# Anticipated climate changes reveal shifting in habitat suitability of high-altitude selaginellas in Java, Indonesia

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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. 2020. Anticipated climate changes reveal shifting in habitat suitability of high-altitude selaginellas in Java, Indonesia. Biodiversitas 21: 5482-5497.* High-altitude ecosystems with humid and cool climate are the preferred habitat for some *Selaginella* species (selaginellas). Such habitats are available in Java, Indonesia, which also has fertile soils with rich mineral contents resulted from volcanic activities. However, the high-altitude ecosystems in Java are threatened by various anthropogenic activities as well as changes in climate conditions, potentially affecting some *Selaginella* species. This study aimed to investigate the shift in suitable habitat of four species of high-altitude *Selaginella* spp. (*Selaginella involvens*, *S. opaca*, *S. ornata*, and *S. remotifolia*) in Java Island under current and future climate conditions predicted by several representative greenhouse gas concentration pathways. Presence data of *Selaginella* localities were collected from field survey between 2007 and 2014 across the island, as well as occurrence points from the Global Biodiversity Information Facility database. A total of 1,721 occurrence points data along with environmental and climate data were used to develop species distribution models using MaxEnt. Future habitat distributions were projected under four climate scenarios to see the shift in suitable habitat and altitudinal ranges. The results showed that the distribution of the four high-altitude *Selaginella* species are strongly influenced by altitude, annual average temperature, and annual rainfall. In the present time, 37.32% (48,974 km$^2$) of the area of Java has been predicted to be suitable for high-altitude *Selaginella*. Under the optimistic climate scenario (RCP 2.6), the highly suitable area will likely to decrease by almost 35% in the year 2080, whereas the medium and low suitable areas will reduce by about 37.2% and 18.3%, respectively. Under the pessimistic scenario (RCP 8.5), about 21.2% of low suitable areas will be lost in 2080, whereas the medium and highly suitable areas are predicted to decrease by around 38.1% and 33.4%, respectively. Under the pessimistic scenario, there will be upward shift by 51.1 m in the year 2030 from the current's mean altitude and will shift by almost 150 m in the year 2080. The maximum altitude of predicted suitable habitat is also predicted to increase to reach almost 3500 m asl in the year 2080. The results of this study imply that habitat shift of four high-altitude *Selaginella* species varies depending on the scenario, but in all cases, the losses are greater than gains.

**Keywords:** *Selaginella*, high-altitude ecosystems, Java, climate change

## INTRODUCTION

Java Island (Indonesia) is located in equatorial zone and geographically lies 7°29′30″S 110°00′16″E, covering an approximately 138,793.6 km$^2$ area of land. This island is almost entirely of volcanic origin which contains thirty-eight mountains, forming an east-west spine that has at one time or another been active volcanoes (Thomson 2013). The highest volcano in Java is Mount Semeru (3,676 m), whereas the most active volcano on the island, and also in Indonesia, is Mount Merapi (2,930 m). Like most islands in the equatorial zone, Java Island has only two seasons, i.e. wet season (during October-April) and dry season (during May-September). Java Island has a wide range of precipitation rates that can be divided into three categories of area. The western region (Banten and West Java Province) and central region (Central Java Province and Special Region of Yogyakarta) have the same average rainfall at about 2000 mm per year. Eastern area of Java (East Java Province), compared to the western region, has lower precipitation at about 1900 mm per year. The areas with high altitude have a higher precipitation rate and in some high-altitude areas in Java precipitation could reach up to between 3000 and 5000 mm per annum (Qian et al. 2010). Likewise, the average temperature of Java Island can be ranged differently according to its altitude feature. Coastal areas have an average temperature of between 22 °C and 32 °C. Whereas in the areas with an altitude of between 400 and 1350 m asl

(above sea level), the average temperature ranges between 18 °C and 29 °C. Higher altitude areas (above 1350 m asl) generally have lower temperatures, in this case, the lowest temperature in Java Island can reach minus 4 °C which was recorded in Ranu Pani area (Mount Semeru) (Hariyati et al. 2013).

The geographical and climatic condition of Java along with the rich biological diversity made this island categorized as one of the 25 identified biodiversity hotspots by Myers et al. (2000), overlap with the four closest biologically richest hotspots, such as Indo-Burma, Peninsular Malaysia, Wallacea, and the Philippines. This island is a suitable habitat for about 25 species of *Selaginella* which five of them endemic species to Java Island (Setyawan 2008; Setyawan et al. 2016), making it as the island with the richest diversity of *Selaginella* species in Indonesia (Wijayanto 2014). Altitudinally, *Selaginella* grows in lowlands and highlands, and there are some species that grow in between the two areas, each with its own preference (Setyawan 2008). Four of the most predominant and prominent species of high-altitude *Selaginella* in Java are *Selaginella opaca* Warb., *Selaginella ornata* (Hook & Grev.) Spring., *Selaginella remotifolia* Spring., and *Selaginella involvens* (Sw.) Spring (Setyawan 2012; Setyawan et al. 2012, 2013, 2015c). However, the high-altitude ecosystems of this island are currently under threat from various anthropogenic activities, including conversion into agriculture land especially for vegetable production, expansion of settlements and tourism, and forestry. There is another threat to these high-altitude ecosystems which is often overlooked, namely climate change (Setyawan et al. 2020).

Climate is one of the most important factors influencing the sustainability of plant species, vegetation pattern, and structure and ecology of forest (Kumar 2011). Climate has long been identified as a primary control of the geographic distribution of plant species (Forman 1964). However, current global climate condition is already moving toward dangerous and unprecedented conditions driven by major and pervasive anthropogenic activities on the Earth's atmosphere, land surface, and waters (IPCC 2007). Over the period between 1880 and 2012, The Intergovernmental Panel on Climate Change (IPCC) in the Fifth Assessment Report (AR5) stated that the average global temperature rose by about 0.85 °C. This condition can be seen as a potentially devastating threat to the environment and all life within it (Fitzpatrick et al. 2008; Beckage et al. 2008; Hasanuzzaman et al. 2013). Furthermore, IPCC has developed predictive scenarios on the future of global climate conditions, projecting a further increase in global mean surface temperature by 2.6-4.8 °C above pre-industrial levels, an increase in flood and drought incidences, and spatial and temporal changes in precipitation patterns in the year 2100 (IPCC 2014).

High-altitude ecosystems are likely to be more sensitive to global warming, owing to the contraction of climatically suitable areas for living organisms along with the increase in elevation (Guisan et al. 1995; Theurillat et al. 1998; Diaz et al. 2003; Beniston 2006). Recent study suggested that the unprecedented rates of warming at high elevation ecosystem

during the 21st century are predicted two or three times greater than the rates of warming during the 20th century (Nogue´s-Bravo et al. 2006). These changes are expected to have devastating effects on plant communities in this ecosystem (Guisan et al. 1995; Beniston et al. 1996; Guisan and Theurillat 2000; Walther 2003; Fitzpatrick and Hargrove 2009).

Along with the environmental degradation caused by various anthropogenic activities, climate change is considered will negatively affect the current patterns of plant diversity (Belgacem et al. 2008). These compounding threats are expected to lead to low emergence of annual species, change the life cycle of plants, changes in phenology and the timing of reproduction, and finally reducing plants diversity (Thuiller et al. 2008; Belgacem et al. 2008; Hilbish et al. 2010; Hill and Preston 2015). A number of studies have been conducted in order to measure the ecological impacts of climate change compounded with destructive human activities, and to predict the response of species to different drivers of change (e.g. Dillon et al. 2010; Gilman et al. 2010; Pereira et al. 2010; Salamin et al. 2010; Beaumont et al. 2011; Dawson et al. 2011; McMahon et al. 2011; Bellard et al. 2012; Belgacem and Louhaichi 2013). Impacts of climate change in the early past had already been seen, for instance, during the period between 1983 and 2012, which was considered as the warmest 30-year period in the last 800 years (IPCC 2014), many shifts in the distribution and abundances of species occurred (Camillie and Gary 2003; Root et al. 2003). Moreover, it also has been estimated that approximately 20% of all of the world's plant species are on the verge of extinction (Brummitt and Bachman 2010), and Thomas et al. (2004) in their report stated that about 15-37% of species in their sample of regions and taxa will extinct caused by mid-range climate warming scenarios by the year 2050.

