The future of endemic species in Sumatra

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Summary

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Background: Endemic species inhabiting tropical island ecosystems are particularly vulnerable to threats like habitat loss, overexploitation, and climate change. Sumatra is a perfect example of an island in the tropics that is impacted by these threats. Only a few studies have been performed on the status and the factors driving their ecological distribution. Furthermore, despite the increasing evidence of overhunting, there is no information on the spatial variation of the areas most impacted by hunting.

Aim: To better understand the impact of combined threats of climate change, hunting and habitat loss on the distribution ranges of Sumatra's endemic terrestrial vertebrate species, using Species Distribution Modelling (SDM).

Organisms: Terrestrial vertebrates endemic to the island of Sumatra.

Place of research: The entire Island of Sumatra, both protected and unprotected areas.

Methods: The species distribution modelling is performed by maximum entropy algorithm (Maxent). Derived from a set of environmental variables and georeferenced occurrences, the model indicates a probability distribution in which each grid cell has a predicted suitability of conditions for the species. In addition, the most important biotic, abiotic, and anthropogenic factors influencing their distribution are examined and the efficiency of the protected area is assessed.

Principal findings: In the future, it is predicted that the areas that are currently most species-rich, are expected to lose most of their species with a changing climate. Primary forested land was the most important variable in determining the range of most species. In the future, Sumatra will no longer provide suitable area for 16 or 18 out of the 40 species under the 1st and 2nd scenario respectively. Furthermore, it is predicted that there will be only little overlap between the suitable range of taxa and the protected areas.

Conclusion: This study can be used by future conservation efforts to acquire knowledge on the drivers behind the distribution of endemic species in Sumatra. As well as the effectiveness of the existing protected areas currently and in the future.

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Introduction

Habitat loss and fragmentation are globally one of the most important threats that have a negative impact on biodiversity (Jacobson et al., 2019; IPBES, 2019). Although these threats are two different processes, they are interdependent and usually occur together (Hanski, 2015). The consequences of the combined effects of these threats are a decrease in population size, species richness and a reduction of their original geographical distribution (Lino et al., 2019). Consequently, species distribution ranges and human-dominated land overlap, leading to human-wildlife interactions (Nyhus, 2016). A significant part of these interactions has negative consequences for both humans and animals (Slater & Abdullah, 2020; Nyhus, 2016).

Another major threat to biodiversity is overexploitation, which can lead to extinction of species in areas that otherwise provide suitable habitat (Benítez-López et al., 2017). Humans have hunted for millennia to acquire food and income, but due to the demand from growing human populations and an increase in the commercialization of wild meat, currently, the rates have become unsustainably high (Benítez-López et al., 2019).

Furthermore, climate change is a significant threat to wildlife (Román-Palacios & Wiens, 2020; Pacifici et al., 2018). Climate affects species by determining their distribution and abundance at a location. Species must either adapt *in situ*, move to a habitat with favourable conditions or they are moved towards extinction (Holt, 1990; Bellard et al., 2012). The various effects of climate change on populations can alter the interactions of species at the community level (Bellard et al., 2012), so the response of a species to climate change may indirectly impact another species that relies on this species.

Particularly, species inhabiting tropical island ecosystems are susceptible to multiple climate change factors, like the loss of suitable climatic conditions (Courchamp et al., 2014). The area of each island is limited, which restrains the species from moving to favourable conditions (Itescu, 2018). Furthermore, tropical species generally have a narrow fundamental niche, which makes them more vulnerable to climate change, as it restricts their ability to adapt (Janzen, 1967; Gómez et al., 2016). Moreover, tropical islands are home to a lot of endemic species, which are particularly vulnerable to global changes, caused by both biotic and abiotic characteristics like unique species interaction and poor habitat availability (Leclerc et al., 2020; McPherson & Nieswiadomy, 2005). An endemic species is a species that naturally only occurs in a single geographical area. Therefore, they are highly adapted to their specific environment, which makes a change such as degradation or destruction of their habitat, a significant threat (Burlakova et al., 2011).

The use of protected areas is a measure of species conservation and to counteract these threats (Rambe et al., 2021; Gallardo et al., 2017). However, because of climate and land-use changes, many species are expected to shift beyond the borders of the protected areas, which will lead to a revision of species composition and diversity (Kharouba & Kerr, 2010). The consequences of this difference in species diversity on ecosystem functioning are unknown (Hoffmann et al., 2019; Araújo et al., 2011). Therefore, it is still unclear if the use of protected areas is enough to overcome these threats.

Besides, a growing body of research is being performed to understand the effect of all these different threats and how their relative importance varies across taxonomic groups however, this is not yet clear (Evans et al., 2011; Scheele et al., 2017; Pacifici et al., 2018). The impact of threats to several species remains poorly understood because tropical areas are generally insufficiently studied (Pacifici et al., 2018). In addition, the impact of environmental factors on the distribution is mostly undetermined (Rahman et al.,2022; Pereira et al., 2012). Important studies have been performed on the population and behavioural ecology of many species, but only a few studies have been performed on the status and the factors driving their ecological distribution (Rahman et al., 2022; Pereira et al., 2012). Moreover, despite the increasing evidence of overhunting, there is no information on the spatial variation of the areas most impacted by hunting (Benítez-López et al., 2019). Likewise, the impact of climate change on protected areas is examined, however they did not compare the impacts inside and outside the protected areas (Araújo et al., 2011). With increasing threats, it is important to know the drivers of the distribution of endangered endemic species to prioritize protecting certain areas (Rahman et al., 2022) and effectively mitigate biodiversity loss (Wang et al., 2022; Araújo et al., 2011).

Sumatra is a perfect example of an island in the tropics that is impacted by these threats. Hence, this study will be focused on the endemic species of Sumatra and assess the relative strength of all these threats on a taxa and species level. The study aims to better understand the impact of combined threats of climate change, hunting and habitat loss on the distribution ranges of the endemic terrestrial vertebrate species of Sumatra, using Species Distribution Modelling (SDM). The most important biotic, abiotic, and anthropogenic factors influencing their distribution are examined as well as compared for different classes. In addition, the current and future spatial distribution of the species is modelled as well as the effectiveness – in terms of geographical overlap – of existing protected areas to protect these species at present and in the future is assessed. The results can be used to gain knowledge on the current conservation status of endemic species of Sumatra and explore the long-term conservation potential of protected areas. Furthermore, this study can be used to get a better understanding of the impact of each driver separately.

Materials and Methods

Study area & Species

The study area consists of the entire Island of Sumatra, both protected (± 23% of the total area) and unprotected areas. The island is dominated by tropical rainforests surrounding the volcanic Mount Kerinci, but also some sea-level peat swamps can be found. Three protected areas in Sumatra are UNESCO-listed and form the tropical rainforest heritage of Sumatra (TRHS). It covers a total of 2.5 million hectares and consists of three separate national parks, namely Gunung Leuser (GLNP), Kerinci Seblat (KSNP) and Bukit Barisan Selatan (BBSNP). Furthermore, 27 other protected areas are established in Sumatra (See appendix A). For this study, terrestrial (and freshwater) vertebrates endemic to the island of Sumatra were selected. A total of 40 species fit these criteria and thus were included in the study (Table 1). These species belong to multiple classes like Mammalia, Aves, Reptilia and Amphibia and have all types of conservation statuses according to the IUCN red list.

