occurrence per grid cell. Nevertheless, it should be noted that the size of this grid is not the representation of approximate species' dispersal capabilities, but rather as a result of modifying the 10-km radius rule of spatial filtering proposed by Kramer-Schadt et al. (2013) and Boria et al. (2014). The grid creation and point selection were conducted using QuantumGIS software ver. 3.2.0 (QGIS Development Team 2017). (ii) Bias file, produced using Gaussian kernel density map approach and then included it into MaxEnt modeling process through the setting option (Dudik et al. 2005; Elith et al. 2011; Phillips et al. 2017). The remaining six presence records that considered suitable were combined with the data from field study; therefore, a total of 30 points were used in this study.

Figure 1. Area of study, Indonesia. (Base map: Google Physical Maps 2014)

Enviro-climatic variables

Based on the previous screening process on the variables that are expected to have direct effect on the species distribution (e.g., Soria-auza 2009; Hu et al. 2015; Mod et al. 2016; Setyawan et al. 2017; Velazco et al. 2017; Setyawan et al. 2020a; Setyawan et al. 2020b), we collected 19 bioclimatic variables, three edaphic variables, and one altitudinal variable. Bioclimatic ver. 2.0 and altitude layers were collected from WorldClim Bioclimatic datasets website (www.worldclim.org). Global Soil pH (SpH) and soil organic carbon (SOC) datasets were collected from the International Center for Tropical Agriculture (https://dataverse.harvard.edu). Soil type dataset was collected from freely available Food and Agriculture Organization of the UN (FAO-UN) website (http://www.fao.org). Due to the limited availability, other variables considered as important and directly affecting species' occurrence (i.e., biotic interactions, human disturbance, possible future land use/cover change, and species' dispersal capability) were not included.

It has been broadly acknowledged that the high correlation among bioclimatic layers will limit interpretation of the variable's contributions; thus, hindrance the correct inferences on the contribution of each variable for being made. Therefore, by using SDM toolbox Ver. 2.0 (Brown 2014), we performed autocorrelation calculation and automatically omitted the bioclimatic variables yielded correlation values above 0.85 (Spearman's rho coefficient) in the pairwise cross-correlation matrix of each dataset (intra-dataset correlations) (Bedia et al. 2013). The remaining nine bioclimatic variables (i.e., bio_1, bio_2, bio_3, bio_4, bio_12, bio_13, bio_15, bio_17, and bio_19) were then compiled with three edaphic variables (FAO types of soil, Soil pH and Soil Organic Carbon), plus one environmental variable (i.e., altitude) (Table 1).

Future scenarios

The possible expansion of *S. zollingeriana* population may take decades to occur, and throughout that time, the bioclimatic conditions are highly possible to change. Accordingly, the distribution of suitable niches for *S. zollingeriana* to disperse may also change dynamically. To model this dynamic change of niche distribution, we used future bioclimatic scenarios acquired from the CGIAR Research Program on Climate Change, Agriculture, and Food Security website (www.ccafs-climate.org). Following the suggestion from Collins et al. (2011), we selected the HadGEM2-CC (Hadley Global Environment Model-2 Carbon Cycle) global circulation model, which was developed by the Hadley Center United Kingdom, to be used in this study. Projection of future climate conditions is divided into several scenarios representing different greenhouse gas (GHG) scenarios. These scenarios are represented by Representative Carbon Pathways (RCP), namely RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5, and projected for the years 2030, 2050, and 2080 (averaged two decades up and down the year). RCP 2.6 represents the most optimistic projection which assumes that global GHG will increase slowly to reach its peak at 3.1 W/m^2 between

2010-2020, and then with the help of new technologies and climate policies, GHG will decline substantially thereafter to 2.6 W/m^2 by the year 2100 (van Vuuren et al. 2007; Moss et al. 2010). RCP 4.5 and RCP 6.0 are moderate predictions wherein the emission will stabilize at 4.5 W/m^2 and 6.0 W/m^2 respectively (Clarke et al. 2007). The most pessimistic projection is the RCP 8.5 projecting the emissions level will continue to increase throughout the century, reaching around 8.5 W/m^2 as the highest level by the end of the century (Riahi et al. 2011). Assuming the most optimistic and the most pessimistic for future climate conditions and by considering the slow expansion rate of the species, we selected the RCP 2.6 and RCP 8.5 for the years 2030, 2050 and 2080 to be used as variables to model future suitable niche distribution for the species. Due to the limited availability of future projections, the other environmental variables (Soil pH, Soil Organic Carbon) remained unchanged. Furthermore, the same altitude layer was used since this variable is a static variable that remains unchanged with time.

Due to its simplified physics and thermodynamics processes, coarse spatial resolution, and numerical schemes, and incomplete knowledge of climate systems, such climate model contains errors (biases) (Ramirez-Villegas et al. 2013). Therefore, the implementation of bias correction is necessary. Using correction data provided by CGIAR-CCAFS, we implemented three different calibration approaches: (i) Change Factor (CF): in this approach, the raw GCM outputs current values are subtracted from the future simulated values, resulting in "climate anomalies" which are then added to the observational dataset (Tabor and Williams 2010), (ii) Bias Correction, this approach revise the projected raw GCM output using the differences in the mean and variability between observations and GCM, in a reference period (Hawkins et al. 2013), (iii) Quantile Mapping (QM), this approach removes the systematic bias in the GCM simulations and accounts the biases in all statistical moments, however, like all statistical downscaling approaches, it is assumed that biases relative to historical observations will be constant in the projection period (Thrasher et al. 2012).

