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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 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 29% within the limits of the protected areas. Under future scenarios, drastic reductions were observed in different regions, particularly in Ecuador with losses of up to 90.5%. 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 in identifying currently unrecorded populations of Mahogany, as well as in 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 tools for conducting dynamic conservation and restoration strategies that consider the effects of climate change.

Keywords: Mahogany; *Swietenia macrophylla*; Neotropic; Ecuador; Protected areas; forest monitoring

Citation: To be added by editorial staff during production.

Academic Editor: Firstname Lastname

Received: date
Accepted: date
Published: date

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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 CO2 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 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 for 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 the 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, 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 in multiple uses such as the production of cosmetics, antidiabetic, anticancer, control of hypertension, and anti-inflammatory [20–22]. Due to these multiple uses, it is considered one of the most commercially important plant species worldwide [23], reaching prices between USD 1,700 and USD 11,000 per m3 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, being necessary a period of 30 years 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 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 the correct management and conservation of Mahogany in the neotropics.

On a global scale, various forest restoration initiatives are being conducted focused on achieving multiple objectives [34,35], including anticipation of the possible effects of climate change [4,36], recovery of biodiversity [5,37] or enhance 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 do, 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 a 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, being an important point of interest in the scientific community, some authors even mention of the sixth great extinction of species [53]. It is estimated that a large part of the 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 environmental conditions available in their environment [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 evidenced 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 as the reason 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) realized of researchers, professionals, land managers, community leaders and decision makers to restore ecosystems in seventy countries, suggest giving greater emphasis to the use of forest native 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, here, we propose 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 the territory [78,79], and recently ecological restoration strategies fundamentally 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 them, only a partial fraction of the climatic niche of the species was considered (only presence records for the species in one country). This practice has been habitual, but at present, it is not the most appropriate option to generate reliable SDMs [86], especially to project the potential distribution of the species to 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 capturing 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 aim to propose forests management strategies to stakeholders in tropical countries that allow 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.

批注 [A1]: I highly recommend using a method like convex hulls or buffers to select background points, if the entire region in Figure 1 was used as the background for model development. Using too large a background area will allow for inaccessible areas to be included in model development, leading to AUC score inflation and erroneous models.

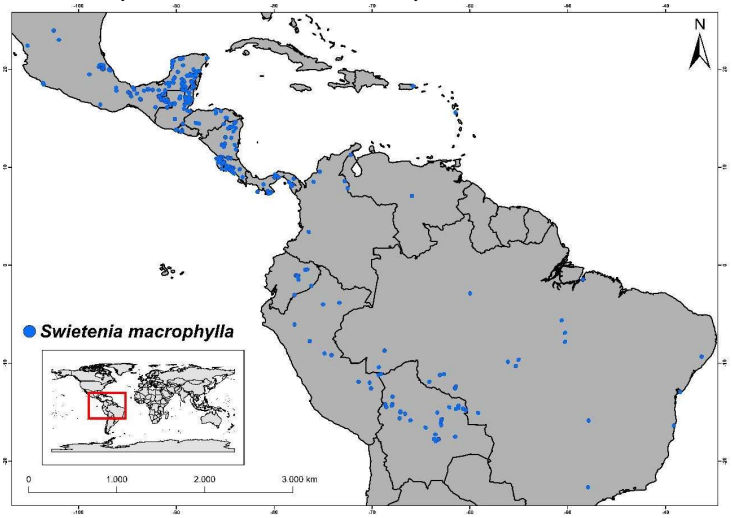


Figure 1. Study area. Presence records of Mahogany (blue dots) in its native distribution area.

2.2 Presence records

Some 2217 presence records for Mahogany were collected from two types of information sources, being online biodiversity databases, such as Global Biodiversity

Information Facility (GBIF; www.gbif.org) and Tropicos (www.tropicos.org), besides scientific publications [17,93–96]. 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 [97–99].