Species distribution modelling

The species distribution modelling is performed by a machine-learning technique called the maximum entropy algorithm (Maxent) (Phillips et al., 2006). Derived from a set of environmental variables and georeferenced occurrences, the model indicates a probability distribution in which each grid cell has a predicted suitability of conditions for the species. Occurrence data were first collected from the Global Biodiversity Information Facility (GBIF). A minimum sample size of 11 was used to achieve accurate distributions following recommendations from Proosdij et al. (2015). If these were not available or the sample size was not bigger than 11, occurrences were extracted from the species' distribution ranges published by the International Union for Conservation of Nature's Red List of Threatened Species (IUCN) (Table 1). For only 8 out of 40 species, sufficient occurrence data were available in GBIF. For the other 32 species, occurance data were obtained by random sampling of the species IUCN ranges in R-studio version 1.1.463 (RStudio Team, 2021) using the packages 'rgdal' (Bivand et al., 2023) and 'sp' (Pebesma & Bivand, 2005). Between 15-50 samples were obtained for these 32 species, the number of samples was dependent on the size of the IUCN range (a relatively small range meant fewer occurrences) and their IUCN conservation status (the more vulnerable a species is, the fewer samples were obtained). For the species for which less than 11 occurrence records were available in GBIF, occurrences were randomly extracted from the distribution ranges as published by the IUCN, after which the available occurrence records of GBIF were added. Next, all the coordinates (from GBIF and those obtained from the IUCN range) were cleaned by removing duplicates, occurrences that were outside of the study area and points that had low accuracy (e.g., fewer than two decimals). The occurrence points of all species together were used to create a bias file, showing sampling effort, which was used in Maxent to reduce sample bias. This leads to an improvement in the model fit (Phillips et al., 2009).

Environmental variables

Although a large range of predictor variables can be important in driving a species range, whether or not they can be used in SDMs depends on the availability. Here, I used bioclimatic, land-use, topographical, and anthropogenic predictor variables (see Table 2). I did not use e.g. biotic variables such as food availability and predation pressure as data on these variables are not available. I used 19 bioclimatic variables available at WorldClim (Fick & Hijmans, 2017) and derived from current climatic data (1970-2000) to predict the current distribution ranges of all species. The smallest scale with which these data are currently available are 30-arc seconds (~ 1 km at the equator), which was thus used as the resolution of my study. Furthermore, 14 land-use variables were downloaded from Land-Use Harmonization2 (LUH2) (Hurt et al., 2020) at a 15 arc-minutes scale covering the same time period. These variables were downscaled to match the same resolution as the bioclimatic variables using the package 'Raster' (Hijmans, 2023) in R-studio (RStudio Team, 2021). In addition, using the packages 'Raster' (Hijmans, 2023) and 'spatialEco' (Evans & Murphy, 2021), I calculated three topographical variables (slope, aspect and normalized topographic position index [NTPI]) based on the SRTM30 digital elevation model (Hijmans et al., 2004) at a 30-arc second resolution.

Table 1.

List of Sumatran endemic species included in this study and summary of occurrence data.

Class	Common name	Scientific name	IUCN Status	No. Occ.	Data type	Source
Amphibia	Elongated Caecilian	*Ichthyophis elongatus*	DD	50	Published distribution range	IUCN
	Kodok-langsing	*Ansonia glandulosa*	LC	25	Published distribution range	IUCN
	Kodok-buduk bengkulu	*Ingerophrynus claviger*	LC	25	Published distribution range	IUCN
	Katak-parasut Dempo	*Rhacophorus catamitus*	LC	50	Published distribution range	IUCN
	Katak-parasut Barisan	*Rhacophorus barisani*	LC	49	Published distribution range	IUCN
	Katak-parasut Bintik-hitam	*Zhangixalus achantharrhena*	LC	50	Published distribution range	IUCN
	Katak-tanduk Sumatra	*Megophrys parallela*	LC	25	Published distribution range	IUCN
	Sumatra Caecilian	*Ichthyophis sumatranus*	DD	20	Published distribution range	IUCN
	Kodok-buduk Sumatra	*Duttaphrynus sumatranus*	DD	20	Published distribution range	IUCN
Aves	Hoogerwerf's Pheasant	*Lophura inornata hoogerwerfi*	DD	14	Coordinates	GBIF
	Rück's Blue-flycatcher	*Cyornis ruckii*	CR	25	Published distribution range	IUCN
	Graceful Pitta	*Erythropitta venusta*	VU	50	Published distribution range	IUCN
	Schneider's Pitta	*Hydrornis schneideri*	VU	50	Published distribution range	IUCN
	Blue-masked Leafbird	*Chloropsis venusta*	NT	1 50	Coordinates Published distribution range	GBIF IUCN

	Sumatran Whistling-thrush	*Myophonus castaneus*	NT	12	Coordinates	GBIF
	Sumatran Drongo	*Dicrurus sumatranus*	NT	50	Published distribution range	IUCN
	Sumatran Cochoa	*Cochoa beccarii*	VU	50	Published distribution range	IUCN
	Sumatran Ground-cuckoo	*Carpococcyx viridis*	CR	25	Published distribution range	IUCN
	Short-tailed Frogmouth	*Batrachostomus poliolophus*	NT	9 50	Coordinates Published distribution range	GBIF IUCN
Mammalia	Kloss's Squirrel	*Callosciurus albescens*	DD	50	Published distribution range	IUCN
	Sumatran Clouded Leopard	*Neofelis diardi ssp. diardi*	EN	12	Coordinates	GBIF
	Dwarf Gymnure	*Hylomys parvus*	VU	50	Published distribution range	IUCN
	Black-crested Sumatran Langur	*Presbytis melalophos*	EN	1 50	Coordinates Published distribution range	GBIF IUCN
	Thomas’s Langur	*Presbytis thomasi*	VU	20	Published distribution range	IUCN
	Sumatran Flying Squirrel	*Hylopetes winstoni*	DD	20	Published distribution range	IUCN
	Sumatran Striped Rabbit	*Nesolagus netscheri*	DD	25	Published distribution range	IUCN
	Sumatran Elephant	*Elephas maximus ssp. sumatranus*	CR	11	Coordinates	GBIF

	Sumatran Tiger	*Panthera tigris spp. sumatrae*	CR	14	Coordinates	GBIF
	Sumatran Orangutan	*Pongo abelii*	CR	15	Published distribution range	IUCN
	Tapanuli Orangutan	*Pongo tapanuliensis*	CR	15	Published distribution range	IUCN
	Sumatran Rhinoceros	*Dicerorhinus sumatrensis*	CR	15	Published distribution range	IUCN
Reptilia	Spatula-toothed Snake	*Iguanognathus werneri*	DD	50	Published distribution range	IUCN
	Crested Lizard	*Lophocalotes ludekingi*	LC	50	Published distribution range	IUCN
	Ulmer's reed Snake	*Calamaria ulmeri*	DD	20	Published distribution range	IUCN
	Three-lined Kukri Snake	*Oligodon trilineatus*	LC	25	Published distribution range	IUCN
	Boulenger's Tree Agama	*Dendragama boulengeri*	LC	50	Published distribution range	IUCN
	Bengkulu Reed Snake	*Calamaria alidae*	DD	50	Published distribution range	IUCN
	Sumatran Short-tailed Python	*Python curtus*	LC	50	Published distribution range	IUCN
	Sumatran Green Pit Viper	*Trimeresurus barati*	LC	25	Published distribution range	IUCN
	Etheridgeum	*Etheridgeum pulchrum*	DD	50	Published distribution range	IUCN

IUCN Status, IUCN Red List category; VU, vulnerable; EN, endangered; CR, critically endangered. NO. Occ., Number of Occurrences. Data Type are either coordinates or published distribution range. Coordinates were downloaded from GBIF and published distribution range were downloaded from IUCN.

