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Modelling Climatically Suitable Areas for Mahogany (*Swietenia macrophylla* King) and Their Shifts across Neotropics: The Role of Protected Areas

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Abstract: Mahogany (*Swietenia macrophylla* King) is a species with great economic interest worldwide and is classified as vulnerable to extinction by the IUCN. Deforestation and climate change are the main hazards to this species. Therefore, it is vital to describe possible changes in distribution patterns under current and future climatic conditions, as they are important for their monitoring, conservation, and use. In the current study, we predict, for the very first time, the potential distribution of Mahogany based on data that reflect the total distribution of the species, climatic and edaphic variables, and a consensus model that combines the results of three statistical techniques. The obtained model was projected to future climatic conditions considering two general circulation models (GCM), under two shared socioeconomic pathways (SSP245 and SSP585) for 2070. Predictions under current climatic conditions indicated wide adequate areas in Central American countries such as Mexico and demonstrated a coverage of up to 28.5% within the limits of the protected areas. Under future scenarios, drastic reductions were observed in different regions, particularly in Venezuela, Perú, and Ecuador, with losses of up to 56.0%. On the other hand, an increase in suitable areas for the species within protected areas was also detected. The results of this study are certainly useful for identifying currently unrecorded populations of Mahogany, as well as for identifying locations that are likely to be suitable both now and in the future for conservation management planning. The methodology proposed in this work is able to be used for other forest species in tropical zones as a tool for conducting dynamic conservation and restoration strategies that consider the effects of climate change.

Keywords: mahogany; *Swietenia macrophylla*; neotropic; protected areas; forest monitoring

1. Introduction

Neotropical forests are characterized by hosting multiple biodiversity hotspots [1], particularly in plant terms [2,3]. Current findings indicate that there could be approximately 73,000 species of trees on the planet; of this percentage, it is suggested that some 43% are encountered in the neotropics [4]. These forests are of fundamental relevance in the conservation of biodiversity and mitigation of the effects of climate change, since it is estimated that they allow the capture of 13% of the total annual emissions of anthropogenic CO_2 worldwide [5]. Therefore, various studies have demonstrated that forests in tropical areas provide numerous alternatives focused on the planning and implementation of sustainable forest conservation strategies [4,5]. However, this potential has been limited due to different natural and anthropic disturbances, among the most relevant being the effect of climate change. Recent studies have found that the global mean surface temperature from 1961 to 2019 increased by 0.66 °C [6]. There is scientific evidence that these changes cause shifts and contractions in the altitude range of tropical species [7,8]. For example, a recent investigation, performed on Chimborazo vegetation in Ecuador, indicated a strong displacement of seed plants towards an altitude of 5185 m, which is >500 m to the 4600 m reported by Humboldt in 1802 [9]. On the other hand, global deforestation for agricultural purposes has been very intense in recent decades [10,11], where some 178 million hectares (ha) of forest have been lost from 1990 to 2020, at a rate of 7.8 million ha/year in the period 1990–2000, 5.2 million ha/year in 2000–2010, and 4.7 million between 2010–2020 [12]. Different scientific works have yielded that these tropical deforestation processes cause a reduction in evapotranspiration levels and precipitation at the local level, hence indirectly affecting a wide variety of plant species [13,14]. In many areas, this change in land use begins with the selective exploitation of timber species of high commercial value, an activity that also affects species of global commercial interest, such as Mahogany (*Swietenia macrophylla* King) [15,16], a timber tree whose native range covers much of the Neotropics.

Botanical records indicate that Mahogany is encountered natively in Belize, Brazil, Colombia, Costa Rica, Dominica, Ecuador, El Salvador, French Guiana, Guatemala, Guyana, Honduras, Mexico, Nicaragua, Panama, Peru, Venezuela, and Bolivia [17,18]. Mahogany wood is desired in international markets in the United States, Japan, and Europe due to its high demand for home construction, plywood, boards, boats, and fine cabinetry [19]. In addition, it has chemical properties that are of great importance for multiple uses, such as the production of cosmetics, control of hypertension, and production of antidiabetic, anticancer, and anti-inflammatory substances [20–22]. Due to these multiple uses, it is considered one of the most commercially important plant species worldwide [23], reaching prices between USD 1700 and USD 11,000 per m^3 of wood [24,25]. Its great commercial interest has increased its overexploitation [15]. Mass extraction has generated significant negative impacts on the habitat of this species, with less than one individual per hectare found in small and dispersed populations [26,27]. This species presents a slow growth, and therefore an ineffective natural regeneration, a period of 30 years being necessary for it to be able to develop completely [28]. In addition, it presents a great vulnerability to climatic conditions that affect its germination or pests that limit its growth [29,30]. For all these reasons, it is considered vulnerable to extinction according to the IUCN evaluation categories and is one of the most threatened forest species in the world [31,32]. In addition, due to its conservation status, it was included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) [33]. Therefore, there is a strong need to implement forest restoration strategies that allow for the correct management and conservation of Mahogany in the neotropics.

On a global scale, various forest restoration initiatives focused on achieving multiple objectives are being conducted [34,35], including anticipation of the possible effects of climate change [4,36], recovery of biodiversity [5,37], and the enhancement of rural livelihoods [38,39]. We could highlight the Bonn Challenge [40] and the United Nations Decade for Restoration [41], which aim to reforest 350 million hectares by 2030 [42,43].

However, effective planning is necessary to select suitable species for the future, since most countries, especially tropical ones, do not perform climate vulnerability studies in order to select the species and sites to restore. If they would perform these studies, they would achieve effective development and adaptation to a changing world in a context of climate change [44].

Climate change represents a challenge for ecosystems and biodiversity in areas with potential for forest restoration [4,45]. Climate variability, intensity, and increased frequency of extreme weather events could increase tree mortality [46], change phenology [47] and physiology [48], or cause migration to higher and cooler elevations [49] and even an accelerated increase in extinction rates [50]. Different recent studies estimate that between 39 and 41% of plant species are at risk of extinction globally [51,52]. Biological extinctions are advancing at an exceptional rate; this being an important point of interest in the scientific community, some authors even mention the sixth great extinction of species [53]. It is estimated that a large portion of species modify their geographic distribution as a response to changes in climatic conditions [54]. However, the most influential threat facing trees in reforested locations is related to their dispersal capacity [55,56]. The dispersal ability of most trees is limited to external factors such as wind and living organisms [57]. In this sense, a greater incidence of climatic changes and a decrease in dispersal capacity could increase the vulnerability of forest species [58]. This vulnerability also depends on their ability to resist and adapt to the existing environmental conditions [59,60]. For example, generalist species have a higher resistance to various climatic conditions compared to specialist species [61]. Under this premise, it is known that native forest species are able to be both generalists and specialists, which is why they have a high potential to be considered in forest restoration programs [62].