In the last few decades, attention toward understanding the potential effect of climate changes on the sustainability of species leads to a marked increase of interest in the use of Ecological Nice Modeling (ENM) (Merow et al. 2013; Fourcade et al. 2014). ENM, also known as Species Distribution Modeling (SDM), was developed in the mid-1980 (Booth et al. 2014), comprehensively involving the utilization of statistic, ecology, Geographic Information System (GIS), and even Remote Sensing (RS) to develop estimation of suitability niche for species across predefined landscapes (Franklin and Miller 2009), while also can be extrapolated through different space and time (Guissan and Thuiller 2005; Elith and Leathwick 2009; Franklind and Miller 2009).

Such modeling can be conducted using a variety of methods including heuristic models (e.g. BIOCLIM— Beaumont and Hughes 2002), combinatorial optimization (e.g. GARP-Fitzpatrick et al. 2007), statistical models (e.g. GAMs-Jensen et al. 2008), and machine learning (e.g. ANN— Ostendorf et al. 2001, Berry et al. 2002, Harrison et al. 2006; MaxEnt —Phillips et al. 2006) (Sinclair et al. 2010). Each of these approaches, indeed, has its own advantages and disadvantages. Nevertheless, one of the most growing approaches of ENM is Maximum Entropy (MaxEnt) algorithms (Belgacem and Louhaichi 2013).

MaxEnt modeling has a great potential for identifying the distribution and habitat selection of wildlife given its reliance on only presence locations and has shown higher predictive accuracy than many other methods (Phillips et al. 2006; Baldwin 2009; Franklin and Miller 2009; Elith and Frankling 2013; Peterson et al. 2011; Remya et al. 2015). Being a general-purpose machine learning method, MaxEnt offers a simple and precise mathematical formulation to characterize the probability of distribution across user-defined landscape (Phillips et al. 2006; Merow et al. 2013). Furthermore, its ability extends to utilize different environmental scenarios to estimate the changes of probability of occurrence of species (Beaumont et al. 2007), therefore, allowing user to evaluate the impact of climate changes on the probability distribution of species (e.g. Rondini et al. 2006; Botkin et al. 2007; Randin et al. 2008; Engler and Guisan 2009; Garavito 2015; Setyawan et al. 2017).

Since high-altitude plants are expected to shift to higher altitude than currently occupied (Grabherr et al. 1994; Nilsson and Pitt 1991), the utilization of ENM along with relevant approaches to model the effect of climate changes on high-altitude *Selaginella* in Java and its altitudinal shifts that may occur is pivotal importance as preliminary information on how changes on climate may affect these species. The changes in climate condition in the past has already impacted habitat of *Selaginella*, as a part of plant communities, in several places (e.g. Boettger 2009; Cao et al. 2010; Bezrukova et al. 2012), it will likely affect the distribution of this genera under future climate condition in Java Island as well. This study aimed to investigate the shift in suitable habitat of four species of high-altitude *Selaginella* spp. (*Selaginella involvens*, *S. opaca*, *S. ornata,* and *S. remotifolia*) in Java under current and future climate conditions predicted by several representative greenhouse gas concentration pathways.

## MATERIALS AND METHODS

### Study area

This study was conducted to investigate the shift of predicted suitable habitat for high-altitude *Selaginella* in Java Island, Indonesia. All of the locality points were collected in the mountainous areas of Java. Records points were selected carefully to represents the geographical distribution of high-altitude *Selaginella* spp. (*Selaginella involvens*, *S. opaca*, *S. ornata,* and *S. remotifolia*) (Figure 1).

### Procedures
#### Locality data

Presence data of *Selaginella involvens*, *S. opaca*, *S. ornata,* and *S. remotifolia* were obtained during our field survey across the island. To ensure the high-confidence level of species identification, all of the specimens obtained were identified using several references on *Selaginella* of the Malay Archipelago and the adjacent regions, both early (Alston 1934, 1935a,b, 1937, 1940) and latest literature (Wong 1982, 2010; Tsai and Shieh 1994; Li and Tan 2005; Chang et al. 2012; Zhang et al. 2013) as well as our precedent publications (e.g., Setyawan 2012; Setyawan et al. 2012, 2013, 2015a,b,c; Setyawan and Sugiyarto 2015). We tried to minimize bias in sampling intensity (Elith et al. 2006; Yackulic et al. 2013) during the data collection by covering as wide areas as possible while also attempting to cover all of the possible climatic and micro-climatic variability of Java Island. From this work, we were able to collect in total of 1330 occurrence points of those four high-altitude *Selaginella* species, which were found distributed in highland areas of western, central, and eastern parts of the island. None coordinate error-correction was conducted for these data as we ensured that the level telemetry error on modern GPS used in this study (normally between 0.01 km and 0.05 km), which is smaller than the resolution of predictor variables, has little effect on the accuracy of models (Montgomery et al. 2011).
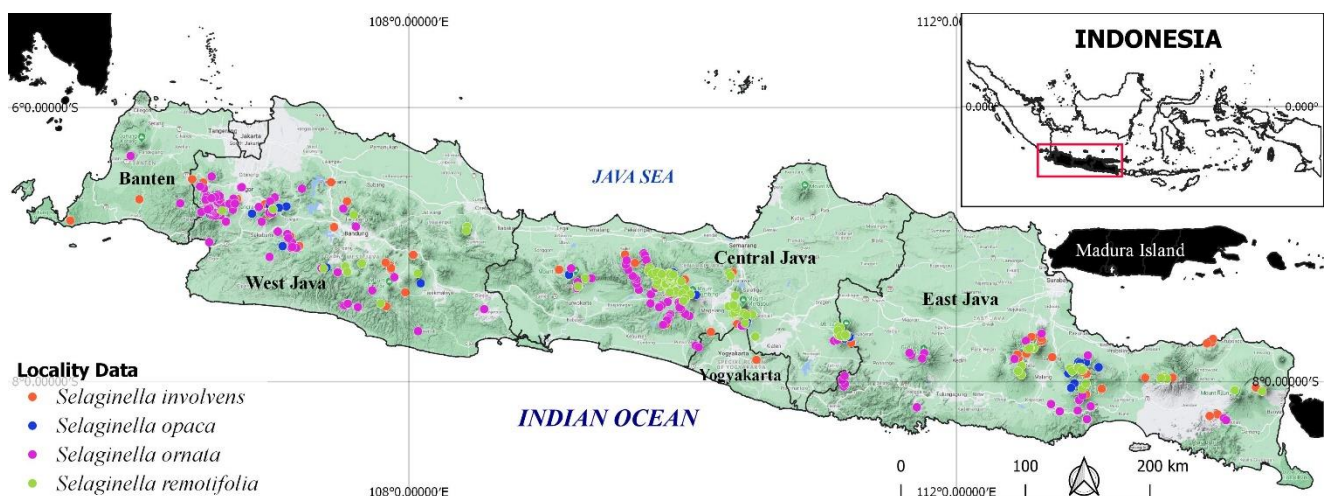


**Figure 1.** Map of point occurrence of selaginellas (*Selaginella* spp.) in Java Island, Indonesia used in this study. (Basemap source: Google Terrain Layer)

Additionally, we retrieved 965 occurrence points for all of those species in Java Island from the Global Biodiversity Information Facility database (http: //www.gbif.org[a,b,c,d]). We carefully verified all of the occurrence points acquired from the GBIF, and the errors that may occur were corrected using Google Earth software (Google Earth Pro 2017). Data records with lack of information on latitudinal and longitudinal coordinates were geo-referenced using Biogeomancer Workbench (http: //www.biogeomancer.org), and guided by locality descriptions on each datum (Guralnick 2006). Data records that contain neither clear nor specific locality description and cannot be geo-referenced were omitted. Afterward, 391 locality points from this database were combined with the occurrence points collected from the field survey (1330 locality points) and then were filtered using spatial filtering technique to reduce the effect of sampling bias. In total, 1,721 occurrence points were used in this modeling.