The NTPI is a measure of the difference between elevation at a central point and the average elevation within a radius that is decided on in advance (De Reu et al., 2013). Also, distance to the river and distance to the road were calculated from inland water and roadmaps that were obtained from the Digital Chart of the World (DCW) ranging between the years 1960-1990 (Hijmans et al., 2004). Furthermore, human population density was used as a proxy for hunting intensity as the central place foraging hypothesis states that the hunting intensity increases near human settlements (Benítez-López et al., 2017). The data for human population were obtained from the Center for International Earth Science Information Network (CIESIN) version (CIESIN, 2018) for the time period 2000 and at a resolution of 30 arc-seconds.

To assess the impact of changes in climate and land-use on the distribution ranges of all species, I used data for 2081-2100. Bioclimatic data, also available at WorldClim (Fick & Hijmans, 2017), from two emission scenarios were used of the general circulation model The Beijing Climate Center Climate System Model (BCC-CSM2-MR), namely the Shared Socioeconomic Pathways (SSP) 2-4.5 and SSP 5-8.5 (IPCC, 2021), as its focus is on East Asia (Wu et al., 2019). SSP 2-4.5 was the most optimistic scenario in this study, where the emission of CO_2 until 2050 is projected to be about the same as it is currently and towards 2100 it is projected to decrease (IPCC, 2021). SSP 5-8.5 was the worst emission scenario used in this study, CO_2 emission is projected to be three times higher compared to the current emission (IPCC, 2021). Land-use data from the World Climate Research Program Coupled Model Intercomparison Project (CMIP6), for the same time period and SSP was downloaded from LUH2 (Hurt et al., 2020) at a 15 arc-minutes scale which was then subsequently downscaled to 30-arc seconds. The five topographical variables and human population density were kept static over time due to the assumed lack of changes or the unavailability of trustworthy projections for the future.

To reduce correlation between predictor variables, several environmental variables were selected per species by performing a correlation matrix in which the least important variable amongst a pair that highly correlated with one another ($R>0.7$) was omitted. The jackknife procedure was applied to evaluate the importance of the variables (Phillips et al.,2006). The jackknife shows the training gain of each variable when the model is run in isolation and compares it with the training gain with all variables. This can be used to explore the relationship between habitat suitability and environmental variables (Abolmaali et al., 2018).

Model validation and performance

Feature selection of Maxent was performed in Rstudio (Rstudio Team, 2021), using an R-package called 'ENMeval' (Kass et al., 2021). ENMeval can assist in feature selection as it calculates performance metrics made with different settings but using the same data (Kass et al.,2021). The results of ENMeval were examined for the models with the lowest delta AICc. The Akaike Information Criterion (AICc) corrected for small samples sizes, considers both model goodness-of-fit and complexity. So, the model with the lowest AICc value (Δ AICc=0) is considered the best model (Burnham & Anderson, 2004). The features settings and regularization multiplier of this model were used in Maxent. This was carried out for every class of animals separately.

Table 2.
Environmental variable list

Group	*Variable*	*Description*
Topographical	Slope	
	Aspect	
	Normalized TPI	
	Distance to river	Distance to the nearest river. Calculated from river map (Hijmans, 2021)
	Distance to road	Distance to the nearest road. Calculated from road map (Hijmans, 2021)
Climatic	Bio1	Annual Mean Temperature
	Bio2	Mean Diurnal Range (Mean of monthly (max temp—min temp))
	Bio3	Isothermality (bio2/bio7) (×100)
	Bio4	Temperature Seasonality (standard deviation *100)
	Bio5	Max Temperature of Warmest Month
	Bio6	Min Temperature of Coldest Month
	Bio7	Temperature Annual Range (BIO5-BIO6)
	Bio8	Mean Temperature of Wettest Quarter
	Bio9	Mean Temperature of Driest Quarter
	Bio10	Mean Temperature of Warmest Quarter
	Bio11	Mean Temperature of Coldest Quarter
	Bio12	Annual Precipitation
	Bio13	Precipitation of Wettest Month
	Bio14	Precipitation of Driest Month
	Bio15	Precipitation Seasonality (Coefficient of Variation)
	Bio16	Precipitation of Wettest Quarter
	Bio17	Precipitation of Driest Quarter
	Bio18	Precipitation of Warmest Quarter
	Bio19	Precipitation of Coldest Quarter
Land-use	primf	Forested primary land
	primn	Non-forested primary land
	secdf	Potentially forested secondary land
	secdn	Potentially non-forested secondary land
	pastr	Managed pasture
	range	Rangeland
	urban	Urban land
	C3ann	C3 annual crops
	C3per	C3 perennial crops
	C4ann	C4 annual crops
	C4per	C4 perennial crops
	C3nfx	C3 nitrogen-fixing crops
	secma	Secondary mean age (units)
	secmb	Secondary mean biomass density (units)
Anthropogenic	Human pop	Hunting intensity

The model was produced in Maxent for every species separate with their selected features settings, regularization multipliers and set of environmental variables. All models were replicated 10 times by cross-validation, for both future scenarios. Thereafter, probability maps were created for every species for the current as well as for the two future scenarios. This was done by taking the average of the 10 replicated models. Afterwards, these probability maps were converted to binominal habitat suitability maps using the maximized sum of sensitivity and specificity as a threshold (Nenzén & Araújo, 2011). Current and future habitat suitability maps for each species were overlayed with each other to assess the percentage suitable area that was gained, remained stable, or lost in future. Furthermore, all current species-specific habitat suitability maps were overlayed with each other to obtain a current species richness heatmap. The same was done for the future. These current and future species richness heatmaps were then overlayed with the protected area map from Sumatra (UNEP-WCMC, 2023) to assess the effectiveness of the current protected areas to conserve biodiversity at present as well as in future.

Results

Model performance

Of the generated species models, 36 out of 40 had a mean AUC $\geq$ 0.7 (Table 3), which means that they have a high confidence level. The other 4 models had a mean AUC between 0.3 and 0.7, so these models' generated projections with low confidence. Nonetheless, they were used during this study.

Table 3.
Mean AUC of the generated species models, together with the three most important variables predicting the distribution of every species. For abbreviations of the important variables see Table 2.

Class	Species	Mean AUC	Important variables
Amphibia	Elongated Caecilian	0.958	c3per, secma, c4ann
	Kodok-langsing	0.977	primf, pastr, secdf
	Kodok-buduk Bengkulu	0.984	bio16, bio17, bio19
	Katak-parasut Dempo	0.947	c4per, bio5, primf
	Katak-parasut Barisan	0.974	bio18, bio9, pastr
	Katak-parasut Bintik-hitam	0.991	bio8, human pop, bio4
	Katak-tanduk Sumatra	0.981	bio9, slope, primf
	Sumatra Caecilian	0.997	human pop, primf, bio4
	Kodok-buduk Sumatra	0.999	bio9, bio16, primf
Aves	Hoogerwerf's Pheasant	0.814	bio8, primf, c3per
	Rück's Blue-flycatcher	0.974	bio4, bio3, c3nfx