To ensure the quality of the presence data information [100], we relied on the present literature that provides methodological suggestions with the aim of generating a reliable database that can be used in ecological modelling [86,101,102]. Consequently, a protocol based on three steps was applied, being firstly to initially mitigate the effect of seasonality collection [103], preserving records collected in years after 1950. Secondly, to consider that presences collect duplicate samples of the same individual who rest in different institutions, therefore records that presented the same geographic coordinates were eliminated. Finally, the possible sampling bias associated with collection patterns was attenuated [104], for this a distance of 5 km was applied between each record. All the steps conducted in this process were executed through the use of the packages (spThin [105], SpeciesGeoCoder [106]) developed in the R environment. The final database included 313 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 2.0 climate data repository (https://www.worldclim.org/) were used at a resolution of 2.5 arc-minutes (approximately 5 x 5 km²) [107]. 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 of the Coupled Model Intercomparison Project Phase 6 (CMIP6, [108]) were considered. Two GCMs (MRI-ESM2.0 [109], MIROC6 [110]) were chosen to consider the variability and uncertainty associated with the creation of future climate models and their influence on spatial predictions [111,112]. Additionally, two shared socioeconomic pathways (SSPs) were used, being 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 database at a resolution of 1 km² [113], they were resampled at a resolution 2.5 arc-minutes. 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 [114], possible pseudo-estimates of predicted areas [89], and interpretative complexity of the models [115]. A Pearson correlation coefficient ($r > 0.8$) was applied between pairs of variables [116]. Highly correlated variables were removed based on the threshold mentioned above. Finally, the models generated for Mahogany included eleven environmental variables (see, Table 1).

批注 [A2]: Why was 2.5arcmin selected and not 30arcsec? The finer resolution will generate better models and allow for more precise predictions. All environmental data used in these analyses are available at 30arcsec.

Table 1. Environmental variables used in the creation of distribution models of *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 [117] were generated, using the biomod2 package [118] by combining predictions generated by three statistical techniques, being generalized additive models (GAM, [119]), boosted regression trees (BTR, [120]), and random forests (RF, [121]). These were used using their default parameters and settings. The predictive accuracy of the models was evaluated by selecting a repeated random sample (ten times), where the 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 [122]. 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 a AUC value < 0.8 [123] were eliminated. Finally, a consensus model was generated through the weighted average of their AUC values. Subsequently, the projection was realized 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. [124]. 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% [125].

批注 [A3]: Using the ensemble model in BioMod2 is excellent. I do recommend testing other sets of model parameters other than just default though. The default parameters are very general and need to be fine-tuned.

批注 [A4]: I recommend adding in other evaluation metrics (eg, AICc, CBI, Omission Rate) other than just AUC.

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), stability (i.e., potential areas where the species is potentially present now and is likely to be present in the future). 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.

批注 [A5]: Was this resampled to the same resolution as the input variables for the ENM? If not, they should be resampled to the same resolution.

2.6 Representativeness of distribution areas of Mahogany *in the network of protected areas*

An intersection was realized between current or future models; and a map of the global network of PA obtained from https://www.protectedplanet.net/en. This occurred below the premise that PAs provide a greater survival advantage in terms of conservation to endangered species, in addition to be a more effective in situ conservation strategy in the short and long term [126–128].

3. Results

3.1 Statistical performance of the models

The validation performed suggests that the consensus model generated for Mahogany was statistically reliable, indicating robust predictive performance, since the AUC value obtained was 0.98.

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 647,388 km2 (Figure 2), which are found in an altitudinal pattern between 0 and 2662 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, the coastal region and the centre of the Ecuadorian Amazon. Particularly, Mexico stands out for being the country with the highest proportion of suitable areas with 36.37% of the total potential distribution of the species.

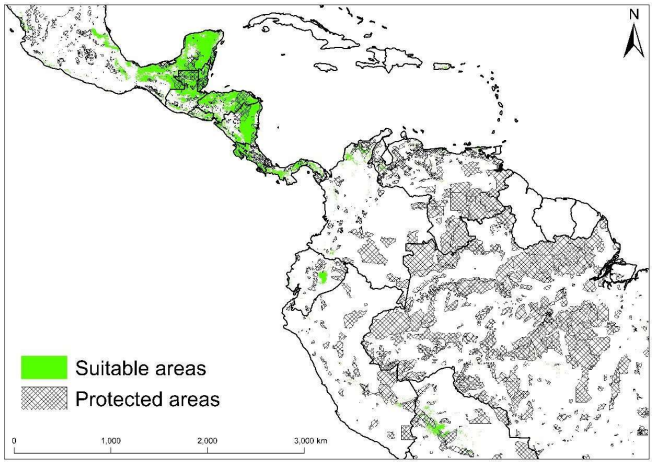


Figure 2. Potentially suitable areas for *Mahogany* under current conditions predicted in the binary model.