The availability of global biodiversity database and environmental datasets has induced the increasing number of regional to continental-wide SDM studies (Hijmans et al. 2005; Kozak et al. 2008). However, strong geographic biases are often exhibited in occurrence data derived from collection of records and/or opportunistic observation (Stolar and Nielsen 2015). Therefore, sampling bias correction is highly important and advised strongly to be conducted to minimize the influence of sampling bias on modeling prediction ability and later interpretation (Fourcade et al. 2013; Kramer-schadt et al. 2013; Fourcade et al. 2014). Fourcade et al. (2014) in their study proposed five sampling bias correction methods which were carefully designed to minimize the effect of four types of sampling biases that may occur within the occurrence points. Subsequently, we identified the type of sampling data biases contained in our presence data and then conducted two out of those five proposed sampling bias correction methods. The first was Spatial filtering, which was conducted by creating a grid of 2x2 km cell size and randomly select only one point of occurrence per grid cell. The size of the grid cell is not the representation of approximate species' dispersal capability, but rather as a careful modification of 10-km radius rule of spatial filtering proposed by Kramer-Schadt et al. (2013) and Boria et al. (2014). QuantumGIS software ver. 3.0.0 (QGIS Development Team 2018) was used in the grid creation and random points selection processes. The second method was Bias file utilization; bias file is a probability surface that represents the intensity of sampling effort across the area of study and gives a gradual weight to random background data used for modeling (Fourcade et al. 2014). Creating an ideal bias file requires the actual sampling intensity data across the study area. Even though it can be roughly estimated by the aggregation of occurrences from closely related species (Phillips et al. 2009), such datum is very limited in availability and hard to generate. In consequence, we created bias grids by deriving a Gaussian kernel density map of the occurrence locations using SDMToolbox of ArcGIS, and then rescaled it from 1 to 20 (Fourcade et al. 2014). Bias file was later used by fed it into MaxEnt software during modeling process through setting options (Dudik et al. 2005; Elith et al. 2010; Phillips et al. 2017).

### Environmental and climate data

The model in this study was built using environmental and bioclimatic variables which were selected based on earlier screenings of related variables considered as the main factors affecting the distribution of species. We first collected 19 bioclimatic and three environmental variables which were expected to have direct effect on plant growth and survival, based on preceding studies (e.g. Soria-auza 2009; Hu et al. 2015; Mod et al. 2016; Setyawan et al. 2017; Velazco et al. 2017). The bioclimatic layers ver 2.0 (Fick and Hijmans 2017) plus altitude layer were acquired from WorldClim Bioclimatic datasets website (www.worldclim.org). Bioclimatic layers were produced by interpolating the average monthly climate data from between 9,000 and 60,000 weather stations at approximately 1 km$^2$ (30 arc-second) spatial resolution (Fick and Hijmans 2017). Soil types and geological features of Java Island were collected from freely available Indonesian Geospatial Information Agency's (Indonesian: Badan Informasi Geospasial, abbreviation: BIG) website. These datasets were then pre-processed in advance through several processes including image cutting, resampling of data in a geographic coordinate system of WGS48 at a resolution of 1 km$^2$ (0.008333 decimal degree), and file format converting into ASCII format. All of these processes were performed using QuantumGIS software ver 3.0.0.

Certainly, issues of redundancy and multi-collinearity will raise as a consequence of high inter-dependency between some of the bioclimatic variables (Bedia et al. 2013). Although neglecting these issues will not affect the predictive quality of model greatly (Elith et al. 2011), it does, however, negatively affects model interpretability, limit any inference of the contribution of any correlated variables, and also hampering the ability of the model for extrapolation (Brauner and Shacham 1998; Van Gils et al. 2012, 2014). Therefore, in order to avoid these effects, we omitted the bioclimatic variables yielding correlation values above 0.95 (Spearman's rho coefficient) in the pairwise cross-correlation matrix of each dataset (intra-dataset correlations) (Bedia et al. 2013). We used SDM toolbox ver. 2.0 (Brown 2014) in ArcGIS ver. 10.3 to perform calculation and automatically removed each one of the two correlated variables. Finally, the remaining twelve variables (i.e. bio_1, bio_2, bio_3, bio_4, bio_12, bio_13, bio_15, bio_18, and bio_19) along with three environmental variables (i.e. altitude, soil type, geological features) were then compiled to be used as predictor variables in this study (Table 1).

### Future climate projections

We used the future climate scenarios of the WorldClim datasets projected with the Earth System configuration of the Hadley Global Environment Model-2 Carbon Cycle (HadGEM2-CC) which were developed by the Hadley Center, United Kingdom (Collins et al. 2011). HadGEM2-CC was produced by modeling the physical climate along with the earth system components and couplings.

**Table 1.** Climate and 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 | Ishotermality | ×100 |
| bio_4 | Temperature Seasonality | ×100 |
| bio_12 | Annual Precipitation | mm |
| bio_13 | Precipitation of Wettest Month | mm |
| bio_15 | Precipitation Seasonality | mm |
| bio_18 | Precipitation of Warmest Quarter | mm |
| bio_19 | Precipitation of Coldest Quarter | mm |
| javasoil | Soil type | |
| javageologi | Geology features | |

Key features of targeted physical performance are El Nino Southern Oscillation (ENSO) and land-surface temperature biases (Koo et al. 2015). Therefore, the physical climate in the HadGEM2-CC family can sustain a realistic vegetation distribution (Collins et al. 2008). This system model has been used to perform all the CMIP5 (Coupled Model Inter-comparison Project Phase 5) centennial experiments including ensembles of simulations of the RCPs (Shrestha and Bawa 2014). We selected four RCP (Representative Carbon pathways), which represents the future greenhouse gas (GHG) emission trajectories, namely RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5 in three different periods of time (2030, 2050, and 2080). RCP 2.6, the most optimistic projection, projected that global GHG emission (measured in CO2-equivalents) will increase slowly to reach its peak at 3.1 W/m2 in between 2010-2020, with the emissions declining significantly thereafter to 2.6 W/m2 by the year 2100 (Van Vuuren et al. 2007; Moss et al. 2010). Emissions in RCP 4.5 is assumed to be stabilized at 4.5 W/m2 by the year 2100 due to the variety of strategies and technologies implemented to reduce GHG emissions level (Clarke et al. 2007). Likewise, the emissions in RCP 6.0 is projected to reach its peak around 2080 and stabilizes by the year 2100 at 6.0 W/m2. In RCP 8.5, emissions continue to rise throughout the 21st century, reaching around 8.5 W/m2 as the highest level by the end of the century (Riahi et al. 2011).

It has been known that these climate scenarios contain systematic error (biases) due to the limited spatial resolution, simplified physic and thermodynamic processes, and numerical schemes or incomplete knowledge of climate system processes (Ramirez-Villegas et al. 2013). Therefore, we implemented bias correction data provided by CGIAR-CCAFS under three different calibration approaches: (i) 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); (ii) 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 present-day observational dataset (Tabor and Williams 2010); (iii) Quantile Mapping (QM), this approach removes the

systematic bias in the GCM simulations and account for 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).

*Model development*

In total, 1,721 occurrence points and twelve variables were then used to build the models using freely available MaxEnt software ver. 3.4.1 (Phillips et al. 2017). MaxEnt was chosen as it has been proved to give better results than other modeling algorithms with the basis of presence-only data (PO) or presence-background (PB) along with environmental variables (Philips and Dudik 2008; Summers et al. 2012). Further consideration to use MaxEnt in this study was because the aim of this study is in accordance with the good performance of MaxEnt to model the effect of climate change on the potential shifting range of species (e.g. Kou et al. 2011; Johnston et al. 2012; Duan et al. 2016). Furthermore, MaxEnt also offers a wide variety of setting options which will be different in each case and occasionally requires species-specific settings (Merow et al. 2013). Hence, we tried to ensure that the setting options were adjusted to our specific study aims, hypothesis, and our intended assumptions (Peterson et al. 2011; Araujo and Peterson 2012; Merow et al. 2013). The adjusted parameters were as follow: (i) Convergence threshold was set to $1×10^{-6}$. (ii) The number of replicated runs was set to ten times (the averaged value is the one used as the result) using "cross-validate" as the replicated run type. Using "cross-validate" means to split the data ten times (10% per partition), train the model ten times on 90% of the data, and test it each time on the 10% partition alternately. (iii) Maximum iterations were set to 5,000 for each run to allow the model to have adequate time for converging, Furthermore, to avoid over-fitting and assuming that the species respond directly to the predictors (vs to correlated factors), we decided to "smooth" the model by choosing only hinge features (Elith et al. 2010). Considering that we used a large collection of occurrence from diverse regions to be projected to different climate condition, the default "regularization multiplier" value was doubled to accommodate aforementioned type of data and aim of study (Elith et al. 2006; Merow et al. 2013; Radosavljevic and Anderson 2013). We used the "projection" feature to extrapolate the model into different climate projections in order to predict the impact of projected future climate conditions to the redistribution of potentially suitable habitat for both species (Van der Wall et al. 2009).