	Graceful Pitta	0.922	bio8, slope, primf
	Schneider's Pitta	0.926	bio8, slope, c4per
	Blue-masked Leafbird	0.882	bio8, c3per, slope
	Sumatran Whistling-thrush	0.959	bio6, distanceto_river, human pop
	Sumatran Drongo	0.456	bio6, slope, primf
	Sumatran Cochoa	0.916	bio8, slope, c3nfx
	Sumatran Ground-cuckoo	0.960	bio5, bio4, slope
	Short-tailed Frogmouth	0.888	bio8, primf, c4per
Mammalia	Kloss's Squirrel	0.924	bio7, bio4, secdf
	Sumatran Clouded Leopard	0.941	c4per, secdf, bio2
	Dwarf Gymnure	0.986	bio17, bio5, primf
	Black-crested Sumatran Langur	0.861	bio7, bio4, bio19
	Thomas’s Langur	0.935	bio4, bio15, pastr
	Sumatran Flying Squirrel	0.999	bio7, bio13, secmb
	Sumatran Striped Rabbit	0.957	bio4, bio5, range
	Sumatran Elephant	0.934	bio2, c3per, secdf
	Sumatran Tiger	0.951	c3per, bio2, secdf
	Sumatran Orangutan	0.903	distanceto_road, pastr, bio7
	Tapanuli Orangutan	0.997	c4ann, pastr, c3fnx
	Sumatran Rhinoceros	0.289	bio19, secdn, range
Reptilia	Spatula-toothed Snake	0.474	bio6, secmb, bio19
	Crested Lizard	0.983	bio16, range, bio14
	Ulmer's Reed Snake	0.997	bio7, bio12, primf

	Three-lined Kukri Snake	0.909	slope, c4per, bio4
	Boulenger's Tree Agama	0.939	c4ann, bio7, human pop
	Bengkulu Reed Snake	0.841	bio4, bio7, range
	Sumatran Short-tailed Python	0.789	c3per, range, secdf
	Sumatran Green Pit Viper	0.695	c4ann, bio7, distanceto_road
	Etheridgeum	0.996	urban, range, bio19

Important environmental variables

The predicted suitable range of the majority of species was determined by a variety of variables (Table 3). When pooling all species together, primary forested land was the most important predictor variable, appearing in the top three most important predictor variables for 11 out of 40 species (Figure1).

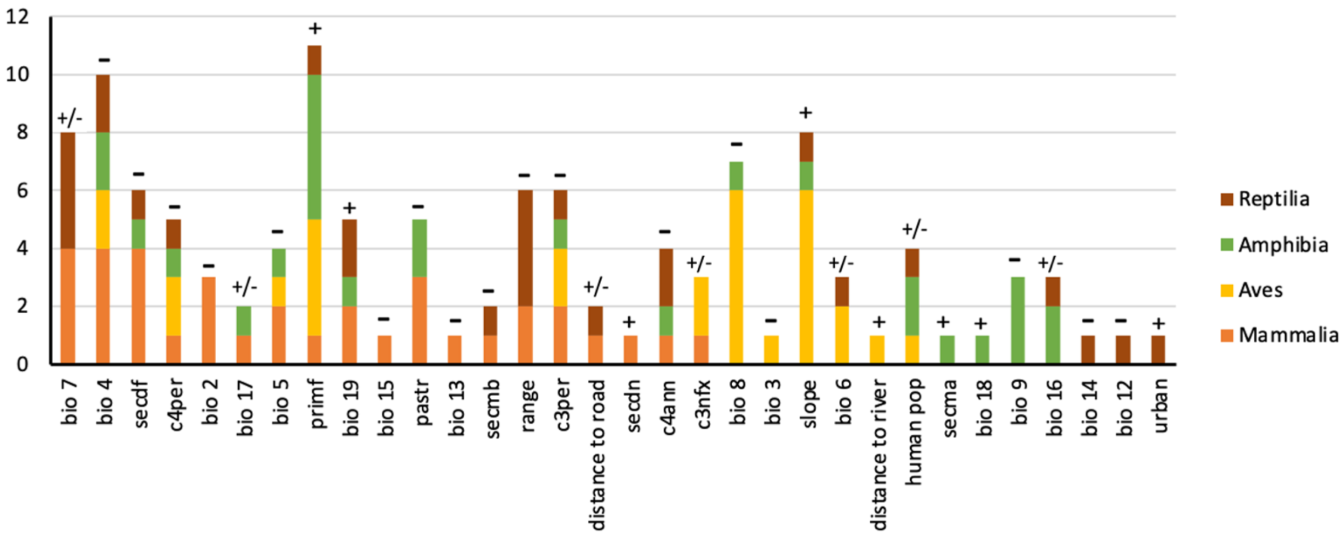


Figure 1.

The frequency of appearing in the top three most important predictor variables per class. For abbreviations of the top three important variables see Table 2. The response of the species on the increasing variables are predominately positive = +, some positive and some negative = +/-, and predominantly negative = -.

Most species responded positively to the increase of primary forested land, except for 2 amphibians (*Ichthyophis sumatranus & Rhacophorus catamitus*) and one bird (*Dicrurus sumatranus*). However, the amount of primary forested land is expected to decline in the future (see appendix B).

For most mammals (4 out of 12) the most important environmental variable that determines their distribution is the temperature annual range, which is expected to increase (see appendix B). Of these four species, three responded positively to the increase. Only for the Black-crested Sumatran Langur (*Presbytis melalophos*) suitability decreased with increasing temperature annual range. Moreover, the temperature seasonality was an important variable for 4 out of 12 species. The temperature seasonality is expected to increase in both future scenarios (see appendix B). For two species (*Presbytis thomasi & Callosciurus albescens*) the suitability increased with increasing temperature seasonality, for the other two it decreased (*Nesolagus netscheri & Presbytis melalophos*). The land-use variable potentially forested secondary land was another important variable for most mammals (4 out of 12). The potentially forested secondary land is predicted to expand in both future scenarios (see appendix B), which may lead to a decrease in the suitability of all four mammals.

For most aves (6 out of 10), the slope is one of the most important environmental variable. Three birds (*Erythropitta venusta, Carpococcyx viridis & Chloropsis venusta*) responded positively to an increase in the slope, for two birds (*Hydrornis schneideri & Cochoa beccarii)* the suitability stayed stable with an increasing slope and one bird (*Dicrurus sumatranus*) had a decrease in the suitability until it reached an optimum, after which it remained stable. Next to that, the mean temperature of the wettest quarter was evenly important for 6 out of 10 species. It is expected that the mean temperature of the wettest quarter will increase (see appendix B). The responses of all six birds were similar, with stable suitability till it reached a species-specific threshold at which the suitability decreased.

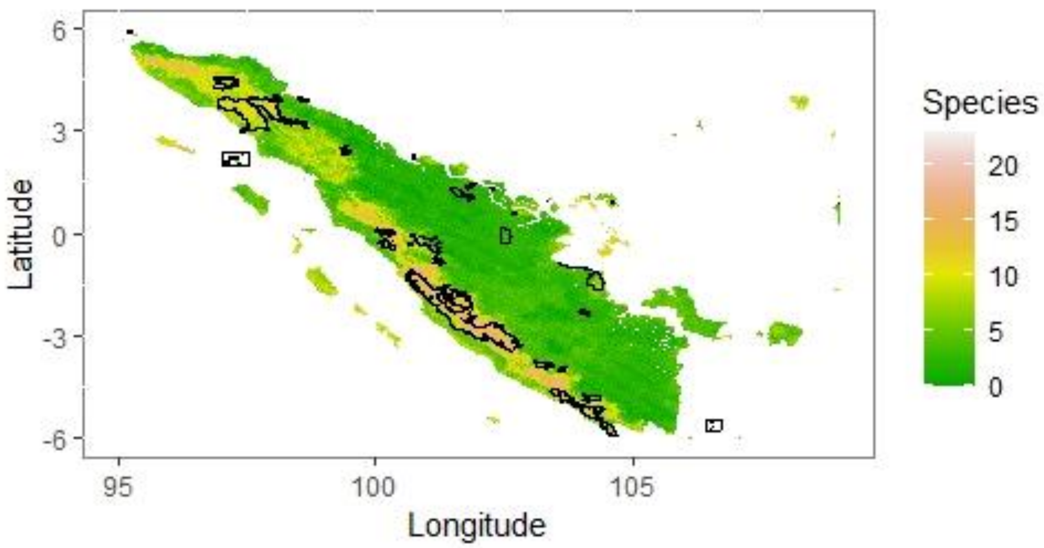
The land-use variables forested primary land appeared most in the top three important predictor variables for amphibians (5 out of 9). For three of these amphibians, the increase in forested primary land resulted in an increase in their suitability. However, for two amphibians (*Ichthyophis sumatranus & Rhacophorus catamitus*) an increase led to a small decrease in suitability.