Table 1. Environmental variables used to build the models

Code	Name	Unit
Alt	Altitude	m asl
bio_1	Annual Mean Temperature	°C×10
bio_2	Mean Diurnal Range	°C×10
bio_3	Isothermality	×100
bio_4	Temperature Seasonality	SD×100
bio_12	Annual Precipitation	mm
bio_13	Precipitation of Wettest Month	mm
bio_15	Precipitation Seasonality (Coefficient of Variation)	mm
bio_17	Precipitation of Driest Quarter	mm
bio_19	Precipitation of Coldest Quarter	mm
Soil_types	FAO soil classification	
soil_carbon	Soil Organic Carbon	
soil_ph	Soil pH	

Modeling

For this study, we used freely available MaxEnt software ver. 3.4.1 (Philips et al. 2017) acquired from the American Museum of Natural History (https://biodiversityinformatics.amnh.org). Several studies have presented the importance of parameter configuration in MaxEnt modeling, rather than using default parameter setting (e.g., Warren and Seifert 2011; Merow et al. 2013; Yackulic et al. 2013; Halvorsen et al. 2015), especially when the number of presence data is small (Merow et al. 2013; van Proosdij et al. 2016; Pearson et al. 2007; Morales et al. 2017). Therefore, we built this model after reviewing and repeatedly testing the various combinations of parameter settings so that the model, which was built using small presence data, would yield more reliable results.

The following parameter settings were adjusted based on the species-specific considerations and reflecting our intended a priori assumptions (Peterson et al. 2011; Araujo and Peterson 2012; Merow et al. 2013). Maximum iterations were set to 5,000 for each run to allow the model to have adequate time for converging along with the Convergence threshold was set to 1×10^{-6}. Each trial was replicated ten times (the averaged value is the one used as the result) using "Bootstrap" as the replicated run type with 20% random test percentage (Merow et al. 2013). The "Bootstrap" used in this study means that for each run a random of 20% of presence data would be sampled as test data. Nevertheless, opposite to subsampling, the sampled data is replaced so that the point may be included in test data more than once. To avoid over-fitting and to assume that the species respond directly to the predictors (vs. to correlated factors), we decided to "smooth" the model by choosing only hinge features (Merow et al. 2013). Along with the default prevalence value of 0.5, we tested several "multiplier regularization (mr)" (1, 2, and 3) and then selected the best mr value based on the calculated TSS and pAUC value, visual evaluation, and jackknife test evaluation (Elith et al. 2006; Merrow et al. 2013; Radosavljevic and Anderson 2013). Considering the aim of this study, which is to model species expansion and to accommodate the small size of presence data, we chose the best multiplier regularization value of 2.00. Since one of the aims of the study is to find the distribution of similar environmental conditions across the country from where the species currently maintain populations (in this case Java Island), we sampled background points at the maximum number of 10,000 from this island only. We used the "projection" feature to extrapolate the model into different climate projections and different islands across the country (van der Wall et al. 2009).

Data analysis

One of the main outputs of Maxent is an ASCII grid representing the distribution of potentially suitable niches of the species across the study area. Using the "logistic" output format, representation of probabilities in the grid is linearly scaled between 0 (lowest) to 1 (highest) probability (Philips and Dudik 2008). To conveniently quantify and compare the predictive grids, we applied binary transformation by categorized the values into two categories (i.e., suitable and unsuitable) using the selected threshold rule. Selecting threshold can be deceptive since one must consider the relative importance differences of commission and omission errors and must emphasize one after the other based on the study objectives. (Phillips and Dudik 2008; Nenzen and Araujo 2011; Bean et al. 2012; Syfert et al. 2013). Norris (2014) and Liu et al. (2016) have explained comprehensively the selection process of a threshold for modeling with presence-only data. Acknowledging the necessity to reduce omission error in the case of modeling species having a possibility to expand in the future, "minimum training presence" was selected as the threshold rule applied in the model. The potentially suitable niche was then reclassified into three classes: low suitability (25-50% probability of occurrence), medium suitability, (51-75% probability of occurrence), and high suitability (>75% probability of occurrence), by using the "natural breaks (Jenks) classification method in Reclassify Analysis of ArcMap ver. 10.3 (ESRI 2011).

We also performed the jackknife test to calculate the variables' relative contribution to the model and quantify the degree to which these variables affect the prediction. Jackknife test shows which variable appears to have the most information that is not present in the other variables and which variable has the most useful information by itself (Phillips and Dudik 2008). The predictive grids, which by default are in ASCII format, were further analyzed using QuantumGIS software ver. 3.2.0 (QGIS Development Team 2017).

The area under the receiver operating characteristic (ROC) Curve (AUC) value, which was produced by MaxEnt and frequently used to evaluate performance model, has been proved to provide limited useful information in the process of evaluating model performance (Lobo et al. 2008; Bahn and McGill 2013; and Aguirre-Gutiérrez et al. 2013). Therefore, several studies used different statistical approaches. Allouche et al. (2006) proposed True Skill Statistic (TSS) as a post-hoc evaluation for the MaxEnt model built by presence-only data and has been used frequently since it was introduced. True Skill Statistic (TSS) (also known as the Youden index) calculation is derived by calculating the summary of sensitivity and specificity minus one (Youden 1950). This approach has been proven to be free from the dependence of prevalence while still keeping all the advantages of kappa which was widely used as an evaluation tool. Cohen's Kappa has been widely used due to its simplicity, the fact that both commission and omission errors are accounted for in one parameter, and its relative tolerance to zero values in the confusion matrix (Manel et al. 2002). However, several studies have criticized the kappa statistic for being inherently dependent on prevalence and claimed that this dependency introduces bias and statistical artifacts to estimates of accuracy (Cicchetti and Feinstein 1990; Byrt et al. 1993; Lantz and Nebenzahl 1996). Consequently, we assume that the use of TSS is more suitable for this study.