However, restoration programs usually consider exotic forest species, generating large extensions of forest monoculture [63,64]. These practices are not recommended because a forest monoculture presents low carbon sequestration rates compared to those seen in native forests [65]. In addition, they present low biodiversity and potentially high vulnerability to climate change [66]. It is important to point out that exotic species can often become invasive, which is a worrying phenomenon since it is estimated that they rank second in reasons for the current global biodiversity crisis [67,68]. For example, these species tend to compete with native species, reducing local biodiversity, and in some cases their eradication is unfeasible because it is considered impracticable in economic terms [69]. Therefore, international standards recommended by the Society for Ecological Restoration (SER), utilized by researchers, professionals, land managers, community leaders, and decision makers to restore ecosystems in seventy countries, suggest giving greater emphasis to the use of native forest species that are often vulnerable to extinction in tropical areas [70,71]. In addition, it is important to note that these species are usually characterized by their dense wood, which is related to greater carbon sequestration, as is the case of Mahogany [72].

Therefore, the identification of areas where the environmental conditions are suitable for the implementation of these reforestation strategies is of vital importance [44]. Therefore, as an optimal tool for this objective, we propose here the use of ecological modelling techniques, commonly known as species distribution models (SDM [73]). The theoretical principle of these models lies in the fact that they correlate data on the presence of species (georeferenced locations) with environmental variables (climate, soil, etc.) to predict the suitable space for the development of an organism for different periods of time (past, present, future) [73–75]. Among the main applications of these models are projections to future climatic conditions to assess how climate change affects plant species [76,77]. They are undoubtedly the most widely used tools to predict the potential distribution of species in the future, but despite their potential to be used in restoration plans, their use has been very limited in this regard. For example, they have made it possible to identify the distribution of timber forest species facilitating their adequate management and conservation in certain territories [78,79], and recently have facilitated ecological restoration strategies principally in the European continent [79–81].

Previous studies have attempted to model the potential geographic distribution of Mahogany in Mexico [29,82,83] and Brazil [84,85]. However, in these countries, only a partial fraction of the climatic niche of the species was considered (only the presence records for the species in one country). This practice has been habitual, but it is not the most appropriate option to generate reliable SDMs [86], especially to project the potential distribution of the species into the future, since the models created under these considerations generate biased predictions [87–89]. Therefore, in the present work, for the first time the entire known native distribution range of Mahogany is considered, allowing the capture of all the environmental variability available for the species and generating more reliable climate change predictions [90].

In this context, due to the current state of conservation of Mahogany and its commercial importance, this study proposes the identification of suitable areas under present conditions and different climate change scenarios with the potential to be used in restoration and/or reforestation with Mahogany in its native distribution area. Furthermore, the areas predicted by the models were compared with the network of protected areas (PA) with the aim to propose forests management strategies to stakeholders in tropical countries that allow for the conservation of the species in the short and long term.

2. Materials and Methods

2.1. Study Area

The extent of the calibration area has a key impact on the results of the SDMs [91,92]. We designed our study area based on prior knowledge of the actual distribution of the species in the region from 33° N to 35° S and from 119° W to 35° W (Figure 1). Specifically, we bounded the study area to the south to include Brazil, to the north to include Mexico, to the west by the Pacific Ocean, and to the east by the Atlantic Ocean. The study region is considered a global biodiversity hotspot [93,94]. In this zone the environmental conditions stand out for presenting an annual mean temperature that oscillates between 1 to 29.3 °C [95], annual precipitation between 0 to 7150 mm [95], and altitude in an approximate range of 0 to 6650 m above sea level (m.a.s.l.) [96].

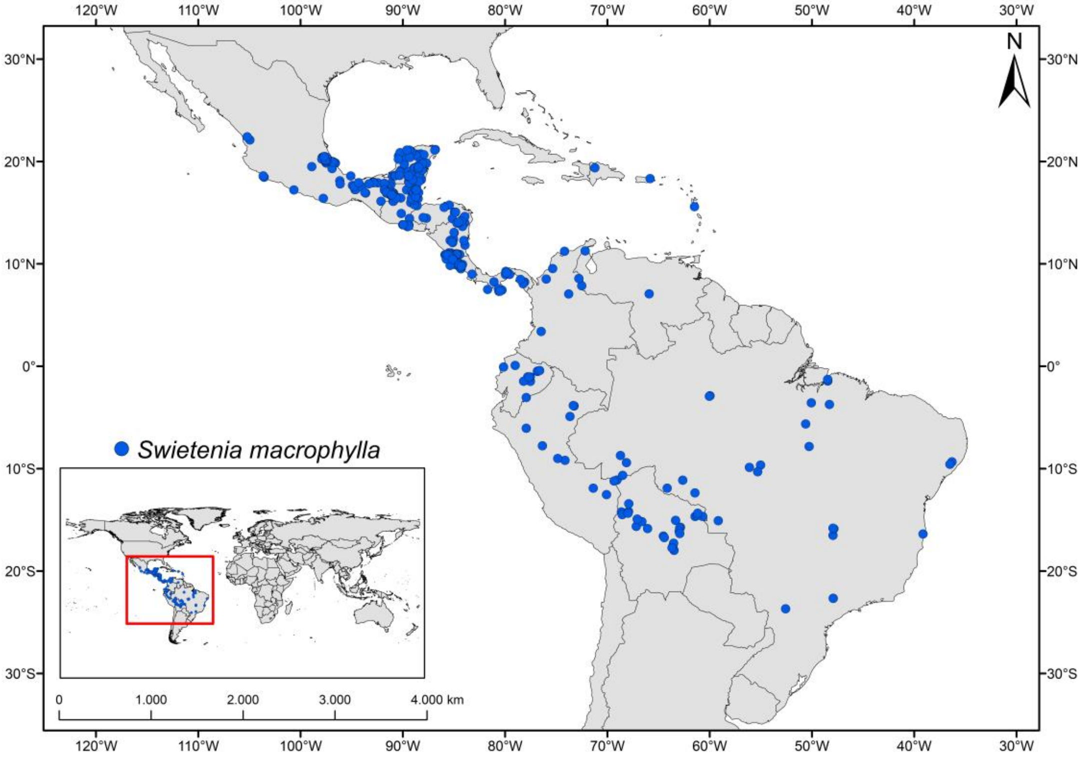

Figure 1. Study area. Presence records of Mahogany (blue dots) in its native distribution area.