3.3 *Changes in the potential geographic distribution of Mahogany in the future*

Considering that the resulting models predict fractional and distant potential areas between each country included in the study area, an area of interest between Peru and Bolivia was selected as an example, where the models predicted potential changes (stability, loss, gain) in the future in the distribution of Mahogany (Figure 3). However, all the areas predicted by the models are presented in Table 2.

Based on future climatic conditions, with a moderate emissions scenario (SSP2-4.5), the models suggest that around 92.3% 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 224,323 km2. However, we encountered that in El Salvador it is expected that 100% of the suitable areas will remain stable in the future. On the contrary, in Ecuador small extensions of stable areas are forecast that only represent 9.5%. Similarly, in a severe emissions scenario (SSP5-8.5), a 5.2% 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 the 87% species. Specifically, patterns similar to those previously described in the SSP2-4.5 scenario were identified, with El Salvador again being the country with 100% of potentially stable areas. Similarly, it is also expected that in Mexico the species will have large extensions of suitable areas in the future.

Particularly, a drastic loss of suitable areas of 90.5% was evidenced in Ecuador. Specifically, these reductions are expected to be most evident in the Amazonian region of

批注 [A6]: I think it is important to note that these models predict where suitable habitat (per the input variables) will be, not necessarily where the species will be. Some of the results is framed well in this context, but the title of this section should be rephrased to keep consistent.

Ecuador in the provinces of Pastaza and Napo (Figure 4b). Similarly, due to a scenario of bleak emissions (SSP5-8.5), it is expected that there will be almost twice as many predicted losses as those reported by the model for the scenario (SSP2-4.5). In general, the models anticipate possible reductions equivalent to 13.4% in the distribution range of the species. Again, it is evident that Ecuador would be the country with the highest rate of loss of predicted suitable areas for *Mahogany* with 87.2% (Figure 4c). On the other hand, it is noted, with this scenario, it is forecasting that El Salvador will begin to generate reductions in suitable habitat of 3.5%.

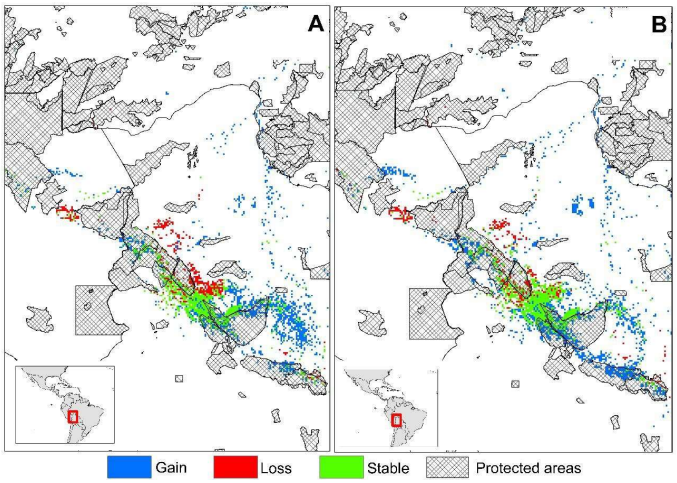


Figure 3. Changes in the potential distribution of *Mahogany* in the future (a) Potential changes predicted in future climate scenario SSP2-4.5; (b) Potential changes predicted in future climate scenario SSP5-8.5.