RESULTS AND DISCUSSION

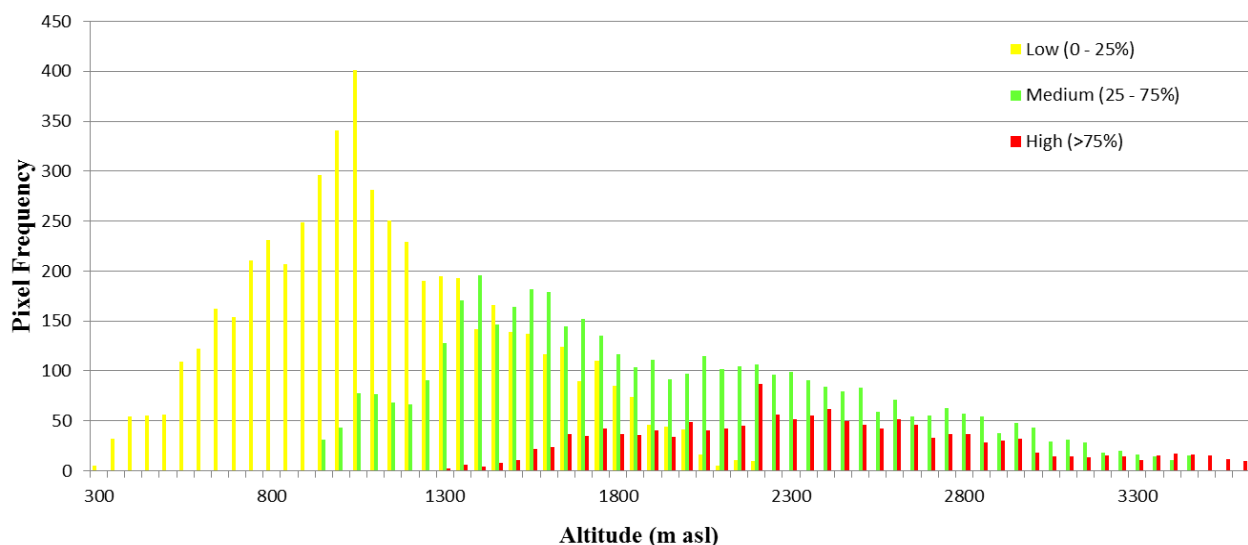*The current distribution of potentially suitable niche of* S. zollingeriana *in Java Island*

The model built using 30 presence data along with twelve enviro-climatic variables depicts the spatial distribution of potentially suitable niche for *S. zollingeriana* across the Java Island wherein this species is suggested endemically maintaining its population. Subsequent to categorizing the output into binary categories (suitable vs. unsuitable), the predicted suitable habitat were then reclassified into three classes by using the "natural breaks (Jenks) classification method i.e., low suitability (25-50% probability of occurrence), medium suitability (51-75% probability of occurrence), and high suitability (>75% probability of occurrence) to allow us to project the distribution of potentially suitable niche in different suitable level under different climate condition.

The model predicted roughly 17.22% (22,095 km^2) of the Java Island area is potentially suitable niche for *S. zollingeriana*. This number consisted of 10.93% (14,028 km^2), 4.75% (6,097 km^2), and 1.54% (1,970 km^2) of low, medium, and high suitability areas, respectively (Figure 2).

The potentially suitable niche is distributed mainly in the mountainous areas of the island. Nevertheless, the surrounding lowland areas are also predicted to be potentially suitable although they have low suitability category. Altitudinally, the low probability areas were mainly distributed in lower-end up to higher areas at the altitude of between 300 and 2100 m asl, whereas medium probability areas were mainly distributed at a higher altitude of between 1300 and 2800 m asl. Moreover, the high probability areas were also mainly distributed in the highland region at the altitude of 1800 to 3600 m asl (Figure 3).
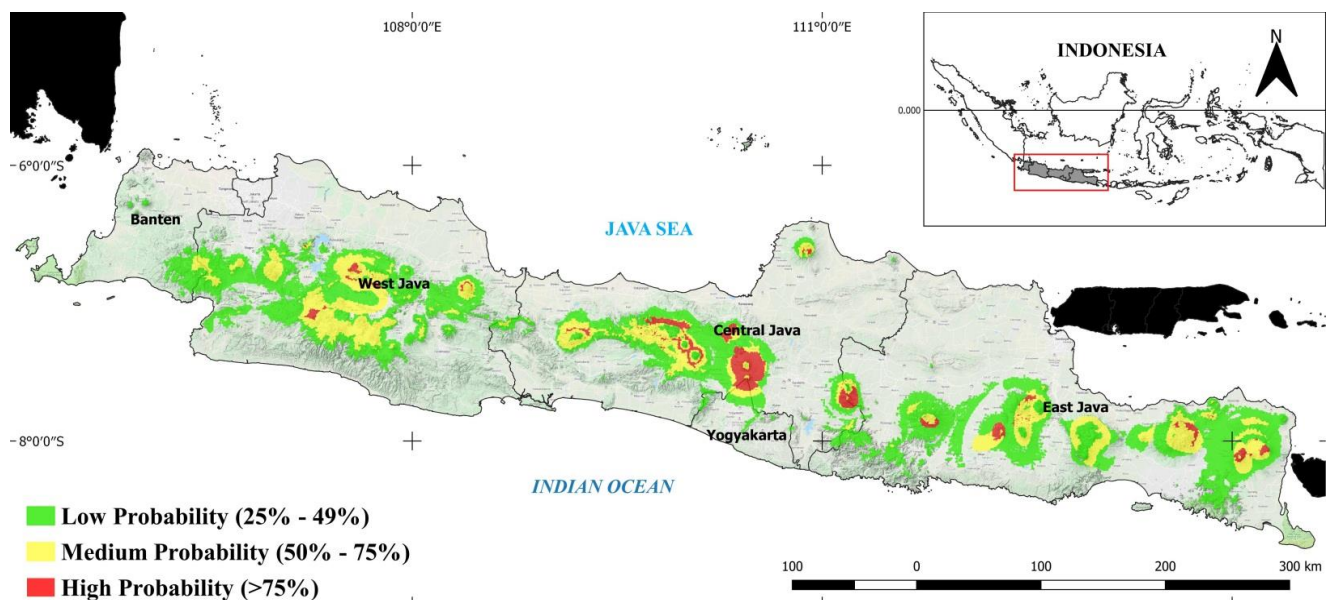
Figure 2. Predicted distribution of potentially suitable niche for *S. zollingeriana* in Java Island under current climate conditions. (Base map: Google Physical Maps 2014)