2.2. Presence Records

Some 4569 presence records for Mahogany were collected from two types of information sources; online biodiversity databases, such as the Global Biodiversity Information Facility (GBIF; www.gbif.org accessed on 16 January 2023), the Integrated Digitized Biocollections (iDigBio, https://www.idigbio.org accessed on 16 January 2023), sistema distribuído de informação que integra dados primários de coleções científicas (SpeciesLink, https://splink.cria.org.br accessed on 16 January 2023), the Botanical Information and Ecology Network (BIEN, https://bien.nceas.ucsb.edu/bien accessed on 16 January 2023), BIOWEB (https://bioweb.bio/portal accessed on 16 January 2023), and the Programa Nacional de Monitoreo de la Biodiversidad de Ecuador (SINMBIO, https://bndb.sisbioecuador.bio/bndb/index.php accessed on 16 January 2023), as well as scientific publications [17,97–101]. The data download was performed using the following packages: OccCite [102], PlantR [103], BIEN [104], and Ridigbio [105]. In the process of obtaining the data, only records reported in botanical collections were considered, as they are of vital importance to clarify the taxonomy of plants and identify their main habitats. Additionally, these present great potential for the creation of ecological models focused on the conservation of threatened species [106–108].

To ensure the quality of the presence data [109], we relied on the existing literature that provides methodological suggestions with the aim of generating a reliable database that can be used in ecological modelling [86,110,111]. Consequently, a protocol based on three steps was applied, the first step being to initially mitigate the effect of seasonality collection [112] through preserving records collected in years after 1950. Secondly, to take into account that presences collect duplicate samples of the same individuals that are stored in different institutions, records that presented the same geographic coordinates were eliminated. Finally, the possible sampling bias associated with collection patterns was attenuated [113] by applying a distance of 1 km between each record. All the steps conducted in this process were executed through the use of packages developed in the R environment (spThin [114], SpeciesGeoCoder [115]). The final database included 407 presence records.

2.3. Environmental Data

Two databases were used as independent variables. On the one hand, the 19 bioclimatic variables available in the Worldclim 2.1 climate data repository (https://www.worldclim.org/ accessed on 16 January 2023) were used at a resolution of 30 s (approximately 1 km^2) [95]. In order to predict future changes in the distribution areas of *S. macrophylla*, the projections of the general circulation models (GCM) until the year 2070 from the Coupled Model Intercomparison Project Phase 6 (CMIP6, [116]) were considered. Two GCMs (MRI-ESM2.0 [117], MIROC6 [118]) were chosen to consider the variability and uncertainty associated with the creation of future climate models and their influence on spatial predictions [119,120]. Additionally, two shared socioeconomic pathways (SSPs) were used; specifically, SSP2-4.5 and SSP5-8.5 for each GCM. The selected SSPs represent conservative (SSP2-4.5 predicts an increase of up to 2.7 °C by 2100) and pessimistic (SSP5-8.5 predicts an increase of up to 5 °C by 2100) conditions.

On the other hand, layers of different soil properties at a depth of 0 to 5 cm were obtained from the SoilGrids (https://www.soilgrids.org accessed on 16 January 2023) database at a resolution of 1 km^2 [121]. In relation to the selection of variables used in the creation of models, the initial set was reduced to mitigate the effects related to multicollinearity [122], possible pseudo-estimates of predicted areas [89], and interpretative complexity of the models [123]. A Pearson correlation coefficient ($r > 0.8$) was applied between pairs of variables [124]. Highly correlated variables were removed based on the threshold mentioned above. Finally, the models generated for Mahogany included eleven environmental variables (see Table 1).

Table 1. Environmental variables used in the creation of SDMs for Mahogany.

Category	Variable	Description	Unit
Bioclimatic variables	bio3	Isothermality	°C
	bio5	Max temperature of warmest month	°C
	bio6	Min temperature of coldest month	°C
	bio17	Precipitation of driest quarter	mm
	bio18	Precipitation of warmest quarter	mm
	bio19	Precipitation of coldest quarter	mm
Soil variables	bdod	Bulk density of the fine earth fraction	kg dm^{-3}
	nitrogen	Total nitrogen (N)	g kg^{-1}
	phh2o	pH (H_2O)	-
	sand	Sand (>0.05 mm) in fine earth	%
	soc	Soil organic carbon in fine earth	g kg^{-1}

2.4. Species Distribution Models

Consensus models [125] were generated using the biomod2 package [126] by combining predictions generated by three statistical techniques; generalized additive models (GAM, [127]), boosted regression trees (BTR, [128]), and random forests (RF, [129]). Following Brun et al. [123], three different parametrization complexity options were compared. For GAMs we established the degree of freedom in the smooth terms to 1.5, 3, and 10 for simple, intermediate, and complex parameterization options. Simple, intermediate, and complex RF models were trained with the minimum number of observations in the terminal nodes to 40, 20 and 1, respectively. Finally, the complexity of BRTs was varied by training 100, 300, and 10,000 trees for simple, intermediate, and complex options. The predictive accuracy of the models was evaluated by selecting a repeated random sample (ten times) where 80% of the data was used to train the models and the remaining 20% to evaluate them. For each replicate, the accuracy of the model was assessed using the Area Under the ROC Curve (AUC) statistic [130]. The evaluation of the predictive performance of the models aims to assess the accuracy of the predictions, thereby guaranteeing confidence in the results obtained. Those models that presented an AUC value < 0.8 [131] were eliminated. The relative importance of each independent variable was calculated by a repeated random permutation test [126]. Finally, for each parametrization option a consensus model was generated through the weighted average of their AUC values. The three parametrization options were compared by means of different statistics: AUC [130], partial AUC [132], TSS [133], and omission value [134]. The complex option obtained better results (see Table 2). Subsequently, the complex consensus model was projected to each GCM (MRI-ESM2.0, MIROC6) and their respective SPPs (SSP2-4.5 and SSP5-8.5). Next, the median of the replicates was calculated and applied for each future scenario, following the procedure used by Simoes et al. [135]. To calculate the area predicted by the models and conduct the respective comparisons between the current and future predictions, all the models were binarized using a commission error of 5% [136].

Table 2. Comparison of the three parametrization options (complex, intermediate, and simple) employed to generated ensemble models thought different statistics.

Model	AUC Media	TSS	Partial AUC	Omision Rate 5%
Complex	0.93	0.74	1.85	0.050
Intermediate	0.93	0.74	1.71	0.049
Simple	0.93	0.74	1.69	0.051

2.5. Changes in the Potential Geographic Distribution of Mahogany

The differences in the predicted areas between the current model and the two future scenarios (SSP2-4.5 and SSP5-8.5) were calculated. Specifically, areas with potential range loss (i.e., potential areas where the species is currently present but is likely to be absent in the future), gain (i.e., potential areas where the species is currently absent, but is likely to be present in the future), and stability (i.e., potential areas where the species is potentially present now and is likely to be present in the future) were considered. On the other hand, the potential changes in the altitudinal ranges in the potential areas predicted by the future models were also estimated. In this sense, the pixels predicted by the models were used as a mask to extract their corresponding altitude values. In order to perform this process, a 250 m resolution Digital Terrain Model (DTM) derived from the Shuttle Radar Topographic Mission (SRTM) was downloaded [96]. The DTM was resampled to a resolution of 1 km^2.