*Model evaluation*

Model performance evaluation was conducted using the Area Under the Receiver Operating Characteristic (ROC) Curve (AUC) produced by the MaxEnt itself and True Skill Statistic (TSS) which was calculated using sensitivity and specificity values. AUC value ranges from 0 (lowest) to 1 (highest), whereby value between 0 and 0.5 represents that the model is no better than just random prediction, value below 0.7 is low, value between 0.7 and 0.9 is good, and value above 0.9 indicates high discrimination or indicates

that the model is far better than random prediction (Araujo et al. 2005). Despite having been proved that AUC does not necessarily provide useful information to assess and/or to evaluate the model performance (by Lobo et al. 2008; Bahn and McGill 2013; and Aguirre-Gutiérrez et al. 2013), we reported it to illustrate that the models in this study perform better than any model with a set of random predictors. Additionally, we calculated the True Skill Statistic (TSS) (also known as the Youden index), as an additional measurement to evaluate the performance of the model (Youden 1950; Allouche et al. 2006). Another measurement of model evaluation was demonstrated by several studies using Kappa statistic (e.g. Duan et al. 2014; Ali and Hossein 2016; Bagheri et al. 2017). However, regarding the use of Kappa value, its value is highly correlated to prevalence of the locality points and the size of the study area (Lobo et al. 2008; Fourcade et al. 2017), hence, would generate some sort of bias or misunderstanding. Moreover, due to the fact that both AUC and Kappa are weighting omission and commission errors equally (Allouche et al. 2006; Lobo et al. 2008; Jimenez-Valverde 2012; 2014; Fourcade et al. 2017), Kappa, just like AUC, is more reliable if it is applied in PA (Presence-Absence) model. Consequently, we assume that the utilization of TSS in this study, wherein using presence-only data, is more suitable than the use of Kappa statistics.

## Data analysis

By using the "logistic" output format, we retrieved prediction maps which depict the distribution of potential ecological niche of species across the study area and the changes of its distribution under future climate projections (Philips and Dudik 2008) which were linearly scaled between 0 (lowest) to 1 (highest). All of the maps produced by MaxEnt were in ASCII file format. We imported the ASCII file containing the probability of habitat suitability into QuantumGIS software ver. 3.0.0 and reclassified it into three classes: low suitability (25-50 % probability of occurrence), medium suitability, (50-75% probability of occurrence), and high suitability (>75 % probability of occurrence). The reclassification was conducted to allow us to compare the changes in every class over time and space by comparing the total area of predicted habitat under current and projected future climate conditions by counting the number of "presence" grid cells and multiplied it by their spatial resolution. The lowest suitability value was acquired using selected threshold rule. Indeed, in the process of selecting threshold rule, one should avoid arbitrariness and should incorporate consideration of relative importance difference between commission error and omission error (Phillips and Dudik 2008; Nenzen and Araujo 2011; Bean et al. 2012; Syfert et al. 2013). By considering that reducing omission error is more important determinant than reducing commission error, Norris (2014) proposed "minimum training presence" or "fixed cumulative value 1" as the most appropriate rule. However, Liu et al. (2016) stated that those proposed threshold rule may be more convenient for modeling rare species, but in the case of more common species, reducing commission error should be considered more than lowering the omission error. Therefore, following Liu et al. (2016), we selected "maximum training sensitivity plus specificity" threshold rule to be used in this study. Additionally, we also retrieved the variables' relative contribution to the models and quantify the degree to each variable affect the prediction. We also retrieved alternate estimation of variable importance by running the jackknife test. Jackknife test will shows which variable has the most information that is not present in the other variables and which variable has the most useful information by itself (Phillips et al. 2009). A separate analysis, which focused on observing the potential change of altitudinal distribution of high-altitude *Selaginella*, was conducted by comparing the mean values of the predicted areas under current and future climate scenarios conditions using independent sample T-test (Shrestha and Bawa 2014).

## RESULTS AND DISCUSSION

### Results

*Model evaluation and variables importance*

According to the calculations of the relative contributions of environmental variables to the MaxEnt models under the current scenario, there are three variables which are considered have the most contribution to the model, i.e. Altitude (alt), Annual mean temperature (bio_1), and Annual precipitation (bio)_12) (Table 2). Altitude made the largest contribution with 53.8%, followed by annual mean temperature and annual precipitation with 13.2% and 7.3%, respectively, making the cumulative contributions of these factors of 74.3%. Thus, suggesting that the distributions of high-altitude *Selaginella* are strongly influenced by these three variables. Similarly, the results of jackknife test suggested that Altitude and Annual mean temperature give the highest gain when used in isolation (Figure 2), which means that these variables appear to have the most useful information by itself and, therefore, provide the highest contribution to the model (Phillips et al. 2008). Furthermore, The environmental variable that decreases the gain the most when it is omitted is mean diurnal range (bio_2) which therefore appears to have the most information that is not available in the other variables (Phillips et al. 2008).

**Table 2**. Percentages of variables contribution to the model

| Environmental variables | Contribution (%) |
|---|---|
| Altitude (Alt) | 53.8 |
| Annual Mean Temperature (°C *10) (bio_1) | 13.2 |
| Mean Diurnal Range (Mean of monthly (max temp-min temp)) (bio_2) | 5.7 |
| Isothermality (bio_3) | 3.7 |
| Temperature Seasonality (standard deviation *100) (bio_4) | 2.2 |
| Annual Precipitation (bio_12) | 7.3 |
| Precipitation of Wettest Month (bio_13) | 0.4 |
| Precipitation Seasonality (bio_15) | 3 |
| Precipitation of Warmest Quarter (bio_18) | 1.2 |
| Precipitation of Coldest Quarter (bio_19) | 0.8 |
| Soil type (javasoil) | 2.8 |
| Geology features (javageologi) | 5.9 |
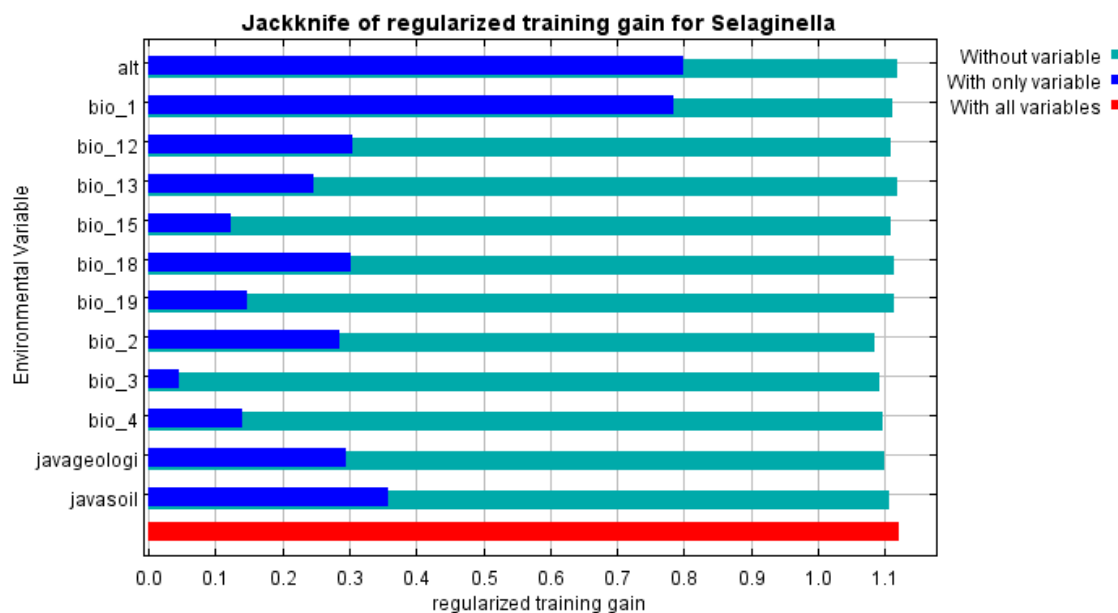
**Figure 2.** Results of jackknife test of relative importance of predictor variables for high-altitude *Selaginella*

Response curve produced by MaxEnt illustrates how each variable affects the prediction by showing how the logistic prediction changes as each variable varied (Phillips et al. 2006). As has been stated before, altitude is the most important determinant in the model, with the response curve indicates positive correlation between altitude level and probability of occurrence. The probability of occurrence gradually increases to above 50% at the altitude of about 800 m asl and then reaches its peak at around 2,300 m asl before a slight decrease at higher altitude, but still at high probability (Figure 3.A). Response curve of the second most important variable (Annual mean temperature) depicts that the probability of presence is high in the area that has annual mean temperature of between 15 ℃ and 22 ℃ (Figure 3.B). Areas which have either lower or higher mean temperature per annum than the aforementioned range have lower probabilities. Response curve of annual precipitation rate (bio_12) also projects positive correlation between probability of presence and annual precipitation rate. The best rate of annual precipitation for the presence of species is predicted at an above 3000 mm year$^{-1}$ (Figure 3.C).