Figure 3. Predicted altitudinal distribution of potentially suitable niche of *S. zollingeriana* in Java Island under current climate condition

Model evaluation

Prior to interpreting the results further or using them in any procedure, a post-hoc model evaluation is commonly performed to assess the relative predicting performance and statistical significance of the model (Peterson et al. 2011). The AUC values may have been accentuated to be misleading and do not provide a strong reflection of model accuracy; however, we retrieved the AUC value of 0.954 to, by some degrees, illustrate that the model built in this study performed better than any model built using set of random predictors and to illustrates the discrimination ability of the model (Lobo et al. 2008; Peterson et al. 2008; Jimenez-Valverde 2012, 2014; Fourcade et al. 2014, 2017). Additionally, the True Skill Statistic (TSS) value, which has been proposed as an alternative metric of evaluation (e.g., Allouche et al. 2006; Hijmans 2012; Phillips and Elith 2010), was retrieved by calculating the summary of sensitivity and specificity minus one. The TSS value of 0.789 means that the model has a better ability at discerning the presence and background points given the threshold supplied than any random model. Therefore, the value gives the impression that model built in this study have a good degree of agreement, good predictive capacity, and also can be interpreted as evidence for the real ecological phenomenon, based on environmental variables used, rather than statistical artifacts (Allouche et al. 2006; Li and Guo 2013).
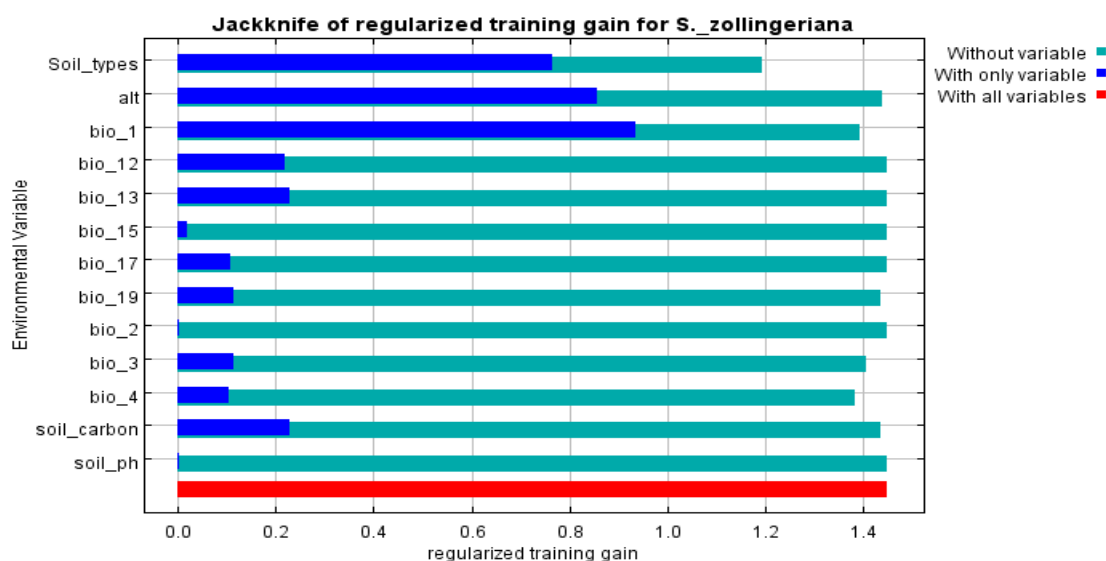
The dominant environmental variables and their significance on the probability of species' presence

According to the relative contributions of environmental variables generated by Maxent (Table 2), the top three variables that significantly affect the distribution of *S. zollingeriana* were as follows: (i) Altitude (Alt), (ii) Annual mean temperature (Bio_1), and (iii) Soil

types (Soil_types). The combination of these three variables contributed to a total of 88.5% to the MaxEnt model, whereas the rest of the variables contributed each less than 5%. Additionally, we retrieved the alternative estimation of variable importance to the models via the jackknife test (Figure 4). The results depicted that the highest environmental variable with the highest training gain, when used in isolation, is annual mean temperature (bio_1), which means that this single variable appeared to have the most useful information by itself and proved to have the highest permutation importance value of 50.4%. Moreover, the environmental variable that decreases the gain the most when it is omitted is soil types (Soil_types), which therefore appears to have the most information that is not present in the other variables (Phillips and Dudik 2008).

Table 2. Percentage of variable contribution to the final model

| Variables	Description	Contribution (%)
Alt	Altitude	35.5
bio_1	Annual Mean Temperature	27.2
Soil_types	FAO soil classification	25.8
bio_3	Ishotermality	3.9
bio_12	Annual Precipitation	3.1
bio_13	Precipitation of Wettest Month	1.9
bio_19	Precipitation of Coldest Quarter	1
soil_carbon	Soil Organic Carbon	0.8
bio_15	Precipitation Seasonality (Coefficient of Variation)	0.5
bio_12	Annual Precipitation	0.3
bio_4	Temperature Seasonality	0
bio_17	Precipitation of Driest Quarter	0
soil_ph	Soil pH	0

Figure 4. Results of jackknife test of relative importance of predictor variables for the model

The response curves were presented to show how each of the dominant environmental variables affects the MaxEnt prediction. These plots of curves reflect the dependence of predicted suitability both on the selected variable and on dependencies induced by the correlation between the selected variable and other variables (Phillips et al. 2008). The response curve between the presence probability of *S. zollingeriana* and altitude (alt) (Figure 5a) shows that the probability of species' presence is increasing gradually along with the increase of altitude. The presence probabilities are higher than 50% at the altitude of about 800 m asl and then reached their peak (probability 70%) at about 1,100 m asl before gradually decreased to 60% probability at the altitude of higher than 1,500 m asl. The next response curve (Figure 5b) shows the optimum annual mean temperature (bio_1) for this species' niche ranged between 12^0C and 21^0C before the probability presence gradually declined at the mean temperature above 22^0C. Furthermore, the third most dominant variable affecting species niche is soil types. The figure shows that there are three types of soil having the highest probability of species' presence, i.e., Be: Eutric Cambisols (code: 4475), Lo: Orthic Luvisols (code: 4535), Nd: Dystric Nitosols (code: 4543). These types of soils are inherently fertile of the tropical soils because of their high nutrient content and deep, permeable structure; thus mostly exploited for agriculture purposes (FAO 2019) (Figure 5c).