For 4 out of 9 reptiles, the temperature annual range and the land-use variable rangeland mostly determines their distribution. Two reptiles (*Calamaria ulmeri* & *Dendragama boulengeri)* responded positively to the increase in the temperature annual range. For the other two (*Calamaria alidae & Trimeresurus barati*) the suitability declined. All four reptiles responded negatively regarding the increasing rangeland. But whereas the temperature annual range is predicted to increase, the amount of rangeland is expected to have a slight decrease (see appendix B).
Human population was an important predictor variable for 3 species, of which 2 amphibians (*Ichthyophis sumatranus* & *Zhangixalus achantharrhena*) and one reptile (*Dendragama boulengeri*). The suitability of the amphibians increased with the increasing human population, whereas the suitability of the reptile decreased. Distance to the road was an important predictor for one mammal (*Pongo abelii*), which responded positively to an increasing distance to the roads and one reptile (*Trimeresurus barati*) for which the suitability declined as the distance to the road increased. Distance to the river was important to predict the range of the Sumatran Whistling-thrush (*Myophonus castaneus*). With increasing distance to the river, the suitability of the Sumatran Whistling-thrush increased till it reached an optimum after which it stayed stable.

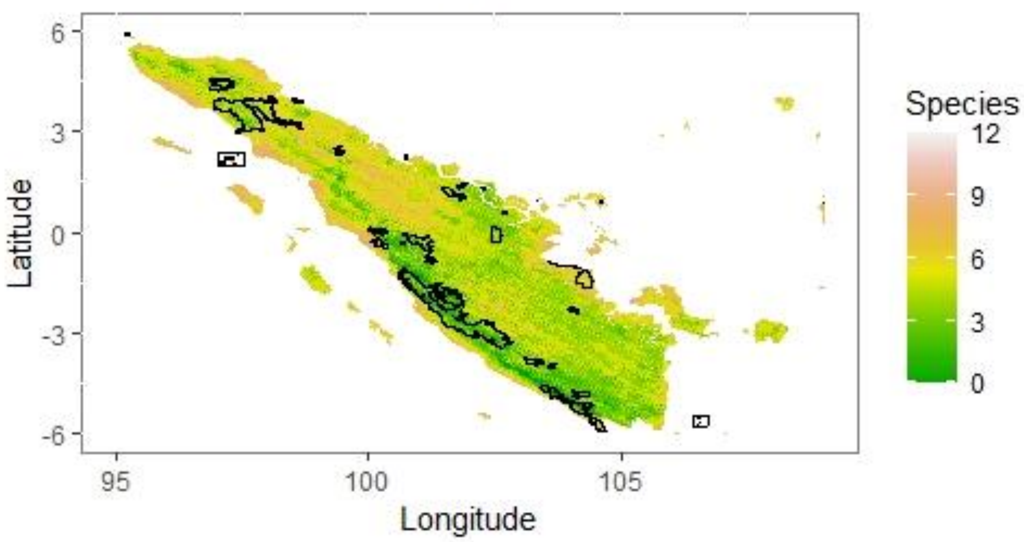
Changes in species richness

Currently, the mountain range, Bukit Barisan on the western side of Sumatra, is the most species-rich (Figure 2A) based on my model predictions. However, the areas that are currently most species-rich, are expected to lose most of their species with a changing climate. The main difference between the two future predictions is that for SSP 2-4.5 certain species hotspots (Figure 2B) can be found that cannot be found any longer for SSP 5–8.5 scenario (Figure 2C).

A



B



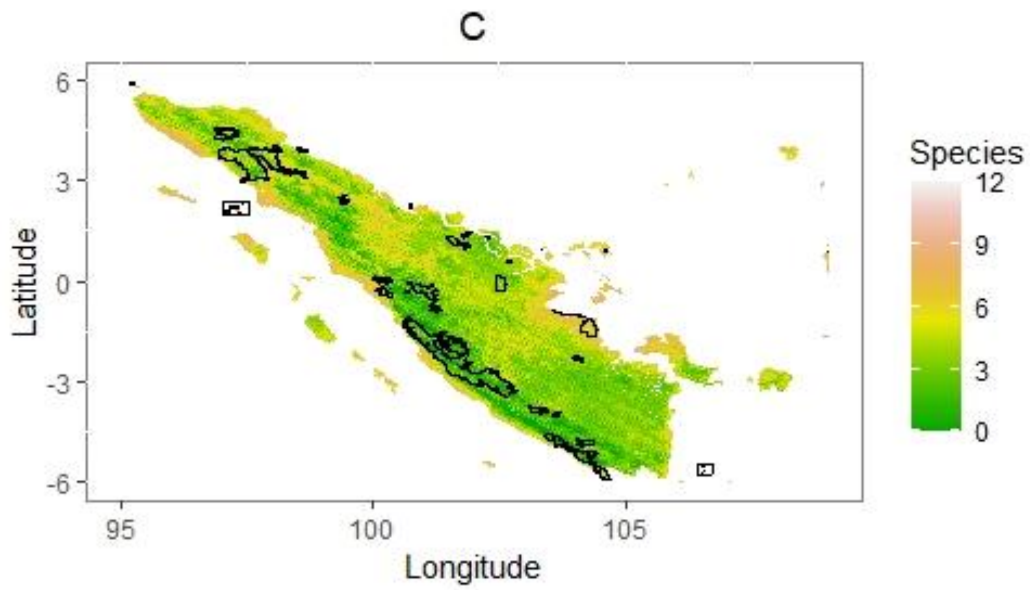


Figure 2.
The distribution of endemic species (A) currently, under (B) SSP 2-4,5 and (C) SPP 5-8,5.

It is predicted that Sumatra will no longer provide suitable area for 16 out of the 40 species under the SSP 2-4.5 scenario (44% amphibians, 60% aves, 42% mammals, 11% reptiles). Another 15 species will lose between 50 to 99% of their current range, of which 50% of the aves, all amphibians, 43% of the mammals and 88% of the reptiles (Table 4).

For the second future scenario (SSP 5-8.5), there is no suitable area left for 18 of the 40 species (44% amphibians, 60% aves, 58% mammals, 11% reptiles). 12 of the 22 remaining species are predicted to lose between 50 to 99% of their current distribution, of which 25% of the aves, all amphibians, 20% of the mammals and 75% of the reptiles (Table 4).

Table 4.

Percentage of suitable range lost <30%= ⇩ , 30-50%= ↓ (green) , 50-70%= ↓ (red) , >70%= ↓ (black) and new suitable range <30%= ⇧ , 30-50%= ↑ (green) , 50-70%= ↑ (red) , >70%= ↑ (black) or no suitable range left= ✕ under SSP 2-4,5 and SSP 5-8,5 for every species as well as the total suitable range (= lost suitable range + new suitable range) that is lost or gained.