The performance of MaxEnt model in term of predictive accuracy and statistical significance are often investigated by evaluating the AUC value and performing additional statistical calculation (Peterson et al. 2011). The AUC value obtained from the model's result in this study was 0.860, which indicate that the model has a good discrimination ability and the model performs better than any model with a set of random predictors (Lobo et al. 2008; Peterson et al. 2008; Jimenez-Valverde 2012, 2014; Fourcade et al. 2017). Additional evaluation of the model was conducted using True Skill Statistic (TSS) by calculating the summary of sensitivity and specificity minus one. The data acquired to calculate the value were obtained from background prediction and sample prediction file from the MaxEnt result. The retrieved TSS value of 0.86 gives the impression that the model built in this study have a good degree of agreement, good predictive capacity, and also can be interpreted as evidence for real ecological phenomenon, based on climatic and environmental variables used (Allouche et al. 2006; Li and Guo 2013).
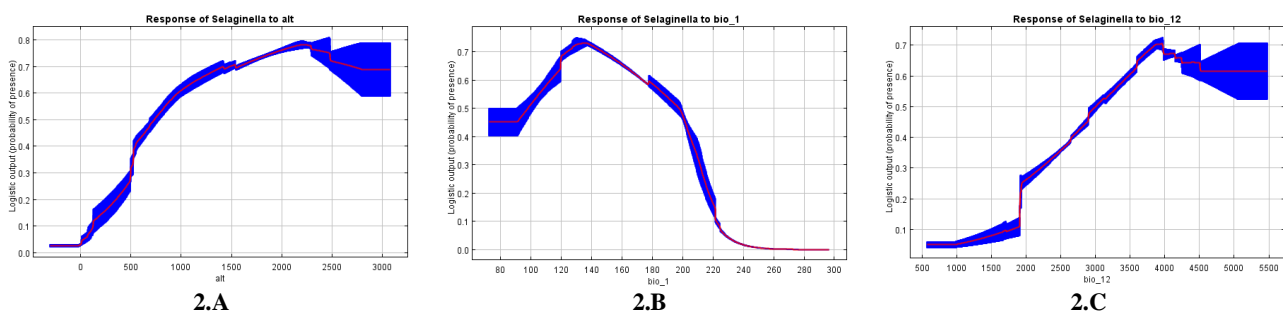


**2.A**  **2.B**  **2.C**

**Figure 3.** Response curves from MaxEnt of the most important variables to the species distribution model: A. Response curve for Altitude; B. Annual mean temperature (in ℃*10); C. Annual Precipitation (in mm year-1). 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)

*Predicted suitable habitat under current climate*

Projected distribution of predicted suitable habitat for high-altitude *Selaginella* under current climate condition is shown in Figure 4. Subsequent to categorized the output into two categories (suitable vs unsuitable) using the aforementioned threshold rule (see Methods), the predicted suitable habitat were then reclassified into three classes: low suitability (25-50% probability of occurrence), medium suitability, (50-75% probability of occurrence), and high suitability (>75% probability of occurrence) to allow us to compare the changes in every class of probability under future climate projection. According to the result, about 37.32% (48,974 km²) area of Java Island was predicted to be suitable for high-altitude *Selaginella*. The number consisted of 17.73% (23,272 km²), 12.37% (16,239 km²), and 7.21% (9,463 km²) of low, medium, and high probability areas, respectively (Figure 7).

The predicted suitable habitats were distributed across the mountainous areas of Java Island, from western to eastern part of the island. The high probability of suitable areas was mainly concentrated in Central and East Java, whereas West Java and Banten province dominated by low and medium probability areas. Altitudinally, the low probability areas were mainly distributed at the altitude of between 500 and 1291 m asl, medium probability at between 1292 and 1734 m asl, and high probability at above 1734 m asl (Figure 5).
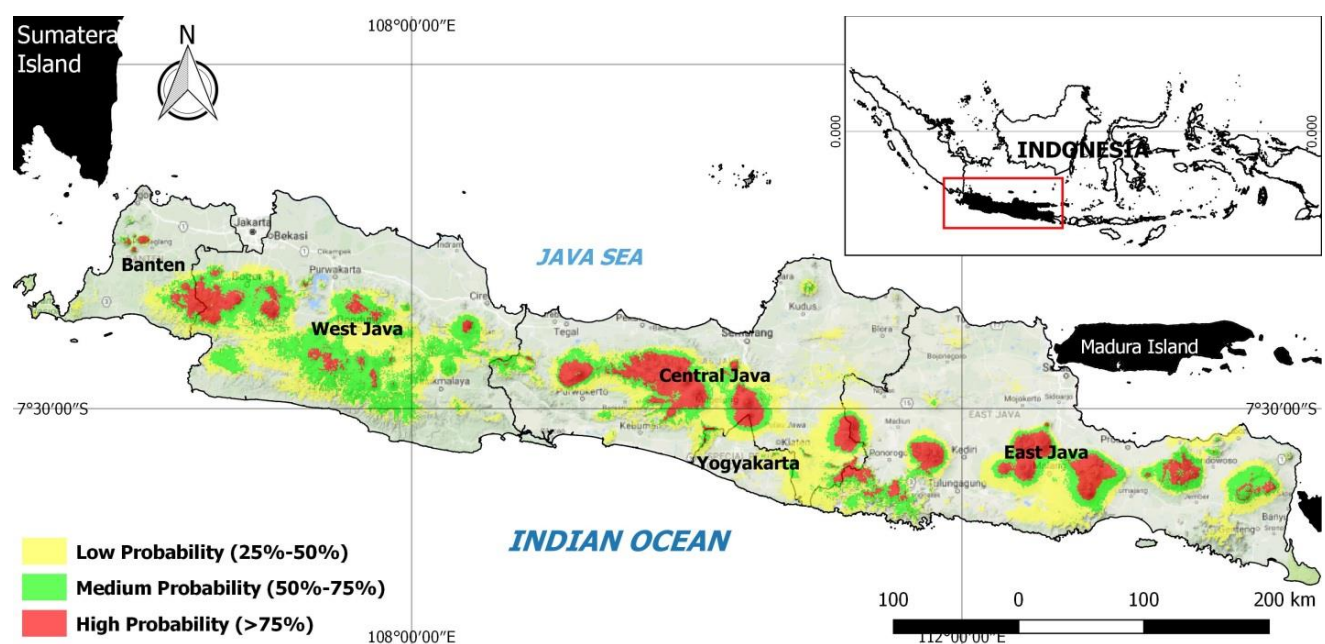