Table 2. 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	%
Belice	24287	23479	96,7	808	3,3	85	0,3	23560	97,0	837	3,4	565	2,3
Bolivia	28121	19609	69,7	8512	30,3	29644	105,4	21431	76,2	6690	23,8	32558	115,8
Brasil	7744	4180	54,0	3564	46,0	16066	207,5	4372	56,5	3688	47,6	44878	579,5
Colombia	17576	14804	84,2	2772	15,8	12518	71,2	15011	85,4	2614	14,9	25969	147,8
Costa Rica	32311	30187	93,4	2124	6,6	3128	9,7	30142	93,3	2609	8,1	5771	17,9
Dominica	698	499	71,5	199	28,5	0	0,0	474	67,9	250	35,8	0	0,0
Ecuador	10685	1010	9,5	9675	90,5	400	3,7	1395	13,1	9322	87,2	3410	31,9
El Salvador	2744	2744	100,0	0	0	940	34,3	2749	100,2	96	3,5	1070	39,0
Guatemala	67842	66691	98,3	1151	1,7	7034	10,4	61843	91,2	6066	8,9	7655	11,3
Honduras	81627	79950	97,9	1677	2,1	8271	10,1	79872	97,8	1997	2,4	11062	13,6
México	235431	224323	95,3	11108	4,7	53759	22,8	194540	82,6	41389	17,6	44631	19,0
Nicaragua	93748	92771	99,0	977	1,0	9536	10,2	91500	97,6	2518	2,7	20526	21,9

Perú	3768	2318	61,5	1450	38,5	6061	160,9	1643	43,6	2125	56,4	10586	280,9
Panamá	29632	25621	86,5	4011	13,5	6280	21,2	27421	92,5	2654	9,0	14451	48,8
Puerto Rico	1296	748	57,7	548	42,3	350	27,0	573	44,2	735	56,7	100	7,7
Venezuela	9878	8293	84,0	1585	16,0	15737	159,3	6842	69,3	3108	31,5	27272	276,1
Total	647388	597227	92,3	50161	7,7	169809	26,2	563368	87,0	86698	13,4	250504	38,7

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 26.2% across its entire native range. In this context, it is expected that the species will have new areas for its adaptation and survival through a progressive ascent of 556 m over time. It is identical that the largest proportion of forecast gains is centered in Brazil, Peru, Venezuela and Bolivia. Also, small increases were seen in Ecuador, especially in areas of the provinces of Pastaza and the provinces of Guayas, El Oro, Manabí and Esmeraldas, which is encouraging considering the potential losses previously predicted by the models. Furthermore, it should be emphasized that the models did not predict suitable new areas in the Dominican Republic, with a 0% win rate.

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 12.5%. In general, the models predict gains of potentially suitable areas for the species of 38.7%. Particularly, it was possible to evidence patterns of profits that were equally higher in the previously mentioned countries. However, there was also a substantial increase in gains in suitable areas in Colombia. On the other hand, again the models anticipate a zero rate (0%) of earnings in the Dominican Republic.

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 of some 29% (Table 3).

Table 3. 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	24287	9304	38,3	9176	98,6	128	1,4	10	0,1	9212	99,0	107	1,2	133	1,4
Bolivia	28121	12554	44,6	9761	77,8	2793	22,2	11763	93,7	10410	82,9	2144	17,1	15577	124,1
Brasil	7744	1973	25,5	1529	77,5	444	22,5	5894	298,7	1417	71,8	580	29,4	13060	661,9
Colombia	17576	1630	9,3	1300	79,8	330	20,2	1374	84,3	1475	90,5	164	10,1	2302	141,2
Costa Rica	32311	12822	39,7	11904	92,8	918	7,2	1993	15,5	11740	91,6	1158	9,0	3272	25,5
Dominica	698	161	23,1	133	82,6	28	17,4	0,0	0,0	124	77,0	44	27,3	0,0	0,0
Ecuador	10685	130	1,2	39	30,0	91	70,0	0,0	0,0	109	83,8	34	26,2	138	106,2
El Salvador	2744	696	25,4	696	100,0	0	0	420	60,3	722	103,7	8	1,1	551	79,2
Guatemala	67842	32869	48,4	32493	98,9	376	1,1	1255	3,8	28182	85,7	4734	14,4	835	2,5
Honduras	81627	26781	32,8	26707	99,7	74	0,3	2912	10,9	26761	99,9	98	0,4	4505	16,8
México	235431	39287	16,7	36631	93,2	2656	6,8	8521	21,7	31974	81,4	7482	19,0	7634	19,4
Nicaragua	93748	39077	41,7	38592	98,8	485	1,2	2638	6,8	38290	98,0	873	2,2	7088	18,1
Perú	3768	645	17,1	507	78,6	138	21,4	1288	199,7	299	46,4	346	53,6	2023	313,6