Possible species expansion in the future based on potential niche distribution

The model which was built for Java Island was then projected into future climatic condition to a wider extent across Indonesia to simulate the possible niche distribution in other islands of the country (Figure 6). The lowest *S. zollingeriana* presence threshold to predict and map the suitable niche was set at the "minimum training presence" threshold (probability $_{presence}$ = 0.23). The presence probability above the threshold was then reclassified into three probability classes (see method). Overall, the model predicted the possibility of species expansion into the other four big islands (i.e., Sumatera, Borneo, Sulawesi, and Papua). Nevertheless, the distribution of the potentially suitable niche is non-uniform wherein in some islands the niche distribution is wider while in the others distribution is narrower. The possible explanation for this phenomenon is due to the inherent differences in environmental conditions among the big islands. Following the result of variable contribution and jackknife calculation, discrepancies in altitude, temperature, and Isothermality conditions are predicted to influence the distribution pattern of suitable niches in these islands significantly.

A

B

C
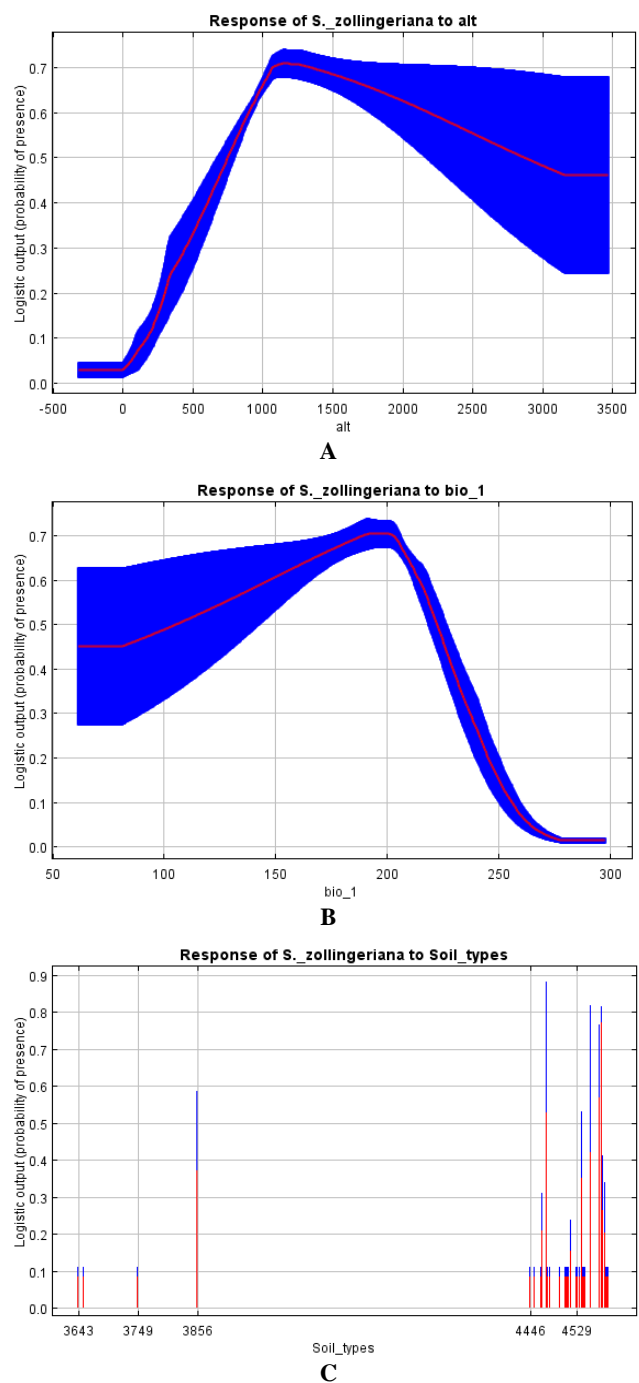
Figure 5. Response curves from MaxEnt for the most important variables for the species distribution model: A. Altitude; B. Annual mean temperature (in ^{0}C*10); C. FAO soil types classification. The curves show the mean response of the 10 replicate MaxEnt runs (red) and the mean +/- one standard deviation (blue, two shades for categorical variables).
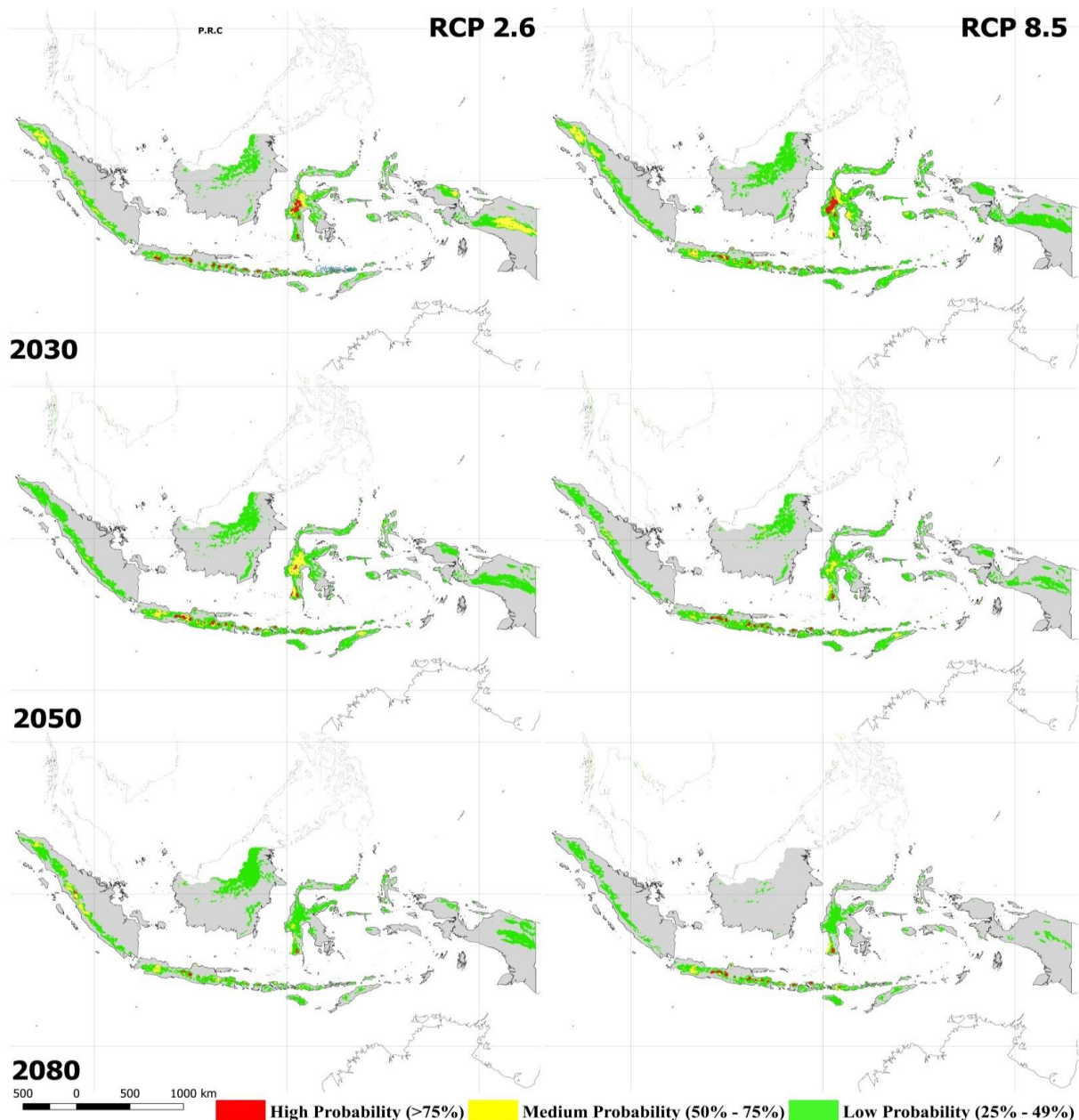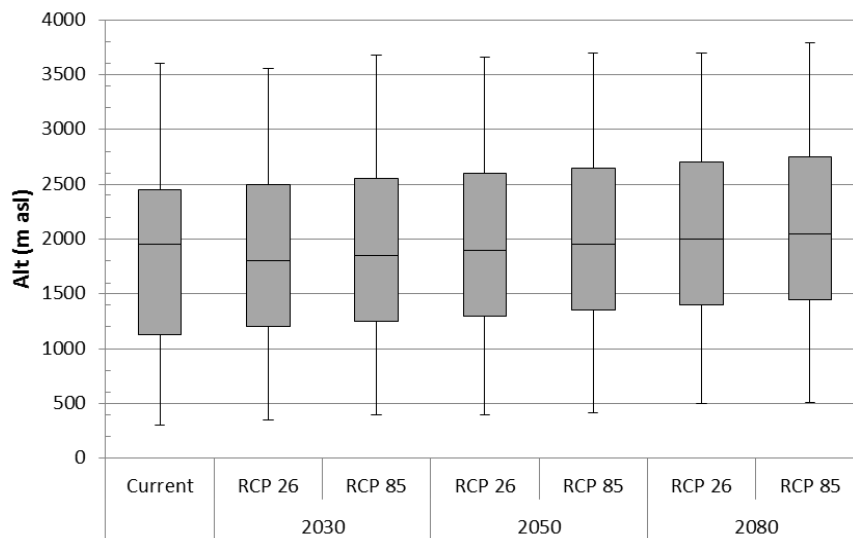
Figure 6. Predicted distribution of potentially suitable niche for *S. zollingeriana* across Indonesia under two different future climate scenarios