**Figure 4.** Predicted distribution of suitable habitat for high-altitude *Selaginella* under current climate condition (Base map: Google Physical Maps 2014).
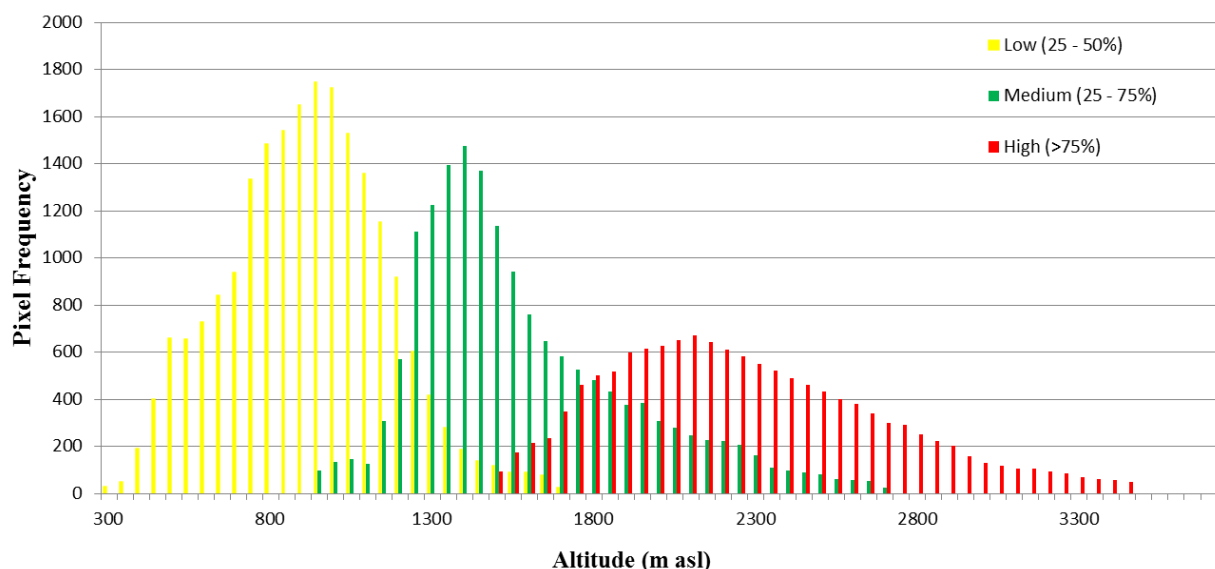


**Figure 5.** Predicted altitudinal distribution of high-altitude *Selaginella* suitable habitat under current climate condition

*Predicted suitable habitat under future climate scenarios*

We used the "projection" feature in MaxEnt along with four future climate scenarios (RCP) in three different time periods to model the predicted suitable habitat of the four high-altitude *Selaginella* in the future. The results of the predicted suitable habitat under future climate were then analyzed and compared with current prediction (Figure 6). Under the RCP 2.6 climate scenario, the high probability area will likely decrease by almost 35% in the year 2080, whereas the medium and low probability areas will reduce by about 37.2% and 18.3%, respectively. Likewise, under the RCP 4.5 and 6.0 scenarios (medium GHG emission scenario), there will be a gradual decrease of suitable areas which are approximately greater than the decrease of areas under the RCP 2.6 scenario. Under these medium scenarios, in 2080, about 18.1%, 37.5%, and 25.1% of low, medium, and high probability areas will be lost respectively. The RCP 8.5 scenario is predicted to have the most negative effect on the distribution of suitable habitat of high-altitude *Selaginella*. Under this climate projection, about 21.2% of low probability areas will be lost across the given periods of time, whereas medium probability areas predicted to decrease by around 38.1% during the same time periods. High probability areas are expected to decrease by about 33.4% in the year 2080 (Figure 7).
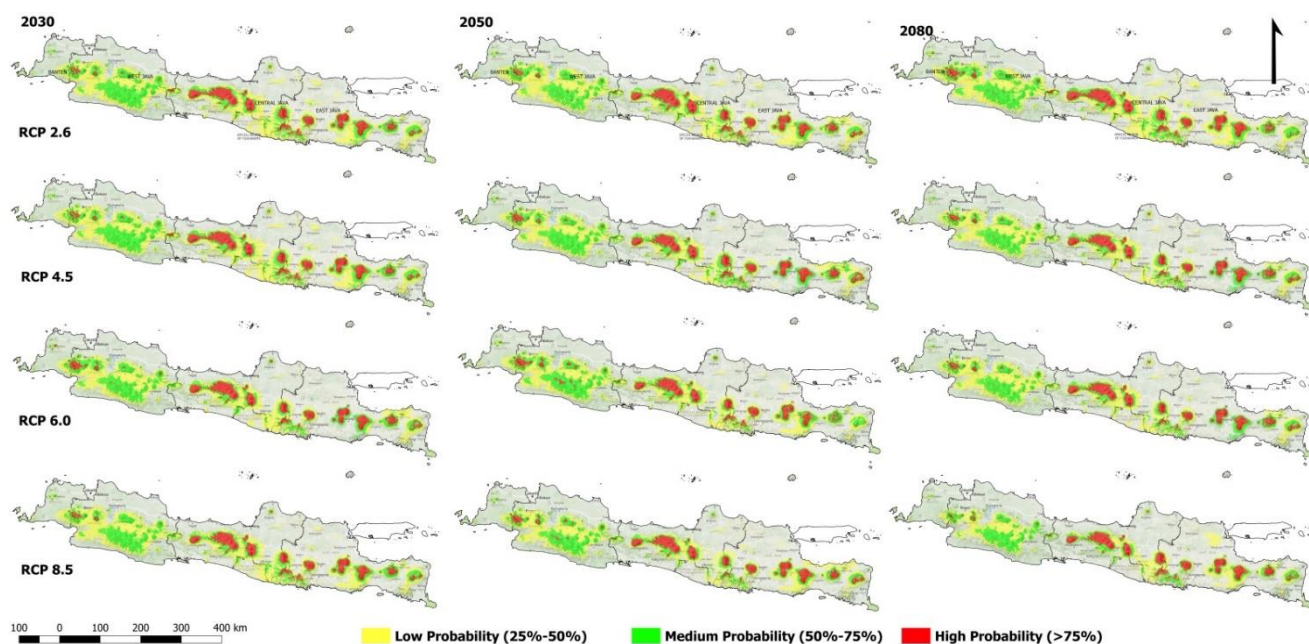


**Figure 6.** Predicted distribution of climatically suitable habitat under future climate projections
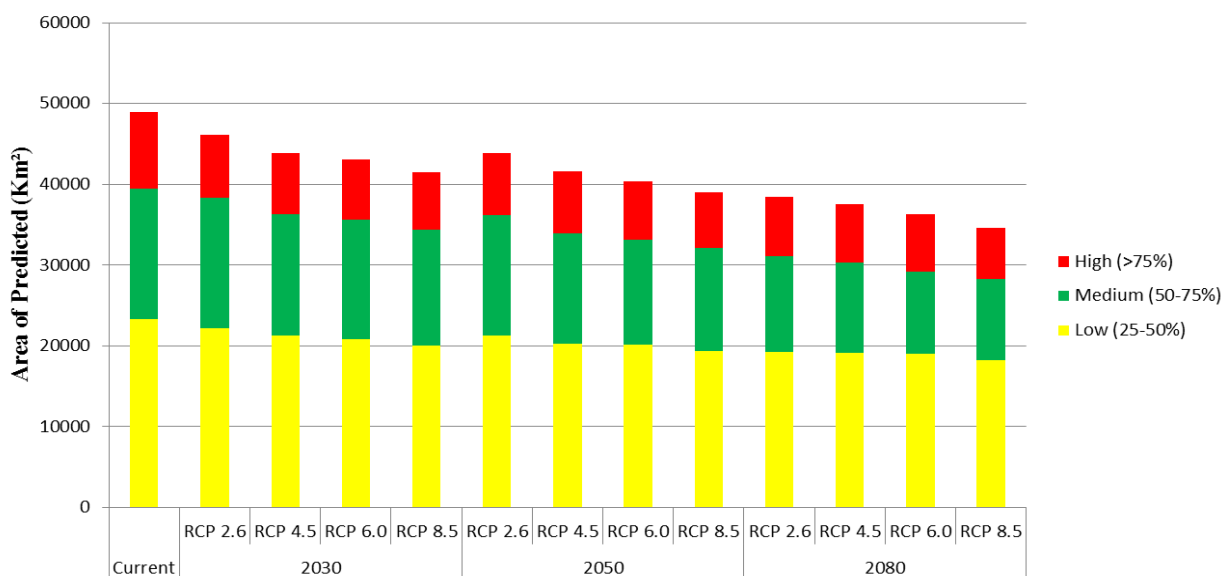


**Figure 7.** Estimated areas of the predicted suitable habitat under current and future climate projections

The projected climate changes are also predicted to affect the altitudinal distribution of high-altitude *Selaginella*'s suitable habitat (Figure 8, Table 3). The models show that despite there will be upward shifts in average distribution of suitable habitat under the RCP2.6, RCP 4.5, and RCP 6.0 in 2030, the shifts, however, are still statistically insignificant (p = 0.01), which mean that the upward shifts in this year and under aforementioned projections are small and still no noteworthy. The upward shift in the year 2030 is statistically significant only under RCP 8.5 climate projection, wherein the mean altitude was predicted to increase by 51.1 m from current's mean altitude. Further upward shifts on the distribution of high-altitude *Selaginella*'s suitable habitat are predicted in 2050 and 2080 under all of RCP projections. In the year 2080 and under RCP 8.5 climate projection, the altitudinal mean will shift by almost 150 m from current average altitude. The maximum altitude of predicted suitable habitat is also predicted to increase to reach almost 3500 m asl in the year 2080 (RCP 8.5), since the effect of climate changes not only affecting the average altitude, but also affecting the minimum and maximum altitudinal distribution of predicted suitable habitat (Figure 8). All of these shifts beyond the RCP 8.5 (2030) were calculated to be statistically significant (Table 3).