Panamá	29632	4056	13,7	3433	84,6	623	15,4	1071	26,4	3578	88,2	650	16,0	2205	54,4
Puerto rico	1296	113	8,7	65	57,5	48	42,5	16	14,2	59	52,2	55	48,7	13	11,5
Venezuela	9878	5558	56,3	5051	90,9	507	9,1	8172	147,0	4318	77,7	1278	23,0	15205	273,6
Total	647388	187656	29,0	178017	94,9	9639	5,1	47327	25,2	168670	89,9	19755	10,5	74541	39,7

Specifically, this coverage of suitable areas was found in greater proportion in Venezuela, Guatemala, and Bolivia. 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 in Ecuador was also noted, with only 1.2% of the suitable areas found within the PAs in force for this country (Figure 4 a).

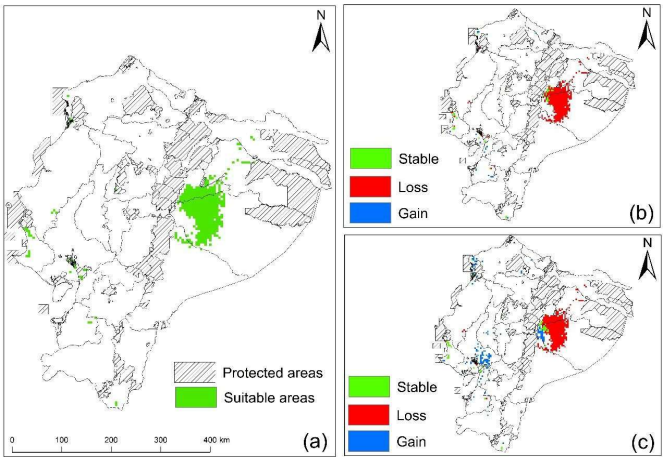


Figure 4. Current and future potential distribution of *Mahogany* in Ecuador (a) Current potential distribution in the national system of PAof Ecuador (b) Potential changes predicted in future climate scenario SSP2-4.5; (c) Potential changes predicted in future climate scenario SSP5-8.5.

In future climate conditions, with an optimistic scenario (SSP2-4.5), the models demonstrated a broad coverage of stable areas within PA of 94.86%. Hereby, in El Salvador, 100% 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 (4.8%) 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 PA of 89.88% is expected.

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 5.14% was reported. Of this percentage, the largest proportion of reductions is expected to be visible in Ecuador with a loss rate of 70% of suitable areas (Figure 4 b). On the contrary, in El Salvador the models predict that there will be no loss of habitat for the species within the PA. Furthermore, with a scenario of not very encouraging emissions (SSP5-8.5), a double of losses is forecast compared to what is indicated in the SSP2-4.5 scenario. Hence, the models suggest losses of suitable habitat of 10.53% within PAs for the species. In particular, it was yielded that Peru would have significant reductions in suitable areas under conservation with predicted losses of 53.6%.

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 25.22% was evidenced considering the models under an 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 Ecuador and the Dominican Republic. Nonetheless, considering an emissions scenario SSP5-8.5, the models foresee an increase in suitable areas possibly under conservation in the future within PAs of 39.72%. It is expected that these increases will be observed in greater proportion in Brazil, Peru, Venezuela, and Ecuador. However, in Ecuador a radical increase in suitable habitat was evidenced with a coverage of 106.2% within PA for the species (Figure 4 c). These findings could be encouraging for *Mahogany* considering the habitat losses predicted by future models in this country.

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 were used considering the global recommendations suggested by the application of species distribution models in a reliable way [101,129]. All this allowed to mitigate possible problems, such as 1) errors associated with sampling bias and spatial aggregation [130]; 2) effects related to multicollinearity [114]; possible pseudo-estimates of predicted areas [91]; interpretive complexity of the models [115].