2.6. Representativeness of Distribution Areas of Mahogany in the Network of Protected Areas

An intersection was realized between current and future models and a map of the global network of PA was obtained from https://www.protectedplanet.net/en (accessed on 16 January 2023). This occurred based on the premise that PAs provide a greater survival advantage in terms of conservation to endangered species, in addition to being a more effective in situ conservation strategy in the short and long term [137–139].

3. Results

3.1. Statistical Performance of the Models

Three types of approaches used in the generation of the consensus model for Mahogany were evaluated, the complex approach being the one that was statistically reliable, indicating a robust predictive performance since it obtained a mean AUC value = 0.93, TSS = 0.74, partial AUC = 1.85 and an omission value of 0.050 (Table 2). On the other hand, the environmental variables with major relative importance to the SDMs were min temperature of the coldest month (Bio 6), pH, and nitrogen (see Supplementary Figure S1).

3.2. Current Potential Distribution of Mahogany

Under current climatic conditions, the predictions of the binary model yielded climatically suitable areas for Mahogany of approximately 1,250,321 km^2 (Figure 2), which are found in an altitudinal pattern between 0 and 2663 m.a.s.l. A large part of the predicted areas was distributed in the eastern, southern and western zones of Mexico, Nicaragua, Honduras, Guatemala, Costa Rica, Panama, Bolivia, Belize, southern Colombia, and the coastal region and centre of the Ecuadorian Amazon. Particularly, Mexico stands out for being the country with the highest proportion of suitable areas with 28.5% of the total potential distribution of the species.

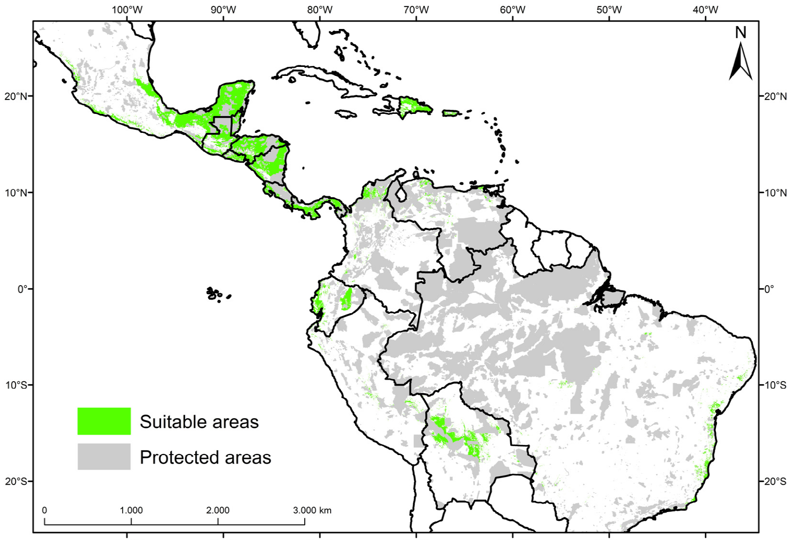

Figure 2. Potentially suitable areas for Mahogany under current conditions predicted in the binary model.

3.3. Possible Changes in the Environmentally Suitable Areas Predicted by Future Mahogany Models

Considering that the resulting models predict fractional and distant potential areas between each country included in the study area, the areas predicted by the models in Ecuador were selected as an example because they predicted significant potential changes (stability, loss, gain) in the future distribution of Mahogany for this country (Figure 3). However, all areas predicted by countries are presented in Table 3.

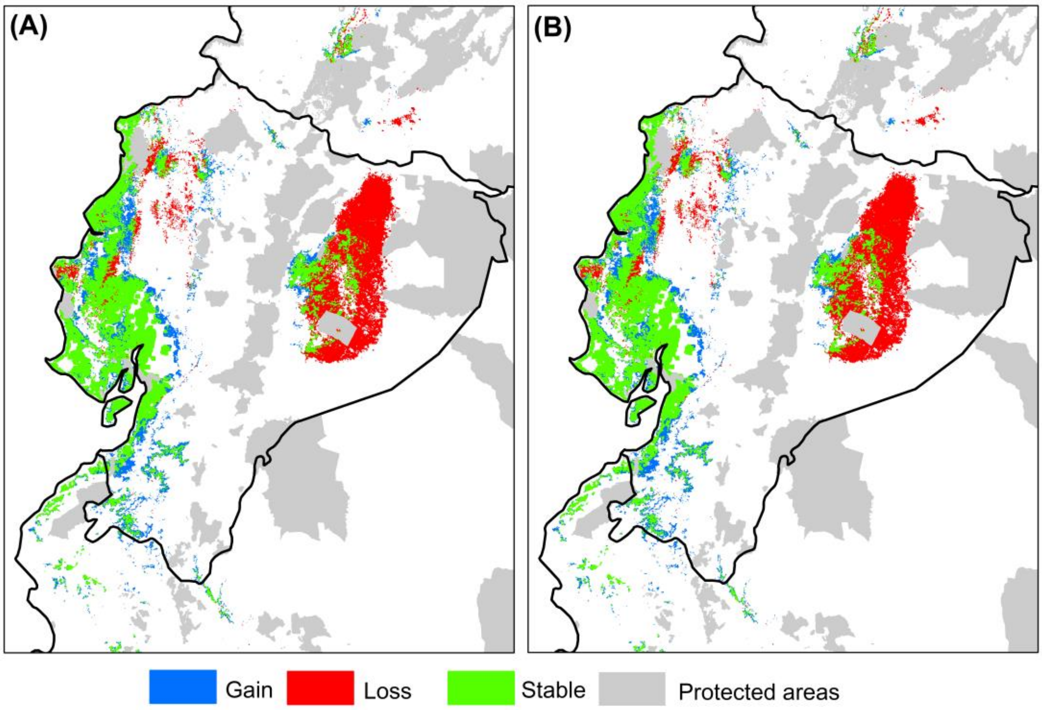

Figure 3. Changes in the potential distribution of Mahogany in the future: (**A**) Potential changes predicted in future climate scenario SSP2-4.5; (**B**) Potential changes predicted in future climate scenario SSP5-8.5.

Table 3. Changes in the potential future distribution of Mahogany in its native range.