## Discussion

Rapid changes on the environmental condition caused by climate changes in the past decades have induced ecologists to increase their focus on the potential response of plant communities to climate change (Hamrick 2004). Several studies (e.g. Parmesan et al. 2003; Colwell et al. 2008; Lenoil et al. 2008; Doak and Morris 2010; Feelay 2012) have reported that range shrinkage and extinction of organisms are examples of ecological impacts of climate changes. Java Island, which is the most densely populated island in Indonesia, will likely to suffer more from the worsening human-induced climate changes. In this study, we have examined how climatic factors affect climatic habitat suitability and geographical range as well as altitudinal distribution of four high-altitude *Selaginella* species.

**Table 3.** Independent T-test of average elevation shift of *Selaginella* habitat under current condition and future climate scenarios.

| Climate scenarios | Year | Mean | SD | P-value |
|---|---|---|---|---|
| Current condition | - | 1530.1 | 633.9 | |
| RCP 2.6 | 2030 | 1550 | 601.8 | 0.29 |
| RCP 4.5 | 2030 | 1559 | 604.3 | 0.26 |
| RCP 6.0 | 2030 | 1561.7 | 608.8 | 0.11 |
| RCP 8.5 | 2030 | 1581.1 | 615.2 | 0.011 |
| RCP 2.6 | 2050 | 1589.2 | 616.4 | 0.001 |
| RCP 4.5 | 2050 | 1592.1 | 627.2 | $3.3 \times 10^{-4}$ |
| RCP 6.0 | 2050 | 1594.8 | 604.2 | $3 \times 10^{-4}$ |
| RCP 8.5 | 2050 | 1601.8 | 599.9 | $1.2 \times 10^{-4}$ |
| RCP 2.6 | 2080 | 1608.1 | 619.9 | $1 \times 10^{-4}$ |
| RCP 4.5 | 2080 | 1627.1 | 585.1 | $1.12 \times 10^{-6}$ |
| RCP 6.0 | 2080 | 1630.7 | 672.8 | $1.1 \times 10^{-6}$ |
| RCP 8.5 | 2080 | 1673.5 | 629.7 | $1 \times 10^{-7}$ |
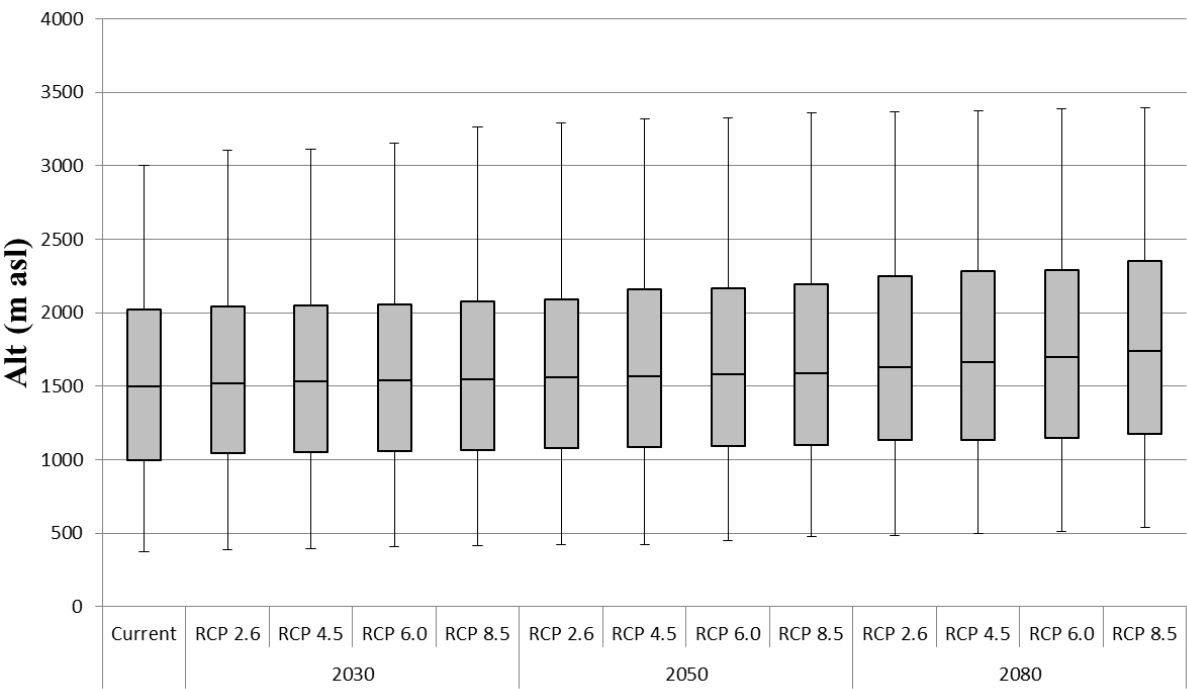


**Figure 8.** Predicted changes in the altitudinal ranges of suitable habitat under future climate projections. The box plots present median, lower quartile, upper quartile, maximum and minimum observations. Altitude is measured in m asl. (meter above sea level)

The results of the model showed that altitude and annual mean temperature were two of the most dominant driving factors of habitat suitability for high-altitude *Selaginella*. The model showed that there is a positive correlation between altitude and the habitat range of high-altitude *Selaginella* and there is a negative correlation between annual mean temperature and such range. Geographical variables, such as elevation, are often related to local precipitation and temperature features (Austin 2002; Körner 2007) and have been considered important determinants of species distribution in mountainous habitats (Körner 2004, 2007; Oluwatobi and Thompson 2015). Temperature, as a regulator of evapotranspiration level, become highly important factor in order to maintain the level of humidity in the region. Water availability, which is measured in annual precipitation (Bio_12), is also another determining factor of habitat suitability for high-altitude *Selaginella*. The positive correlation between the annual precipitation and the probability presence of the species (Figure 2.C), suggests that the four species of high-altitude *Selaginella* require a high level of humidity. Humidity is correlated with many environmental factors that influence the biochemical and physiological processes of plants (e.g. Platt et al. 1993; Wang et al. 1998; Thuiller et al. 2008; Timothy et al. 2009; Bowman 2011; Ruszala et al. 2011). Therefore, the combination of those three factors is expected to be the main role in shaping the ecological adaptation and the distribution pattern of high-altitude *Selaginella*.

A set of future climate scenarios, which was projected under four GHG emission trajectories (the RCP), will likely affect the sustainability of high-altitude *Selaginella* species negatively. The models predicted the losses of suitable habitat will occur gradually across the area of study during the given periods of time. Under the lowest GHG emission projection (RCP 2.6) wherein radiative forcing reaches 2.6 W/m2 by the year 2100 (Meinshausen et al. 2011; IPCC 2014), the annual mean temperature is projected to rise by up to 1.05 ℃ which is predicted to occur mostly in lowland areas (Figure 9.A). Likewise, under the worst scenario projection (RCP 8.5; radiative forcing 8.5 W/m2 by the year

2100), the magnitude of temperature is predicted to increase by about 2.71 ℃ (Figure 9.B). Unlike in the case of temperature, the changes in precipitation would not be the same across the Java Island areas. There will be areas where the amount of precipitation shows a decreasing trend while in other areas there is an increasing trend (Figures 9.C and 9.D). This projection of changes in annual precipitation is in accordance with a study conducted by Siswanto and Supari (2015), which found that during the last 30 years, changes in total annual rainfall across the Java Island vary from-170 to +82 mm/decade. These changes in climate conditions in the future have been predicted to lead to decreasing trends of high-altitude *Selaginella*'s habitat at a rate of between 2.2% and 4.7% per decade. The model results demonstrated that altitude, annual mean temperature, and annual precipitation as three of the most dominant driving factors of habitat suitability of four species of high-altitude *Selaginella*, confirming the fact that changes in these factors have negative impacts on the sustainability of the species in the future.