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 [131]. Previous studies realized 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 [132]. 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 conditions unfavourable climatic conditions for its adaptation [133,134]. Therefore, here, a consensus model approach was used to model the current and future distribution of *Mahogany* [117]. 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 [135,136]. 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 [137–139]. All of the above could be verified, because the models, after the evaluation process of their predictions, were all statistically reliable and yielded AUC values> 0.9. These qualities give high confidence in the predicted adequate area for this species in its native distribution range, for which they could 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 [17,29,83,95,96] 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 represents the climatic niche of *Mahogany*, which allowed to capture all the environmental variability available to the species [54] and therefore 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 to characterize potentially suitable areas in current and future conditions for the species, which allows managing to maximize 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 [140,141]. Hence, the possible sampling biases associated with the greater number of botanical inventories in regions, mainly in Central America. These patterns are fundamentally associated with accessibility (roads, rivers) to the sampling sites [142]. 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 [101,102,129], 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 [143]. This demonstrates that the species presents a great vulnerability to herbivores that limit 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) [144,145]. 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 and even if the attacks are frequent, the intensity of the attacks can cause the death of the plant [146,147].

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 [148]. Therefore, considering all the possible biotic interactions known for the species to be modelled will provide additional information that could be key to anticipate whether these interactions could be positive or negative for the survival of the species [149,150]. Furthermore, recent research indicates that the predictive power of species distribution models could be improved when biotic interactions between species are considered [151,152]. 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 [153]. 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 [154], 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, being found in greater proportion in Mexico and Nicaragua. These findings are consistent with the known distribution ranges previously described for the species [17,95,96]. Mexico has been one of the countries with the largest number of investigations focused on understanding the distribution patterns of *Mahogany* [82,83,155–157]. This is mainly related to the more significant number of occurrence records of the species in this country. Regarding the patterns described in this study, the current model demonstrates adequate areas

in 18 states of Mexico, representing 36.37% 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 [82,83,156].

In relation to the predicted areas in Brazil, it was possible to demonstrate that these only represent 1.19% 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 [158,159]. 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 Pará. 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 [160,161]. 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 to which the species has not been able to access for biogeographical reasons and by the lack of suitable environments under current conditions [17,157,162].

4.4 Changes in the potential geographic distribution of Mahogany in the future

Overall, under future climatic conditions, our models predicted that 92.3% 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, in Ecuador, our models allowed us to identify small extensions of potentially stable areas that only represent 9.5%. This percentage could be considered significantly low and of great concern, since for both emission scenarios (SSP2-4.5 and SSP5-8.5), our models anticipate a drastic reduction of suitable areas of up to 90.5%. These reductions are expected to be mostly detected 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 administrators because, in Ecuador, it is estimated that under current conditions in the last thirty years, the adequate areas available in its extension of presence (EOO) would have been reduced by a percentage equal to or greater than 80%, therefore it is currently considered critically endangered (CR A2cd) in this country [143]. In this context, through the interpretation of our findings, it is expected that the available habitat for the species in Ecuador will be reduced by a further 10.5% until 2070, which allows to anticipate that the populations of *Mahogany* currently reported in provinces de Pastaza, Napo, Orellana, Morona Santiago [143], would be potentially prone to extinction.

Nevertheless, our models forecast possible gains from suitable areas going forward, reporting gains of 26.2% to 38.7% for the conservative (SSP2-4.5) and pessimistic (SSP5-8.5) emissions scenarios, respectively. These gains were forecast in greater proportion in Brazil, Peru, Venezuela, Colombia 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 2662 masl. Hereby, it is expected that the species will have new areas for its adaptation and survival through a progressive ascent of 556 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 [163,164]. However, this process may be slow considering that the transition of the flora towards higher altitude ranges depends directly on its dispersal capacity [165–167].

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 [168], land use change [169], mining [170] and urban expansion [171] could have an even greater impact on the reduction of suitable accessible habitat for *Mahogany*. Therefore, it is interesting to mention that the influence of these activities has currently been evidence, since recent population studies conducted in the province of Pastaza found only 7 individuals in 3 plots of 1.7 hectares [143], 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 in order to identify areas where the species could be under immediate short-term and long-term conservation status, as it could be one of the best in situ conservation strategies [128]. In this context, with the current climatic conditions, our models suggest that 29% of the areas predicted for *Mahogany* would be under conservation within the limits of the PA network, with Venezuela, Guatemala and Bolivia 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 [78,172,173]. 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 [174,175]. This is demonstrated by recent studies, which yielded greater diversity within PAs than outside [176]. 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 1.2% would be found within the existing PAs for this country. However, this percentage disagrees with that suggested by Iglesias et al [143], who indicate that the species has not yet been detected within the national system of PA of Ecuador (SNAP, for its acronym in Spanish). The models detected habitat reductions (loss) for the species within PAs throughout its native range. Such gains are expected to be 5.14% to 10.53% for the SSP2-4.5 and SSP5-8.5 scenarios, respectively. Interestingly, the models indicate that possibly part of these area reductions occur in Ecuador, with a loss rate of 70% of suitable areas.