Species	Total suitable range		Lost suitable range		New suitable range	
	SSP 2-4.5	SSP 5-8.5	SSP 2-4.5	SSP 5-8.5	SSP 2-4.5	SPP 5-8.5
Elongated Caecilian	↓ (red)	↓ (red)	↓ (black)	↓ (black)	⇧	⇧
Kodok-langsing	↓ (black)	↓ (black)	↓ (black)	↓ (black)	⇧	⇧

Kodok-buduk Bengkulu	⇓	⇓	↓ (red)	↓ (red)	↑ (green)	↑ (green)
Katak-parasut Dempo	↓ (red)	↓ (red)	↓	↓	⇑	⇑
Katak-parasut Barisan	✕	✕	✕	✕	✕	✕
Katak-parasut Bintik-hitam	✕	✕	✕	✕	✕	✕
Katak-tanduk Sumatra	↓	↓ (red)	↓	↓	⇑	↑ (green)
Sumatra Caecilian	✕	✕	✕	✕	✕	✕
Kodok-buduk Sumatra	✕	✕	✕	✕	✕	✕
Hoogerwerf’s Pheasant	✕	✕	✕	✕	✕	✕
Rück's Blue-flycatcher	↑	↑	⇓	⇓	↑	↑
Graceful Pitta	✕	✕	✕	✕	✕	✕
Schneider's Pitta	✕	✕	✕	✕	✕	✕
Blue-masked Leafbird	↓	↓	↓	↓	⇑	⇑
Sumatran Whistling-thrush	↓ (red)	↓ (green)	↓ (red)	↓ (green)	⇑	⇑
Sumatran Drongo	↑ (green)	↑ (green)	⇓	⇓	↑ (green)	↑ (green)
Sumatran Cochoa	✕	✕	✕	✕	✕	✕
Sumatran Ground-cuckoo	✕	✕	✕	✕	✕	✕
Short-tailed Frogmouth	✕	✕	✕	✕	✕	✕
Kloss's Squirrel	↑ (red)	↑ (red)	⇓	⇓	↑	↑

Sumatran Clouded Leopard	✕	✕	✕	✕	✕	✕
Dwarf Gymnure	↓	✕	↓	✕	⇧	✕
Black-crested Sumatran Langur	✕	✕	✕	✕	✕	✕
Thomas’s Langur	↑	↑	⇩	⇩	↑	↑
Sumatran Flying Squirrel	⇩	✕	↓	✕	↑	✕
Sumatran Striped Rabbit	✕	✕	✕	✕	✕	✕
Sumatran Elephant	✕	✕	✕	✕	✕	✕
Sumatran Tiger	✕	✕	✕	✕	✕	✕
Sumatran Orangutan	↑ (green)	↑ (green)	⇩	⇩	↑ (green)	↑ (green)
Tapanuli Orangutan	⇩	⇩	↓	↓	↑	↑
Sumatran Rhinoceros	⇩	⇩	⇩	↓ (green)	⇧	⇧
Spatula-toothed Snake	↑ (red)	↑ (red)	⇩	⇩	↑	↑ (red)
Crested Lizard	↓	↓	↓	↓	⇧	⇧
Ulmer's Reed Snake	⇧	⇧	↓	↓	↑	↑
Three-lined Kukri Snake	↓	↓	↓	↓	⇧	⇧
Boulenger's Tree Agama	↓ (green)	⇩	↓ (red)	↓ (green)	⇧	⇧

Bengkulu Reed Snake	✕	✕	✕	✕	✕	✕
Sumatran Short-tailed Python	↓	↓	↓	↓	⇧	⇧
Sumatran Green Pit Viper	↓	↓	↓	↓	⇧	⇧
Etheridgeum	↓	↓	↓	↓	⇧	⇧

The overlap between the distribution of the species and the protected areas in both future scenarios will diminish compared to the current overlap (Table 5). Especially the suitable range of mammals is expected to have the least spatial overlap with the protected areas in both future scenarios. Aves are expected to have the most spatial overlap of their suitable area and the protected areas in the SSP 2-4.5 scenario. For the SSP 5-8.5 scenario the suitable area of both aves and reptilia are expected to overlap the most with the protected areas.

Out of all classes, reptilia are expected to retain the most suitable area inside protected areas, as they have the smallest difference in overlap between current and future scenarios. However, mammals are likely to lose the most suitable range inside protected areas, as the difference in overlap between current and future scenarios is expected to be the largest.

Table 5.
Percentages of overlap between the species distribution and the protected areas.

Class	% Current in protected areas	% SSP 2-4.5 in protected areas	% SSP 5-5.8 in protected areas
Mammalia	17	2	2
Amphibia	23	10	3
Aves	22	14	4
Reptilia	12	5	4

Discussion

The island of Sumatra is impacted by threats like climate change, hunting and habitat loss. Therefore, the aim of this study is to understand the impact of these threats combined on the distribution ranges of the endemic terrestrial vertebrate species of Sumatra. As well as examining the effectiveness of protected areas to overcome these threats.

Endemic species are of special concern when looking at the threat of climate change (Morueta-Holme et al., 2010; McPherson & Nieswiadomy, 2005). As said before their small range is a burden, which limits their ability for dispersal. This makes them less able to keep track of a rapidly shifting climate (Morueta-Holme et al., 2010; Burlakova et al., 2011). Furthermore, if these species will not directly respond to climate change, they are living in ecosystems in which the species diversity is altered as a result of climate change (Thomas, 2010). The change in species diversity will result in a change in the communities, with unknown consequences for the ecosystem functioning (Hoffman et al., 2019; Araújo et al., 2011). Especially endemic species are likely to be susceptible to changes in ecosystem productivity and species interactions created by climate change (Thomas, 2010).

The results of the most important variables showed that ‘primary forested land’ is an important variable for most of the endemic species in Sumatra, but for amphibians in particular. Most endemic species in Sumatra, use tropical rainforests for their habitat, which can explain the importance of primary forested land (Stork et al., 2009). However, three species responded negatively to an increase in primary forested land. One of them being, the *Ichthyophis sumatranus*, an amphibian that can be found in sandy, rocky rivers and slow river flows (Rozi & Samitra, 2020). Only during heavy rains, they tend to come out of the water (Rozi & Samitra, 2020). The other amphibian (*Rhacophorus catamitus*), can be found near the pool of a stream (Streicher et al., 2012).

For mammals, especially the climatic variables that measure the influence of temperature were most important. These findings are supported by other studies on the influence of climatic variables on the distribution of mammals (Rahman et al., 2022; Deb et al., 2018; Rajpar & Zakaria, 2011; Santillán et al., 2018). Nonetheless, the effect of climate change on mammals is very contradictory, so it is very important to get more understanding of these complex interactions (Paniw et al., 2021; Root et al., 2003). Furthermore, the land use variable ‘potentially forested secondary land’ negatively affects the suitability for most mammals. Secondary forests are notably different from primary forest in species composition and diversity (Thompson & Donnelly, 2018; Gibson et al.,2011). From research it can be concluded that especially small mammals have a high tolerance for secondary forests and forest edges (Gibson et al.,2011). Three of the four mammals (*Neofelis diardi ssp. Diardi*, *Elephas maximus ssp. Sumatranus, Panthera tigris spp. Sumatrae)* in this study that had a decrease in suitability with an increase in potentially forested secondary land are large mammals, so are less tolerant to an increase in secondary forests.