Temperature, as the second most dominant factor, allegedly affects both the photosynthetic capability and preservation of photosynthetic apparatus of *Selaginella* species (Jagels 1970, Eickmeier 1985). The negative correlation between temperature and probability of high-altitude *Selaginella*'s presence, depict the possible negative effects of warmer temperature. Soni et al. (2012) in their study stated that *S. bryopteris* shows a very poor mechanism for its stomatal regulation in response to high temperature, which also affects its photosynthesis capability. Furthermore, regarding 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 *S. bryopteris* induced with dehydration stress. Desiccation in this *Selaginella* species can also cause enhanced production of reactive oxygen species (ROS) and increased lipid peroxidation. In consequence, the increasing level of annual mean temperature and the decreasing level of annual precipitation are the most important compounding factors of the sustainability of high-altitude *Selaginella*'s habitat in the future.
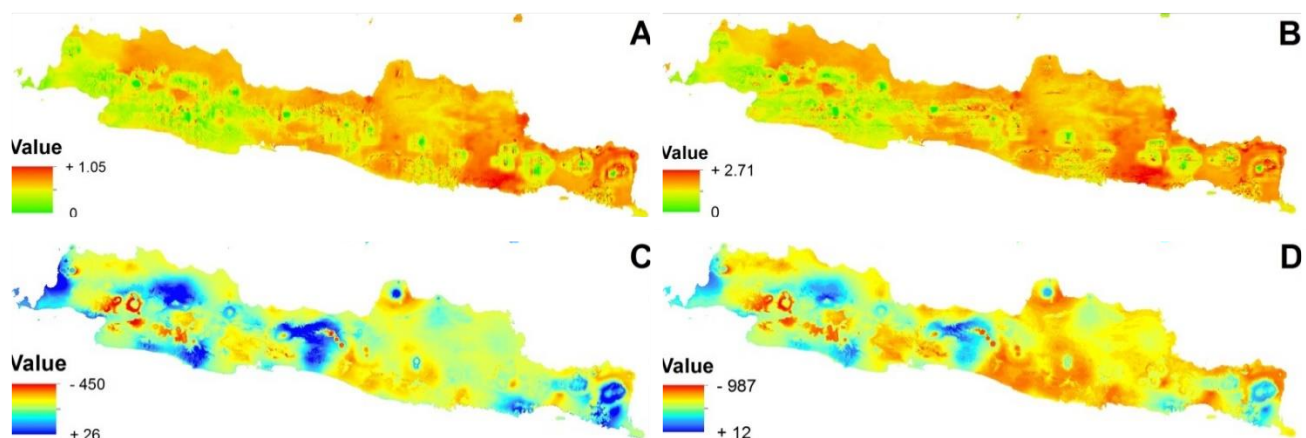


**Figure 9.** Changes in annual mean temperature (bio_1) under RCP 2.6 scenario (A) and RCP 8.5 scenario (B); changes in annual precipitation (bio_12) under RCP 2.6 scenario (C) and RCP 8.5 scenario (D). Colors represent the difference between present climate and future climate (2080-2100). Images were produced by subtracting the value of the future climate variable from the value of the current climate variable on a cell by cell basis.

Several studies have reported that the compounding effects of climate change may threaten the survival of many plant species (e.g. Dillon et al. 2010; Gilman et al. 2010; Pereira et al. 2010; Salamin et al. 2010; Beaumont et al. 2011; Dawson et al. 2011; McMahon et al. 2011; Alice et al. 2012; Bellard et al. 2012; Belgacem and Louhaichi 2013). In response to changes in the environmental condition, plants may develop micro-evolutionary mechanisms to adapt to new conditions, such as reducing photosynthetic rates, growth rates, mineral absorption and tissue regeneration, as well as and increasing concentrations of secondary metabolites (Jochum et al. 2007; Wiens et al. 2009). Plants may also respond by contracting, expanding, or even fragmenting their range of dispersal to follow the changing environments (e.g. Philips et al. 2006; Wiens et al. 2009; Minteer and Collins 2010; Chen et al. 2011; Morueta-Holme et al. 2015). Furthermore, several studies have also reported the early sign of plants migration into higher altitude areas induced by changes in climatic condition (e.g. Zhang et al. 2001; Parmesan and Yohe 2003; Root et al. 2003; Leng et al. 2008; Lenoir et al. 2008; Bertrand et al. 2011; Petitpierre et al. 2016). The modeled altitudinal range of suitable habitat for high-altitude *Selaginella* under future climate condition, in this study, also provide similar signs of range shifting into higher altitude. The shifts occur as the lower land areas are predicted to become drier and warmer, reducing the suitability of habitat at such lowlands and increasing the suitability of wetter and cooler areas at higher altitude (Allen and Breshears 1998; Parmesan and Yohe 2003; Parmesan 2006; Lenoir et al. 2008a,b). However, the shifting may not occur evenly as the shifting will also be constrained by some limitations, including dispersal ability of the spore of *Selaginella* species, natural or anthropogenic barriers, and interaction with other biotic factors (such as herbivory animal). Therefore, to build a proper model that can closely resemble the real-world phenomenon requires enrichment of factors and variables which considered directly or indirectly affecting the sustainability of the species.

Despite several measurements have been taken to minimize the errors in the model caused by bias on the sampling data and to minimize bias on future climate projections and species-specific setting options (see Method), it is inevitable that overestimation and/or underestimation (omission/commission error) may still be contained in the results of the model. Such biases can be caused by several reasons. First, neither the dispersal rate of species nor the demography of meta-population was included in the model, as these parameters are currently unavailable. Cryptogam species, such as *Selaginella*, have a wide dispersal range, and for this reason, modeling their niche is better when absence data is available because it has been known that ENM/SDM using true absence data rather than pseudo-absence data have a lower rate of overprediction (Vaclavik and Meentemeyer 2009). Second, the low resolution of environmental variables used in this study (1 km$^2$) has not yet capable of representing the unique environmental condition that greatly drives the probability of the occurrence of species. Third, the predictors used in this study did not comprehensively represent all of the environmental factors affecting the existence of the species (e.g. biotic factor interaction). Fourth, the lack of human-induced variables, such as land use/land cover changes, deforestation, infrastructure development activities, which can affect the dispersal and habitat shifting of the species. Fifth, the lack of micro-climate variation variables which predicted to affect the existence of species in the study area. Therefore, it is important to note that, like most of the SDM, the "predicted" distribution of suitable habitat does not represent the "true" prediction of the distribution of species, but rather the prediction of the distribution of "suitable" habitat-based only on the variables used in this study. Nevertheless, we may treat the results of this model as an appropriate representation of how the current climate condition shapes the distribution of suitable habitat for high-altitude *Selaginella*, and its predicted redistribution under the effect of future climate projections.

Incorporating dispersal rates, meta-population demography, and other multiple compounding factors, which are expected to have both direct and indirect effect on the target species and its associated biota, is desirable to build a more ideal model (Morin and Thuiller 2009; Sinclair et al. 2010; Ellis 2011). However, such an ideal package of data is currently limited or unavailable. Nonetheless, refining current climate models and incorporating recent development of new climate models provide opportunity to build more precise and ideal model. Future attempts of modeling ENM/SDM are encouraged to incorporate potential human-induced land use/land cover changes, more detailed ecological data, data of biotic interactions between species in the regional ecosystems, and better sampling of presence data that accurately represent the variability of ecological niche of species. Despite all of the presented limitations, this study provides the baseline of understanding the potential effect of climate changes on the distribution of predicted suitable habitat for high-altitude *Selaginella* in Java Island. Based on the results, therefore, we may make an inference and draw a conclusion that future climate conditions will negatively affect the sustainability of high-altitude *Selaginella* by reducing the ability of certain habitat to support the survival of the species. Moreover, habitat shifting to higher altitude areas is also predicted to occur as a result of changes in climate conditions.

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