In Ecuador, the SNAP covers about 20% of Ecuador's surface with 69 PA 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 [177]. 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 [171,178]. Globally, an estimated 14.8% of tree species would be within high human pressure, even within existing PAs [179]. In Ecuador, it is estimated that 72% of the 4,437 threatened native vascular

plants would be encountered outside the areas delimited in the current SNAP [180,181]. Therefore, it is known that the least protected species are usually the most threatened [182], as is the case of *Mahogany*. We may remind that this could be even more serious for Ecuador, considering the increase in mining activities [170]. 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 25.22% for the SSP2-4.5 scenario and 39.72% 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 106.2% within PA 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 [181,183]. 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 [79,184,185]. 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 [186,187], drones applied to monitoring and the current state of forests [188,189]. 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 use of non-timber forest resources and the possible effects induced by global climate change [190].

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 [97,191], such is the case, that it is estimated that ~36% of plants have little information on their distribution in global herbaria, finding that between 11.2 and 36.5% of these species have less than five reported observations [192]. Therefore, it would be essential to increase botanical sampling efforts for the species in tropical areas. In addition, in Ecuador it is necessary to increase efforts to digitize existing botanical collections in national herbaria and 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, for its acronym in Spanish) should be promoted [193].

Nonetheless, currently much of the efforts focused on the survey and inventory of specimens are based on geographical decisions that consider distance, accessibility and available economic resources [194]. As a result, in most inventoried species there is evidence of different types of sampling bias that limit their biological knowledge outside of inaccessible areas, which could be climatically suitable [142,195,196]. In this way, the use of methodologies that allow the identification of optimal areas under geographic and environmental considerations that facilitate the documentation of the greatest number of specimens with less economic resources and human effort [197], is key to obtaining a more complete and enriched database.

Given this urgent need, new methodologies implemented in packages developed for the R programming environment have now emerged, which could help solve current necessities. One of these packages is WhereNext [198], which is based on the use of a generalized model of dissimilarity, whose principle is the understanding of the compositional dissimilarity of two sites through the differences between their conditions and the geographic distance between them, allowing with it, to identify areas that decrease the

average distance between the previously sampled sites and those not yet sampled [199]. 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 [200]. In addition, Biosurvey provides the opportunity to evaluate previously selected post-analysis sites, with climatically suitable areas identified through species distribution models [200]. However, the authors suggest that the areas described by the SDM to be used should to be previously verified by a group of experts in the species of interest [154]. 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.

Author Contributions: Conceptualization, R.J.H.-F., R.M. and B.T.; methodology, R.J.H.-F. and R.M.; software, R.J.H.-F. and R.M.; validation, R.J.H.-F., B.T. and R.M.; formal analysis, R.J.H.-F. and R.M.; investigation, R.J.H.-F., B.T., C.T-T., T.T., M.H.-R., R.L. and R.M.; data curation R.J.H.-F.; writing—original draft preparation, R.J.H.-F., C.T-T., T.T., M.H.-R. and R.L.; writing—review and editing, R.J.H.-F., B.T., C.T-T., T.T., M.H.-R., R.L. and R.M.; supervision R.J.H.-F., B.T. and R.M. All authors have been involved in developing, writing, commenting, editing, and reviewing the manuscript. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: This is not applicable as the data are not in any data repository of public access, however if editorial committee needs access, we will happily provide them, please use this email: rherreraf2@uteq.edu.ec

Acknowledgments: The authors would like to thank the Faculty of Agricultural and Forestry Sciences, Quevedo State Technical University (UTEQ), and Department of Biology, Universidad Autónoma de Madrid, for supporting all the production stages of this document, as well as to all botanists for their efforts in botanical collections in the neotropics.

Conflicts of Interest: The authors declare no conflict of interest.

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