One of the most important variables for birds was the mean temperature of the wettest quarter. Variations in the mean temperature and precipitation can lead plants to flower and produce fruit, which will affect food availability (Deb et al., 2018; Katayama et al., 2019). Low temperatures and high precipitation form a constraint on bird assemblages at tropical elevational gradients. So, bird species at high elevations might benefit from increased temperatures, however extreme drought events could also negatively affect high-elevation assemblages (Santillán et al., 2018; Larsen et al., 2011). This could explain the response of the birds, where their suitability was kept stable until they reached their species-specific threshold after which it decreased.

Land-use variables were the most important drivers of the distribution of amphibians and reptiles. Research has shown that primary and secondary forested land generally have higher species richness and abundance of amphibians and reptiles compared to human-modified landscapes (Thompson & Donnelly, 2018). Due to high deforestation rate in Sumatra, between the years 2000-2009 nearly half of Sumatra's total forest was lost (Uruyu et al.,2008), and it is predicted that another 58.9% of the remaining forest will be lost between the years 2016 and 2050 (Poor et al.,2019). Hence, destruction or changes of primary and secondary land are likely to explain why this study predicts that all reptiles and amphibians lose more than 50% of their current range.

Hunting intensity was found not to be an important variable for most taxa. However, previous studies do show the importance of hunting on the distribution of species (Benítez-López et al., 2019; Romero-Munoz et al.,2019; Blom et al., 2005; Gallego-Zamorano et al., 2020). The way how the hunting intensity was measured could be an explanation for why it was not found as an important variable for more species. A mixed-effects model of not only human population density but also the distance to hunters' access points and species' body mass (Gallego-Zamorano et al., 2020) could give a more reliable variable of hunting intensity, as these are the major incentives of hunting impacts (Benítez-López et al., 2017; Benítez-López et al., 2019).

The species richness map that is created during this study gives insight into the distribution of the species, as defined by environmental variables. Currently, my analyses show that most species-rich areas of Sumatra can be found on the mountain range of the Bukit Barisan. This mountain range includes three UNESCO-listed protected areas that form the TRHS. The TRHS is one of the biggest conservation areas in Southeast Asia, which supports a high diversity of species (UNESCO, n.d). However, this region is predicted to be less or not suitable for the majority of species under both future climate change scenarios modelled in this study, meaning that the TRHS may lose its effectiveness in the future to conserve the endemic species included in this study. Under both future scenarios, the endemic species are driven towards habitats that are currently unsuitable for most species.

Climate as well as land-use change are expected to cause many species to move out of protected areas (Kharouba & Kerr, 2010; Araújo et al., 2011). So, the static boundaries of the protected areas may limit their effectiveness (Hole et al., 2009). Despite this, protected areas stay beneficial in species conservation, as they may act as critical stepping stones or corridors that can facilitate dispersal for some species (Hole et al., 2009). The little overlap between the suitable range of the taxa and the protected areas shows that the existing protected areas are insufficient in assuring conservation, which is in line with other studies (Catullo et al., 2008; Sibarani et al., 2019). In Sumatra, many charismatic mammals now only exclusively survive between the boundaries of protected areas (Pacifici et al., 2020). However, from this study, it can be concluded that especially mammals lose most of their suitable range in protected areas in both future scenarios.

Little data and information were available for many species included in this study, which resulted in the use of occurrences from IUCN, that were less trustworthy. This weakens the intention to identify meaningful ecological variables and predict the distribution ranges. Furthermore, the model predicting species distribution lacked some variables, like food availability, land cover and species interactions. These variables influence the species distributions, but it was beyond the scope of the current study. Data on the spatial overlap of species and their potential prey species may facilitate the interpretation of prey preference and interspecific interactions, which provide insight into ecosystem functions (Allen et al., 2020). This issue can be addressed by including more species and using a joint species distribution model in future research (Wilkinson et al., 2020). Moreover, suitable area does not automatically mean that this is where the species will be found. This can be solved by performing habitat suitability model validation however, this requires reliable occurrence data for all species considered, which are currently not available. Additionally, the performed analysis during this study does not estimate extinction risk, but only which parts of Sumatra contain suitable areas for the species. Nonetheless, this study can be used by future conservation efforts to acquire knowledge on the drivers behind the distribution of endemic species in Sumatra. As well as the effectiveness of the existing protected areas currently and in the future.

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Appendix A- Protected areas of Sumatra

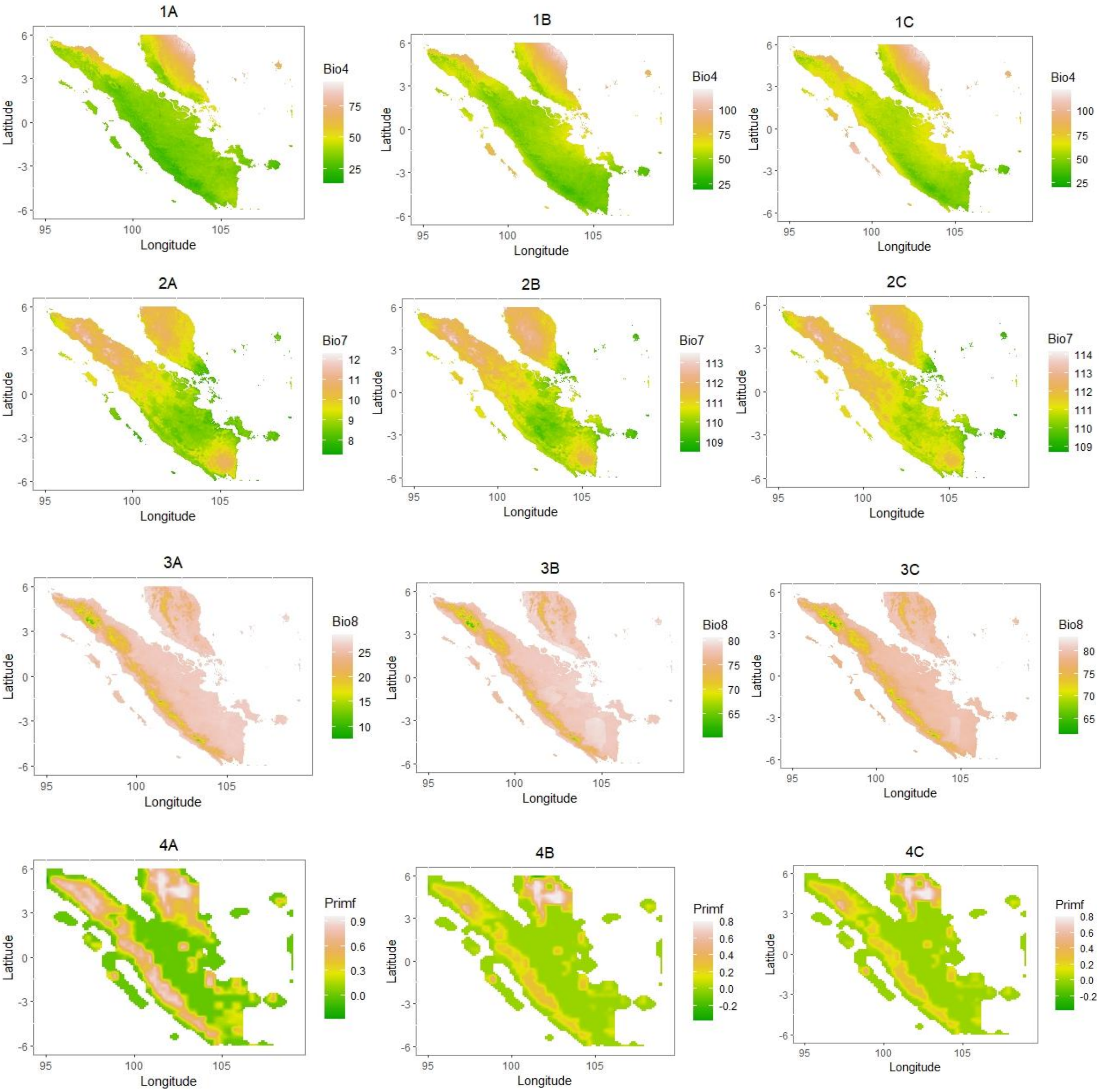
Table A1.
List of protected areas in Sumatra. IUCN-category: Ia - Strict Nature Reserve, Ib- Wilderness Area, II- National Park, III- Natural Monument or Feature, IV- Habitat or Species Management Area, V- Protected Landscape or Seascape, VI- Managed Resource Protected Areas.