Country	Current	SSP2-4.5						SSP5-8.5					
		Stable	%	Loss	%	Gain	%	Stable	%	Loss	%	Gain	%
Belize	26,251	26,196	99.8	55	0.2	0.0	0.0	26,181	99.7	70	0.3	1	0.004
Bolivia	15,2876	114,041	74.6	38,835	25.4	47,652	31.2	118,038	77.2	34,838	22.8	41,876	27.4
Brazil	64,690	54,111	83.6	10,579	16.4	127,285	196.8	47,707	73.7	16,983	26.3	102,627	158.6
Colombia	65,862	54,472	82.7	11,390	17.3	23,827	36.2	47,849	72.7	18,013	27.3	33,427	50.8
Costa Rica	38,259	35,473	92.7	2786	7.3	1606	4.2	33,641	87.9	4618	12.1	2542	6.6
Dominica	834	771	92.4	63	7.6	0.0	0.0	706	84.7	128	15.3	1	0.1
Ecuador	56,900	33,772	59.4	23,128	40.6	11,050	19.4	32,817	57.7	24,083	42.3	20,670	36.3
El Salvador	19,146	19,091	99.7	55	0	3474	18.1	18,945	99.0	201	1.0	3452	18.0
Guatemala	89,556	86,531	96.6	3025	3.4	11,110	12.4	85,836	95.8	3720	4.2	15,023	16.8
Honduras	116,168	115,535	99.5	633	0.5	10,008	8.6	113,661	97.8	2507	2.2	12,299	10.6
México	355,755	342,038	96.1	13,717	3.9	58,797	16.5	324,593	91.2	31,162	8.8	59,811	16.8
Nicaragua	132,988	130,865	98.4	2123	1.6	2469	1.9	129,975	97.7	3013	2.3	3149	2.4
Perú	18,544	10,896	58.8	7648	41.2	17,550	94.6	11,631	62.7	6913	37.3	25,814	139.2
Panamá	61,645	54,667	88.7	6978	11.3	1693	2.7	56,104	91.0	5541	9.0	3672	6.0
Puerto Rico	6928	5517	79.6	1411	20.4	424	6.1	4269	61.6	2659	38.4	219	3.2
Venezuela	43,919	27,086	61.7	16,833	38.3	18,111	41.2	19,326	44.0	24,593	56.0	34,255	78.0
Total	1,250,321	1,111,062	88.9	139,259	11.1	335,056	26.8	1,071,279	85.7	179,042	14.3	358,838	28.7

Based on future climatic conditions with a moderate emissions scenario (SSP2-4.5), the models suggest that around 88,9% of suitable habitat for Mahogany would remain stable (i.e., suitable in the current period and in the future). It is important to point out that the largest proportion of stable areas would be found in Mexico with approximately

342,038 km^2. However, we encountered that in Belize it is expected that 99.8% of the suitable areas will remain stable in the future. On the other hand, Peru is the country with the lowest number of stable future areas with 58.8%. Similarly, in a severe emissions scenario (SSP5-8.5), a 3.1% reduction in suitable stable areas is anticipated compared to that predicted under the conservative scenario (SSP2-4.5), reflecting a percentage of habitat stability for 88,8% of species. Specifically, patterns similar to those described above were identified in the SSP2-4.5 scenario, with Belize once again being the country with the highest proportion of possibly stable areas in the future with 99.7%. Similarly, in El Salvador the species is also expected to have large areas of suitable areas in the future with 99.0%.

On the other hand, in relation to the loss of suitable areas, there was a drastic loss of 41.2% of suitable areas in Peru and 40.6% in Ecuador in a conservative scenario (SSP2-4.5). Particularly in Ecuador, these reductions are expected to be more evident in the Amazon region of Ecuador; specifically, in the provinces of Pastaza and Napo. Similarly, in a gloomy emissions scenario (SSP5-8.5), an increase of 3.2% is expected compared to the expected losses reported by the model for the scenario (SSP2-4.5). Overall, the models foresee possible reductions equivalent to 14.3% in the species' range. Particularly, in this scenario, Venezuela is expected to lose 56.0% of the areas suitable for the species. On the other hand, in second place would again be Ecuador with a predicted loss rate of 42.3% of suitable areas for Mahogany.

The models also forecast possible expansion (gain) of suitable areas. Under an optimistic emissions scenario (SSP2-4.5), potentially suitable habitat gains for the species are anticipated to be 26.8% across its entire native range. The largest proportion of forecast gains are again centered in Brazil, Peru, Venezuela, and Colombia. Furthermore, it should be emphasized that the models did not predict suitable new areas in Belize and Dominica, both of which had a success rate of 0%. The potential increases in suitable areas under a pessimistic emissions scenario (SSP5-8.5) are expected to be greater than those evidenced in comparison to the conservative scenario (SSP2-4.5) with an increase of 1.9%. In general, the models predict gains of potentially suitable areas for the species of 28.7%. On the other hand, the models forecast possible slight area gains in Belize and Dominica with 0.004% and 0.1, respectively. In this context, it is expected that the species will have new areas for adaptation and survival through a progressive ascent of 282 m in an optimistic scenario (SSP2-4.5) and 792 m in a pessimistic scenario (SSP5-8.5).

3.4. Representativeness of Distribution Areas of Mahogany in the Network of Protected Areas

From the intersection of the potentially suitable areas predicted by the models under current and future conditions with the PA network, it was demonstrated that the proportion of suitable habitat for Mahogany under current conditions that would be available within the PA limits would be some 28.5% (Table 4).

Specifically, this coverage of suitable areas was found in greater proportion in Venezuela, Colombia, and Costa Rica. These findings suggest that the species may currently be under conservation in the areas predicted by the models. However, a slight coverage of suitable areas under conservation for the species was also observed in Puerto Rico and Ecuador, with only 4.7% and 5.9%, respectively.

In future climate conditions with an optimistic scenario (SSP2-4.5), the models demonstrated a broad coverage of stable areas within PAs of 89.24%. Thus, in Belize 99.7% of the suitable areas previously predicted by the current model would remain stable. On the other hand, in a dim scenario (SSP5-8.5) a slight reduction (3.51%) in suitable stable areas is anticipated compared to the forecasts provided by the scenario (SSP2-4.5). In general, a stability of suitable habitat within PAs of 85.73% is expected.

Table 4. Changes in the potential future distribution of Mahogany within the network of protected areas.