Considering the pace needed for the species to disperse, the model was not projected into current climate condition but to the future condition as early as 2030 under two different climate scenarios. In general, using the most optimistic GHG emission scenarios produced a wider distribution of possible suitable niches than the more pessimistic scenario that produces a narrower and limited distribution of suitable niches (RCP 8.5). Across the time period to the further future, all of the scenarios projected a declining trend of the availability of suitable niche wherein from 2030 to 2080 the modeled niche declined about 58% and 59% at RCP 2.6 and RCP 8.5, respectively (Table 3). In all of the scenarios, lower probability has a more dispersed distribution than higher probabilities accounted about two-third of suitable niches are categorized as having

a low probability (25%-50%). We then extracted the altitudinal value of the predicted suitable habitat from all scenarios in the attempt of investigating whether there are discrepancies in the altitudinal distribution among the scenarios. Across the periods of time, our models showed that the niche is projected to marginally shifted to higher altitudes. Even though the shifting is relatively small, the figures still represent the changes in climatic variability that may affect the future distribution of the species. From the current distribution to the year 2080 minimum altitudinal distribution shifted higher from about 300 m asl to around 511 m asl. The maximum altitudinal distribution was also projected to become higher from approximately 3600 m asl to about 3786 m asl, whereas the medial also slightly become higher by about 250 m (Figure 7).