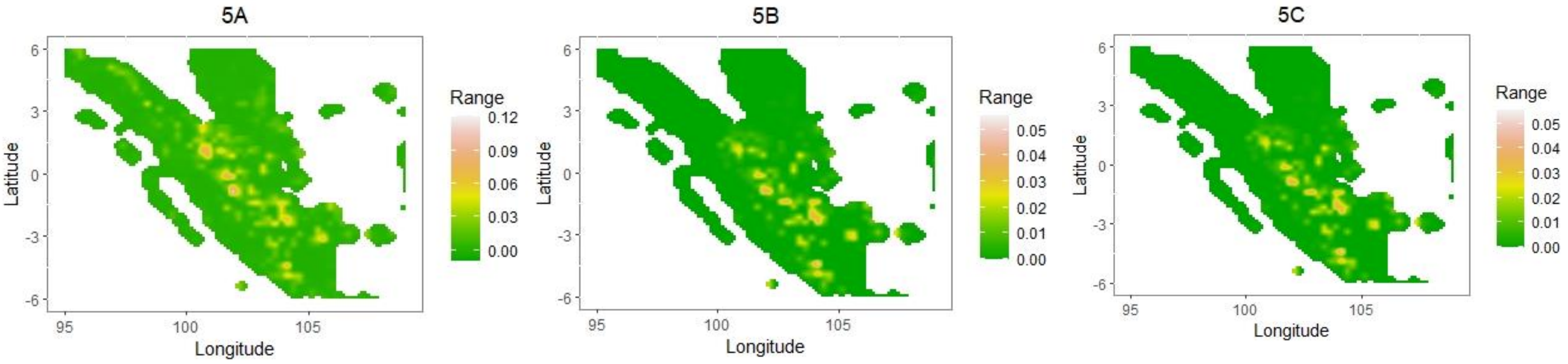
Protected area	***Designation***	***IUCN-Category***
Gunung Leuser	National Park	II
Butik Barisan Selatan	National Park	II
Berbak	National Park	II
Kerumutan	Wildlife Reserve	IV
Dolok Surungan	Wildlife Reserve	IV
Gumai Pasemah	Wildlife Reserve	IV
Isau-isua Pasemah	Wildlife Reserve	IV
Gunung Raya	Wildlife Reserve	IV
Kerinci Seblat	National Park	II
Lingga Isaq	Hunting Park	VI
Sibolangit	Nature Recreation Park	III
Tinggi Raja	Nature Reserve	III
Karang Gading dan Langkat Timur Laut	Wildlife Reserve	IV
Batang Palupuh	Nature Reserve	Not Reported
Lembah Anai	Nature Reserve	Not Reported
Mega Mendung	Nature Recreation Park	Not Reported
Lembah Harau	Nature Recreation Park	V
Malampah Alahan Panjang	Wildlife Reserve	Not Reported
Maninjau	Nature Reserve	Not Reported
Singgalang Tandikat	Nature Recreation Park	VI
Batang Pangean I	Nature Reserve	Not Reported
Gunung Sago Malintang	Nature Recreation Park	VI
Pulau Berkeh	Nature Reserve	Ia
Bukit Rimbang Bukit Baling	Wildlife Reserve	IV
Giam Siak Kecil	Wildlife Reserve	IV
Bukit Batu	Wildlife Reserve	IV
Tasik Tanjung Padang	Wildlife Reserve	IV
Tasik Besat-Tasik Metas	Wildlife Reserve	IV
Bentayan	Wildlife Reserve	IV

Appendix B- Predictions of climatic, topographical, and land-use variables.

Figure B1.

Important climatic, topographical and land-use variables, current status(A) and future predictions for SSP2-4.5(B) and SSP5-5.8(C). 1=Bio4, 2=Bio7, 3=Bio8, 4=Primf, 5=Range, 6=Secdf, 7=Slope. For abbreviations of the important variables see Table 2.




5A
5B
5C
Latitude
Longitude
6
3
0
-3
-6
95
100
105
Range
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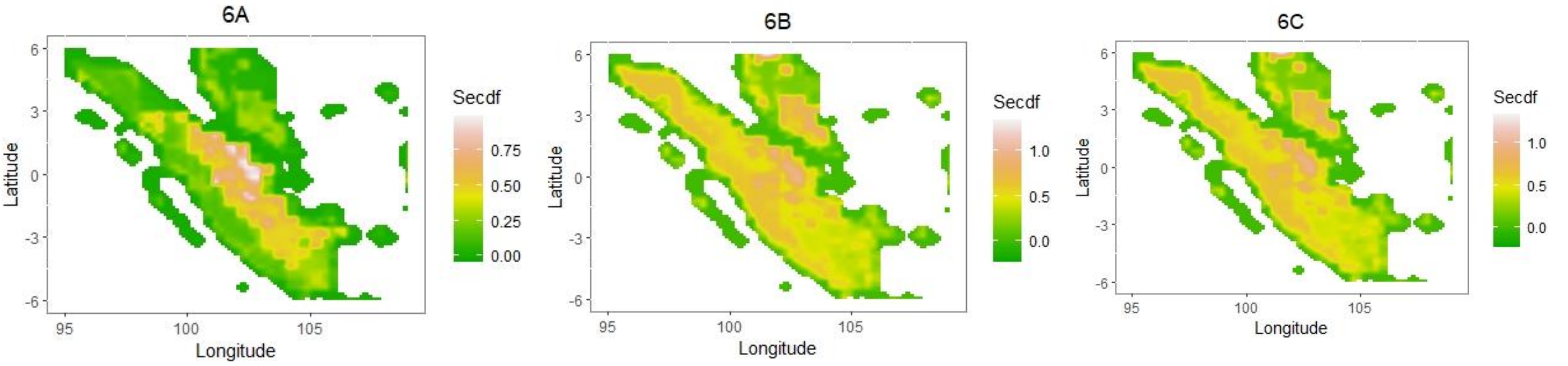
0.06
0.03
0.00
0.05
0.04
0.03
0.02
0.01
0.00


6A
6B
6C
Latitude
Longitude
6
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-6
95
100
105
Secdf
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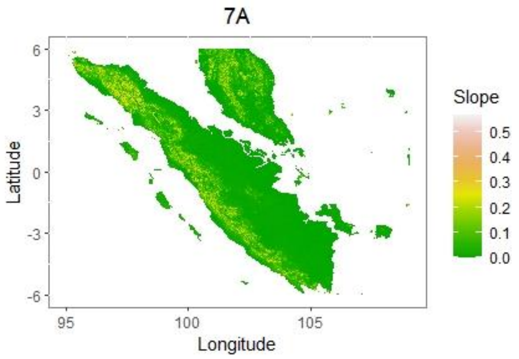
0.25
0.00
1.0
0.5
0.0


7A
Latitude
Longitude
6
3
0
-3
-6
95
100
105
Slope
0.5
0.4
0.3
0.2
0.1
0.0