Country	Current	Protected Areas	%	SSP2-4.5						SSP5-8.5					
				Stable	**%**	**Loss**	**%**	**Gain**	**%**	**Stable**	**%**	**Loss**	**%**	**Gain**	**%**
Belice	26,251	9712	37.0	9681	99.7	31	0.3	0	0.0	9676	99.6	36	0.4	0	0.0
Bolivia	152,876	55,563	36.3	44,194	79.5	11,369	20.5	15,142	27.3	44,577	80.2	10,986	19.8	16,745	30.1
Brasil	64,690	13,714	21.2	10,687	77.9	3027	22.1	53,598	390.8	10,251	74.7	3463	25.3	43,045	313.9
Colombia	65,862	30,973	47.0	26,192	84.6	4781	15.4	11,095	35.8	24,142	77.9	6831	22.1	14,073	45.4
Costa Rica	38,259	17,295	45.2	15,985	92.4	1310	7.6	1330	7.7	15,177	87.8	2118	12.2	2171	12.6
Dominica	834	189	22.7	183	96.8	6	3.2	0	0.0	185	97.9	4	2.1	1	0.5
Ecuador	56,900	3384	5.9	1873	55.3	1511	44.7	582	17.2	1958	57.9	1426	42.1	911	26.9
El Salvador	19,146	2909	15.2	2877	98.9	32	1.1	877	30.1	2837	97.5	72	2.5	1008	34.7
Guatemala	89,556	37,037	41.4	36,836	99.5	201	0.5	906	2.4	36,645	98.9	392	1.1	1429	3.9
Honduras	116,168	31,004	26.7	30,846	99.5	158	0.5	2907	9.4	30,397	98.0	607	2.0	3900	12.6
México	355,755	61,281	17.2	58,697	95.8	2584	4.2	6537	10.7	54,174	88.4	7107	11.6	5830	9.5
Nicaragua	132,988	50,831	38.2	49,997	98.4	834	1.6	739	1.5	49,127	96.6	1704	3.4	631	1.2
Perú	18,544	6255	33.7	3809	60.9	2446	39.1	5738	91.7	3869	61.9	2386	38.1	7278	116.4
Panamá	61,645	12,590	20.4	9828	78.1	2762	21.9	541	4.3	10,276	81.6	2314	18.4	1248	9.9
Puerto Rico	6928	324	4.7	232	71.6	92	28.4	57	17.6	192	59.3	132	40.7	44	13.6
Venezuela	43,919	23,190	52.8	16,016	69.1	7174	30.9	11,670	50.3	11,931	51.4	11,259	48.6	24,905	107.4
Total	1,250,321	356,251	28.5	317,933	89.24	38,318	10.76	111,719	31.36	305,414	85.73	50,837	14.27	123,219	34.59

Based on future scenarios, the models indicated small reductions (loss) of habitat for the species within PAs. In the moderate emissions scenario (SSP2-4.5), a coverage loss of 10.76% was reported. Of this percentage, the largest proportion of reductions is expected to be visible in Ecuador with a loss rate of 44.7% of suitable areas. Furthermore, with a scenario of not very encouraging emissions (SSP5-8.5), a double of losses is forecasted compared to what is indicated in the SSP2-4.5 scenario. Hence, the models suggest losses of suitable habitat of 14.27% within PAs for the species. In particular, it was shown that Venezuela would have significant reductions in suitable areas under conservation with predicted losses of 48.6%.

Finally, the results predict that the species will have new areas potentially suitable for its conservation within the PA network currently in force in the future. A coverage of 31.36% was evidenced considering the models under the emissions scenario SSP2-4.5. Particularly, these area increases are expected to be most notable in Brazil, Peru, and Venezuela. On the contrary, it was also possible to notice null rates (0%) of gain of areas under conservation for the species in Belize and Dominica. Nonetheless, considering the emissions scenario SSP5-8.5, the models foresee an increase in suitable areas possibly under conservation in the future within PAs of 34.59%. It is expected that these increases will be observed in greater proportion in Brazil, Peru, Venezuela, and Colombia. However, in Ecuador a radical increase in suitable habitat was evidenced with a coverage of 313.9% within PAs for the species.

4. Discussion

4.1. Predictive Performance and Strengths of the Models

In the last decade, multiple recommendations have been formulated to improve the quality of species distribution models, thereby improving their reliability, replicability, and use in different forest restoration initiatives [80]. In the present study, ecological modelling techniques that take into consideration global recommendations for the reliable application of species distribution models were used [110,140]. All this facilitated the mitigation of possible problems, such as (1) errors associated with sampling bias and spatial aggregation [141]; (2) effects related to multicollinearity [122]; possible pseudo-estimates of predicted areas [91]; and interpretive complexity of the models [123].

In addition, it has been demonstrated that there is a wide variability in the predictions resulting from the models when using various algorithms individually. This is due to the fact that they are susceptible to the configurations and parameterizations used [142]. Previous studies conducted about Mahogany use the maximum entropy algorithm (Maxent) as the only algorithm to carry out the modelling of the species [29,82–85]. We imply that this selection may be based mainly on the fact that Maxent is one of the algorithms most explored and used in the existing literature [143]. However, recent research also suggests that Maxent's predictive power could be unreliable and possibly biased when making projections to novel future climates, leading to overestimates of predicted areas beyond previously known ranges for the species and under unfavorable climatic conditions for its adaptation [144,145]. Therefore, here, a consensus model approach was used to model the current and future distribution of Mahogany [125]. This approach has been evaluated and the findings suggest that combining predictions from multiple algorithms could improve predictions compared to models generated by separate algorithms [146,147]. Furthermore, our models considered the inclusion of soil variables, since recent evidence suggests that the use of soil variables helps improve current predictions and reduces overestimations in future predictions [148–150]. All of the above could be verified, since the selected modelling approach, after the evaluation process of its predictions, was statistically reliable (see Table 2). These qualities give high confidence in the predicted adequate area for this species in its native distribution range, and they could thus be considered for use in different approaches to conservation and forest restoration. However, it will be essential to confirm the actual presence of Mahogany through the implementation of forest inventories to evaluate the present findings.

One of the main achievements of this study was to include in the creation of the models the entire known native distribution range of Mahogany for the first time. Previous research has been done to model the potential geographic distribution of Mahogany in Mexico [17,29,83,99,100] and Brazil [84,85]. However, locally calibrated SDMs are limited by partial representation of the ecological niche of the species and therefore future projections may be biased [87–89]. Nonetheless, the models generated in this study fully represent the climatic niche of Mahogany, which allows for the capture of all the environmental variability available to the species [54] and therefore allows for more reliable models for the present and projections with less future over-prediction or under-prediction errors [90]. In this way, we consider that the information presented by our models is extremely important in terms of forest restoration and adaptation to the possible effects of climate change, since it allows for the characterization of potentially suitable areas in current and future conditions for the species, which facilitates the maximization of the potential success of conservation strategies and forest landscape restoration programs [65].