Table 3. The dynamics of potentially suitable niche for *S. zollingeriana* across Indonesia under two future climate scenarios in different periods of time

Year	RCP Projection	Area × 10^3 km^2			
		Low	Medium	High	Total
2030	RCP 2.6	343	92.6	32.0	467
	RCP 8.5	308	80.6	28.3	417
2050	RCP 2.6	299	67.2	24.2	391
	RCP 8.5	243	56.5	19.0	319
2080	RCP 2.6	209	53.5	12.7	275
	RCP 8.5	190	49.7	9.1	249

Figure 7. Predicted changes in the altitudinal distribution of potentially suitable niches under current and future climate projections. The box plots present median, lower quartile, upper quartile, maximum and minimum observations. Altitude is measured in m asl. (meter above sea level)

Discussion

This study presents a primary attempt to model the potential range expansion of *S. zollingeriana* by every possible means of species' proliferation, spread, and transportation while under the presumption of its range expansion will be greatly affected by differences in future climate condition. Across Java Island, it has been predicted that about 17.22% (22,095 km2) of its area is suitable for the species based on the variables induced. Moreover, the model predicted the niche distribution of the species in its native island (Java) would be driven by the altitude level, the annual mean temperature, and its isothermality. Geographical variable, such as altitude, often connotes atmospheric pressure, local precipitation and temperature features (Austin 2002; Körner 2007); thus expected to affect greatly on determining the suitability of species in a certain niche. According to literature, Selaginella is a herbaceous plant that will likely grow in the moist or rather wet region. Therefore, elevation and temperature codependency affecting humidity plays an important role in the cause of species' survival. Isothermality (bio_3) is defined as the quantification of how large the diurnal temperature range oscillates with annual temperature oscillations (O'Donnell and Ignizio 2012). Previous studies

(e.g., Jagels 1970, Eickmeier 1986) confirmed the importance of temperature and its stability in ensuring the survival of genus Selaginella.

The niche of *S. zollingeriana* in Java Island is predicted to be distributed widely but fragmented mainly to occur only in the highland areas at above 500 m asl. Discrepancies in local environmental conditions connoted by altitude (i.e., temperature and humidity) are to be expected as the cause of little to none suitable niche found in the lowland areas. Due to the adiabatic nature of the Earth's atmosphere, the denser air in the lowland has a greater heat absorption capacity than the thinner air in the highland areas. Therefore, the mean temperature in highland is expected to be lower than that of lowland areas. Temperature, as the second most dominant variable, allegedly affects both the photosynthetic capability and preservation of photosynthetic apparatus of Selaginella species (Jagels 1970, Eickmeier 1986). The negative correlation between temperature and the probability of species' presence (Figure 5c) illustrates the unsuitability of warmer temperature in lowland areas affecting species survival. For instance, Soni et al. (2012) in their study stated that *Selaginella bryopteris* show a very poor mechanism for its stomatal regulation in response to high

temperature, which also affects its photosynthesis capability. Moreover, in regards to the effect of changes in precipitation level, studies conducted by Deeba et al. (2009) and Pandey et al. (2010) demonstrated drastic inhibition in net photosynthesis and maximal photochemical efficiency when *Selaginella bryopteris* induced with dehydration stress. Desiccation on this Selaginella species can also cause enhanced production of reactive oxygen species (ROS) and increased lipid peroxidation. In consequence, the increasing level of mean temperature and the decreasing level of precipitation is the most important compounding factor in determining the sustainability of Selaginella's habitat in the future.

Those allegations are aligned with the results of the predicted distribution of potentially suitable niches under future climate conditions across the Indonesian archipelago. Projected future climate condition in Indonesia has been predicted will significantly disturb the distribution of potentially suitable niche of *S. zollingeriana*, altering its geographical distribution pattern. Under the lowest GHG emission projection (RCP 2.6), wherein radiative forcing will gradually rise before it stabilizes at 2.6 W/m^2 by 2100, the annual mean temperature will rise to about 0.4-0.7^{0}C in all areas of Indonesia (Meinshausen et al. 2011; IPCC 2014). While under the worst emission scenario (RCP 8.5), the annual temperature will rise to 1.7^{0}C. This condition is predicted to decrease the probability of regional niche to support the existence of *S. zollingeriana*. From the total of 467×10^3 km^2 predicted suitable niche in 2030 under RCP 2.6, the predicted suitable niche would decrease significantly to around half the number (249×10^3 km^2). Global warming is also projected to favor range shifts, especially upward migrations, for many species for which temperatures are the main limiting factor of their geographic distribution (Parmesan et al. 1999; Saxe et al. 2001; Bale et al. 2002; Harvell et al. 2002). Distributional shift assessment using the extracted altitudinal value of the predicted suitable niche under current and future conditions indicate that there will be upward shifting to higher elevation area as the temperature gradually warming. This indication is aligned with certain studies that predicted a shift of forest ecosystems to a higher altitude under projected future climate conditions (e.g., Walther et al. 2003; Bertrand et al. 2011). Even though the shifting figures are relatively small, the finding still illustrates the changes in the suitability level of certain areas/regions affected by climate changes. The increase in temperature and possible occurrence of severe drought, as indicated by precipitation variability in those areas, would increase the level of stress the plants received from its surrounding (Kelly and Goulden 2008). Therefore, it is expected to reduce the species' capability to survive in the drier-warmer lower parts of its altitude range (Allen and Breshears 1998; Lenoir et al. 2008) and increase its competitive ability and tolerance in the wetter and cooler upper parts of its altitude range (Parmesan 2006).