4.2. Model Limitations

It is necessary to point out that there could be certain limitations related to the presence set and the non-consideration of biotic interactions in the generation of our model. Initially, we highlight that the set of occurrences compiled for Mahogany for its native distribution area considered all possible open access databases of biodiversity and records published in scientific articles. However, the uncertainty associated with the spatial precision associated with the data must be considered [151,152]. Hence, the possible sampling biases associated with the greater number of botanical inventories in regions, mainly in Central America, must be acknowledged. These patterns are fundamentally associated with accessibility (roads, rivers, etc.) to the sampling sites [153]. All these points were considered in our study in the data cleaning process based on the methodological suggestions recommended for the development of species distribution models [110,111,140], with the aim of achieving the most reliable model possible. However, we ascertain that our model did not consider the possible biotic interactions that could exist for the species in its native area. For example, a forest inventory conducted in native populations of Mahogany in the province of Pastaza yielded that 93% of the sampled seedlings indicated signs of herbivory in 50% of their leaves [154]. This demonstrates that the species presents a great vulnerability to herbivores that limits its growth and the survival of individuals in its populations [29,30]. Research focused on the phytosanitary control of Mahogany indicated that the most relevant biological threat to the species would be the insect *Hypsipyla grandella* (Lepidoptera: Pyralidae) [155,156]. The larvae of this species attack the terminal buds, particularly of young trees, generating a defective growth of the species which decreases its commercial value. Even if the attacks are not frequent, the intensity of the attacks can cause the death of the plant [157,158].

In addition, it is known that a species can be influenced by different biotic interactions that are able to prevent it from occupying the entire area that corresponds to its ecological niche [159]. Therefore, considering all the possible biotic interactions known for the species to be modelled will provide additional information that could be key to anticipating whether these interactions could be positive or negative for the survival of the species [160,161]. Furthermore, recent research indicates that the predictive power of species distribution models could be improved when biotic interactions between species are considered [162,163]. However, at present, integrating these interactions is still a challenge, as more research is needed to determine whether the incorporation of these variables should be continuous or binary in the development of models [164]. We suggest that it would be necessary to explore in greater depth the influence of this pest on the distribution of Mahogany through the participation of experts in different forest disciplines [165], with a view to precisely characterizing the possible negative effects of this interaction in the future.

4.3. Current Potential Distribution of Mahogany

Based on current conditions, our model suggests that the species could have climatically suitable areas in 16 countries from Central America to South America, with suitable areas being found in greater proportion in Mexico and Bolivia. These findings are consistent with the known distribution ranges previously described for the species [17,99,100]. Mexico has been one of the countries with the largest number of investigations focused on understanding the distribution patterns of Mahogany [82,83,166–168]. This is mainly related to the more significant number of occurrence records for the species in this country. Regarding the patterns described in this study, the current model demonstrates adequate areas in 18 states of Mexico, representing 28.5% of the total distribution of the species. The states with the highest proportion of suitable areas were Campeche, Quintana Roo, and Yucatán. These areas reported by our models are similar to those predicted by models developed in previous research in Mexico and the province of Yucatán [82,83,167].

In relation to the predicted areas in Brazil, it was possible to demonstrate that these only represent 5.2% of the total distribution of the species. In addition, it is important to point out that the areas suitable for the species indicate a widely discontinuous and fragmented pattern, which is similar to that reported in previous studies where it is established that the species would be almost in danger of extinction due to the fact that its populations are very restricted and fragmented [169,170]. Furthermore, considering the spatial distribution of suitable areas in Brazil, previous studies reported that the state of Acre had the most suitable climatic conditions for the species [84,85]. These areas do not coincide with the results obtained in this study, as our models suggest that the largest proportion of areas reported for Brazil would be encountered in the states of Bahia and Espírito Santo. However, both studies indicated a concordance in the prediction of the absence of suitable areas for the species in the north-western region of Amazonas. This pattern could be associated with the presence of large extensions of tributaries and rivers, as is the case of the Amazon [171,172]. On the other hand, the model also reported similar patterns of absence in the north-central region of Colombia. These findings seem to be induced by the presence of large foothills with altitudes which the species had not been able to access for biogeographical reasons and by the lack of suitable environments under current conditions [17,168,173].

4.4. Changes in the Potential Geographic Distribution of Mahogany in the Future

Overall, under future climatic conditions, our models predicted that 88.9% of the areas suitable for Mahogany will remain stable throughout most of its range. For example, the stable areas reported in Mexico were similar to those shown in recent studies where they mention that areas such as Quintana Roo, Yucatán, and Calakmul would be potentially suitable for the habitat of the species in the face of climate change [26,29,83]. On the contrary, our models allowed us to identify that Peru and Ecuador were the countries with the lowest proportion of potentially stable areas with 58.8% and 59.4%, respectively. These reductions are expected to be detected mainly in the Amazon region of Ecuador, specifically in the provinces of Pastaza and Napo. The reductions reported by our models should be of great interest in decision making by local managers since, in Ecuador, it is estimated that under current conditions the suitable areas available in its extent of occurrence (EOO) would have been reduced by a percentage equal to or greater than 80% over the last thirty years. The species would thus be currently considered critically endangered (CR A2cd) in this country [154]. In this context, our findings suggest that Mahogany populations currently reported in the provinces of Pastaza, Napo, Orellana, and Morona Santiago [154] would be potentially prone to extinction.

Nevertheless, our models forecast possible gains from suitable areas going forward, reporting gains of 26.8% to 28.7% for the conservative (SSP2-4.5) and pessimistic (SSP5-8.5) emissions scenarios, respectively. These gains were forecast in greater proportion in Brazil, Peru, Colombia, Venezuela, and Bolivia. However, an encouraging scenario was also reported for Ecuador with small gains in areas in the coastal region, specifically in the provinces of Guayas, Manabí, Esmeraldas, and El Oro. It was demonstrated that the gains in areas occurred in an altitude range higher than that previously reported by our model under current conditions, which was from 0 to 2663 m.a.s.l. Thus, it is expected that the species will have new areas for its adaptation and survival through a progressive ascent of 792 m over time. It is estimated that the increase in global temperature would induce a displacement of forest species towards areas that were previously colder, where environmental circumstances may be more conducive to the adaptation of populations of the species in the future [174,175]. However, this process may be slow considering that the transition of the flora towards higher altitude ranges depends directly on its dispersal capacity [176–178].

This consideration could not be beneficial for the species as the pressure imposed by human activities advances at an accelerated rate compared to biological adaptation processes. For example, in the Amazonian region of Ecuador (ARE), activities such as deforestation [179], land use change [180], mining [181], and urban expansion [182] could have an even greater impact on the reduction of suitable accessible habitat for Mahogany. Therefore, it is interesting to mention that evidence of the influence of these activities has recently been discovered, since recent population studies conducted in the province of Pastaza found only seven individuals in three plots of 1.7 hectares [154], which indicates that the populations of the species could be under great anthropic pressure. However, these figures are even more worrying in inventories performed in Brazil and Mexico, where less than one individual per hectare was found in small and scattered populations [26,27].

4.5. Representativeness of the Potential Distribution of Mahogany in the Network of Protected Areas

Among all the investigations previously conducted for the species considering the use of SDMs in Mexico and Brazil [29,82–85], the current study stands out for being the first to perform an intersection analysis between the predicted areas under current and future conditions and the PA network. This analysis was performed in order to identify areas where the species could be protected under immediate short-term and long-term conservation statuses, as this could be one of the best in situ conservation strategies [139]. In this context, with the current climatic conditions, our models suggest that 28.5% of the areas predicted for Mahogany would be under conservation within the limits of the PA network, with Venezuela, Colombia, and Costa Rica being the countries where the species would find greater opportunity for immediate conservation. These results are extremely important, given that PAs have been considered one of the best strategies for biodiversity conservation, particularly for threatened forest species [78,183,184]. The effectiveness of PAs lies in the fact that they provide adequate conditions for the establishment and survival of many species from different taxonomic groups, in addition to mitigating the effects of overexploitation and selective felling of forest species associated with deforestation processes [185,186]. This is demonstrated by recent studies which have shown greater diversity within PAs than outside them [187]. Therefore, the results evidenced by the model for Mahogany suggest that the species would have optimal conditions for its conservation in these areas.

Subsequently, a slight proportion of suitable areas under conservation was also identified in Ecuador, where our models suggest that 5.9% of suitable areas would be found within the existing PAs for this country. However, this percentage disagrees with that suggested by Iglesias et al. [154], who indicate that the species has not yet been detected within the national system of PAs of Ecuador (SNAP, according to its acronym in Spanish). The models detected habitat reductions (losses) for the species within PAs throughout its native range. Such reductions are expected to be 44.7% to 48.6% for the SSP2-4.5 and SSP5-8.5 scenarios, respectively. Interestingly, the models indicate that possibly part of these area reductions would occur in Ecuador.

In Ecuador, the SNAP covers about 20% of Ecuador's surface with 69 PAs distributed in its four regions (coastal lowland, highlands, Amazonian lowland, and Galápagos). In addition, Ecuador in 2008 implemented the "Programa Socio Bosque", aimed at the conservation of forest resources inside and outside PA and buffer zones [188]. Despite all these initiatives, Ecuador is one of the countries in South America with the greatest expansion of road infrastructure inside and outside the SNAP [182,189]. Globally, an estimated 14.8% of tree species would fall within areas under high human pressure, even within existing PAs [190]. In Ecuador, it is estimated that 72% of the 4437 threatened native vascular plants would be found outside the areas delimited in the current SNAP [191,192]. Therefore, it is known that the least protected species are usually the most threatened [193], as is the case of Mahogany. We suggest that this could be even more serious for Ecuador, considering the increase in mining activities [181]. Additionally, it is necessary to emphasize that Mahogany has a very slow growth rate, fully developing in an average of 30 years [28]. For this reason, PAs play a key role in its in-situ conservation, since they should be areas under continuous conservation, which could provide the species with a safe habitat for its survival and development in the short and long term.

Within such future climatic conditions, our models evidenced a possible increase of 390.8% for the SSP2-4.5 scenario and 313.9% for the SSP5-8.5 scenario. In both scenarios, the models anticipate that profits will be higher in Brazil, Peru, and Venezuela. Particularly, in Ecuador a radical increase in suitable habitat was evidenced with a coverage of 26.9% within PAs for the species. These results could be very encouraging considering the forecasts predicted by our models for the species in the future. Ecuador is one of the countries with the highest global conservation priority that currently requires more connectivity between existing PA areas in the SNAP [192,194]. Recent studies suggest that improving connectivity between PAs could be one of the best initiatives to safeguard current biodiversity and enhance adaptive capacity in the context of future climate change [79,195,196]. However, it is also necessary to improve monitoring within PAs through new current initiatives based on the use of remote sensing for the detection of deforestation hotspots and selective logging [197,198], such as drones applied to monitoring the current state of forests [199,200]. Nonetheless, it is also necessary to encourage environmental education to raise awareness and promote the conservation of forest resources, knowledge of the impacts of human activities on forests, alternative uses of non-timber forest resources, and the possible effects induced by global climate change [201].

4.6. Considerations for Current and Future Monitoring of Mahogany Populations

Herbarium specimens provide essential information that can be used to increase knowledge of Mahogany distribution patterns. However, the limited availability of digitized herbarium collections available for plants is one of the current problems [106,202]. It is estimated that ~36% of plants have little information on their distribution in global herbaria, and that between 11.2 and 36.5% of these species have less than five reported observations [203]. Therefore, it would be essential to increase botanical sampling efforts for the species in tropical areas. In addition, in Ecuador, for example, it is necessary to increase efforts to digitize existing botanical collections in national herbaria. In turn, these data can be shared with the scientific community through open access databases in Ecuador (BIOWEB, SISBIO) and worldwide (GBIF, IDIGBIO, etc.). On the other hand, the continuous monitoring of all forest species through the National Forestry Inventory of Ecuador (ENFI, according to acronym in Spanish) should be promoted [204].

Nonetheless, currently many of the efforts focused on the survey and inventory of specimens are based on geographical decisions that consider distance, accessibility, and available economic resources [205]. As a result, in most inventoried species there is evidence of different types of sampling bias that limit biological knowledge of them outside of inaccessible areas which could be climatically suitable [153,206,207]. In this way, the use of methodologies that allow for the identification of optimal areas under geographic and environmental considerations that facilitate the documentation of the greatest number of specimens with fewer economic resources and less human effort [208] is key to obtaining a completer and more enriched database.

Given this urgent need, new methodologies implemented in packages developed for the R programming environment have now emerged which could help address current necessities. One of these packages is WhereNext [209], which is based on the use of a generalized model of dissimilarity. The principle of this model is the understanding of the compositional dissimilarity of two sites through the differences between their conditions and the geographic distance between them. This allows it to identify areas that decrease the average distance between the previously sampled sites and those not yet sampled [210]. On the other hand, another current alternative is the Biosurvey package, which uses a methodology that considers the environmental conditions available in the study areas and records of the presence of the species [211]. In addition, Biosurvey provides the opportunity to evaluate previously selected post-analysis sites, with climatically suitable areas identified through species distribution models [211]. However, the authors suggest that the areas described by the SDM to be used should be previously verified by a group of experts in the species of interest [165]. Based on this context, in this study we suggest considering the areas predicted by our models under current conditions to be used in future research that could be implemented through the previously described packages, thus achieving the detection of new sites that complement the collections available for the species.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14020385/s1, Figure S1: Relative importance of each independent variable inside the species distribution models. We calculated the mean value (10 replicates models) for each sampling strategy, variable, modelling technique (GLM, BRT, and RF).

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