Alongside the climatic factors, the ability of *S. zollingeriana* to disperse outside of its current geographical range is also likely to be governed by ecological determinants that affect propagule (in case of Selaginella species, is its spore) departure, transport, and arrival, respectively. Several factors potentially will be affected by climate conditions in the process of species' dispersal, i.e., plant fecundity, dispersal pathways, spore delivery sites, and biotic interactions at the new geographical sites (Hampe 2011). Clark et al. (2001) demonstrated on theoretical grounds that variation in fecundity (net productive rate) can exert strong effects on expansion rates. The authors highlight the finding that climate-driven changes in population fecundity could play a key role in future range expansions, even though the authors emphasized regarding fecundity consideration as a variable parameter considerably reduces model-based estimates of past expansion rates. Moreover, numerous experimental studies have shown that elevated CO2 level can significantly increase the pollen, spores, flower, and seed output of individual plants (LaDeau and Clark 2001, 2006a; Jablonski et al. 2002; Stiling et al. 2004; Way et al. 2010), although this increase may be accompanied by decreasing quality of the seeds (most notably is in terms of nitrogen content) (Jablonski et al. 2002; Stiling et al. 2004; Way et al. 2010). In addition, a number of field studies have successfully monitored multi-year patterns of plants fecundity in populations near the (climate-governed) leading edge of species ranges (i.e., Pigott and Huntley 1981; Hofgaard 1993; Holm 1994; Despland and Houle 1997; Meunier et al. 2007). Unsurprisingly, propagules productions are typically linked with favorable climatic conditions. Consequently, future warming may be expected to result in higher long-term average fecundity; however, it may be accompanied by irregular propagule production and decreased propagule quality. Nevertheless, further investigation is needed to understand more about projected future climate conditions with plants fecundity (e.g., genetic-evolutionary component, Allee effects, etc.).

The trajectories of migrating *S. zollingeriana's* propagules are expected to largely be determined by the landscape context of the Indonesian archipelago. It is well known from phylogeographical studies that major geographic barriers have influenced past population and range dynamics (Hewitt 2010). The strong context-dependence of long-distance dispersal and colonization resulting events is possibly the main reason for the exceptionally peculiar nature of past range expansions (Hu et al. 2009; Jackson et al. 2009). Therefore, a better understanding of how the biotic and abiotic environment provokes expansion routes and dispersal pathways is critical for improving predictions of future range shifts. Investigation of future climate changes that might affect dispersal pathways is surprisingly limited. Recently, Trenberth et al. (2007), Kuparin et al. (2009), and Nathan et al. (2011) found that the combination of increasing air temperature and increasing frequency of winds and storms can indeed favor the frequency of long-distance wind-dispersal of propagule, although the effect seems rather small. The impact of future climate change on the behavior of biotic dispersal agents is even more difficult to predict. The only well-known prediction of the effect of climate change on biotic dispersal is that climate-driven changes of bird migration routes and wintering grounds could result in

substantial changes in the abundance of avian seed dispersers (Berthold et al. 1992; Rivalan et al. 2007; Carlo and Morales 2008). Since there is limited information on how *S. zollingeriana* is dispersed in Java, it is difficult on which aspect of propagule dispersal of the species will be significantly affected by future climate changes.

From a landscape perspective, climate changes can result in loosening or constricting climate constraints on plants in the growing area available for colonization as well as increasing connectivity for patches (Hampe 2011). When climate constraints loosening, the propagule pressure required for establishing self-sustaining populations would rapidly decrease since both seed sources and suitable establishment sites become more abundant. Otherwise, constricted climate constraints will increase pressure for propagule to establish self-sustaining populations (Simberloff 2009). Furthermore, climate change is not only influencing the movement and establishment of recruiting colonizer but also imply indirect effects through its mediation of biotic interactions that intervene at different stages of the recruitment process. The fundamental complexity and context-dependence of such biotic interactions burden predictions with a great uncertainty upon future changes in biotic interactions and their consequences on the survival of expanding species (Mitchell et al. 2006; Parmesan 2006). Therefore, further investigations on the true climate constraints of *S. zollingeriana* and its biotic interactions in its native region are pivotal to predict the survival of species' colonization in the new regions.

The major limitations for modeling plant expansion range are the assumption that species are at the equilibrium with their environment and the assumption of niche conservatism, wherein climate niches of the species from the native area can be projected onto new geographical spaces (Gallien et al. 2012; Barbet-Massin 2018). Although *S. zollingeriana* has a sufficiently long history in Java and has been used for traditional uses by the communities to have sampled most of the environmental conditions, its distribution may not yet at equilibrium. Moreover, recent model accuracy techniques (such as TSS) might not be appropriate for range expansion modeling. The not-so-high TSS value of the model (0.789) could also mean either that the variables used in this study do not genuinely capture the enviro-climatic determinants of the species' niche distribution, or that the variables are correct and the species has a huge potential for spreading wider into the new range of suitable niche.

There are three presumptive factors that are likely to affect the accuracy of the model. Firstly, MaxEnt assumes the current distribution data of the species provides a good indication of their true potential range. Whereby this is not entirely correct, the potential range will be under- or over-estimated. The potential range could be overestimated for species occurring in few scattered locations throughout the entire area of study, whereas it could be underestimated for species that currently exist in a small, clumped range. Secondly, despite the bias corrections conducted, unrepresentative data from field studies and databases may have led to an underestimation of the current and potential distribution of less conspicuous species. Lastly, the process of averaging the climatic suitability values per 1 km^2 cell assumes that the mean values represent the location where the species occurs. The likelihood of a significant error in this assumption depends on the variability of the climatic factors in the cells in the study area. At the broad scale at which this study is intended to collect information regarding the possibility of suitable niche in the other islands of Indonesia, these factors may not have a substantial effect on the overall accuracy or usefulness of the results. Further detailed assessments, however, will be necessary for further utilization of this study (e.g., to inform management and planning, conservation efforts, etc.). Despite the limitations mentioned above, it is reasonable to presume the robustness of the predicted trends of suitable niche distribution at the level of acceptable for a primary study. The construction of a more ideal model requires the availability of multiple compounding factors which are expected to have a direct or indirect effect on the target species and its associated biota. Potential human-induced land use/land cover changes in the potential new region of occupation, biotic interactions between species in the new regional ecosystems, more detailed enviro-climatic data, and better representation of variability of species' niche are several examples of variables that are expected to be pivotal in constructing a more ideal model. Nevertheless, with the currently available data, we could make inferences that if the propagules of *S. zollingeriana* could be dispersed across the country, the availability of potentially suitable habitat could be disturbed by the recent and future changes in climate conditions. Therefore, the successfulness of *S. zollingeria's* expansion could severely be hindered by future climate changes.

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