Modeling future tree species distributions under climate change to guide restoration planning: Application to the Brazilian Amazon

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Abstract

Addressing climate change and biodiversity loss requires innovative approaches to ecosystem restoration. This study aims to (1) develop a statistical tool to predict species distribution shifts under future climate scenarios and (2) apply it to 30 key tree species in the Brazilian Amazon, a biodiversity hotspot increasingly threatened by deforestation and climate change.

Using MaxEnt, we modeled species distributions under three climate scenarios (optimistic, medium, and pessimistic) for 2040, 2070, and 2100, integrating bioclimatic and soil variables. The tool generates interpretable maps highlighting areas of stability, expansion, and contraction for each species.

Results reveal a dual effect of climate change: while some species may initially expand their ranges, long-term survival is uncertain, particularly for those with low ecological plasticity. Functional trait analysis identified three species clusters, emphasizing the role of wood density, phenology, and

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plasticity in species selection for restoration.

Our findings highlight the need to integrate predictive modeling with ecological knowledge to guide species selection and enhance restoration success. By prioritizing climate-resilient species, this approach supports ecosystem stability and long-term conservation goals. Strengthening collaboration between scientists and practitioners is essential to refining and scaling these decision-support tools for effective restoration efforts.

Keywords: Ecological restoration, Prediction tool, Species distribution model, Climatic Scenarios, Tropical rainforest.

1. Introduction

The crucial link between climate change and biodiversity loss has been increasingly recognized. Addressing both challenges in restoration projects is essential to ensure ecosystems' resilience for future centuries.

Ensuring the long-term persistence of restored ecosystems requires restoration programs to be informed by a deep understanding of the ecology and evolutionary history of the species involved. This knowledge increases the likelihood of creating habitats suitable for local species while enhancing the ecosystems resilience to climate change.

In response to the growing ecological concerns of citizens, the number of ecosystem restoration projects has increased. For example, activities with significant environmental footprints are strongly encouraged to mitigate their impact by actively contributing to initiatives that promote biodiversity restoration or improve the carbon balance through sustainable practices (IPBES, 2019). Some actual restoration programs prioritize rapid actions and immediate results, even if it involves agricultural or alien species (Montemagni Almeida et al., ults; Suzuki et al., 2021). They provide an instant public image improvement by quickly vegetating degraded areas. However, such actions can harm local ecosystems through invasive competition and resource degradation and fail to restore the degraded ecosystemall the more so that, even in optimistic scenarios, ecosystems will face climatic changes. The most effective restoration strategy implies careful species selection and maximizes intra and inter-specific diversity (Butterfield et al., 2017).

Biodiversity loss has reached a critical point, necessitating actions focused on areas with the greatest potential for success, protection of rare species, and historically rich ecosystems, where diverse survival opportunities for planted species and specimens can be maximized(van Tiel et al., 2024). The Amazon is the largest existing rainforest, supporting the greatest biodiversity on Earth and a major resource for the local population, but it is increasingly impacted and threatened by unsustainable activities (Guayasamin et al., 2024). For instance, in 2022, 15.5% of its surface was dedicated to monocultures and pastures (Project, 2023), with projections suggesting that 40% of Amazon forests could be eliminated by 2050 due to non-sustainable commercial agricultural expansion (Soares-Filho et al., 2006). Its importance encompasses numerous valuable ecosystem services, with regional climate regulation and carbon stock being particularly noteworthy (Guayasamin et al., 2024). Deforestation leads to significant regional climate changes, primarily reducing rainfall, which, in turn, affects rural activities and the maintenance of millions of inhabitants who depend on the natural resources of forests, either for income generation or for the production of their own medicines (Zemp et al., 2017).

Yet, global warming presents a critical challenge to restoration projects by amplifying extreme climatic events (Aleixo et al., 2019). To address these challenges, large-scale forest restoration should prioritize the selection of key native species that deliver multiple ecosystem services and can adapt to climate change within specific regions (Flores et al., 2024).

Species Distribution Modeling (SDM) is a well-established method in biogeography and biodiversity research, particularly in data-scarce areas like tropical forests (Elith and Leathwick, 2009; Rushton et al., 2004), where many species remain understudied (Wilson et al., 2016). Despite its potential, SDM often stays within academia, with limited practical application. To bridge this gap, we developed a tool linking scientific insights to real-world restoration projects. Using SDM, we combined species presence or abundance data with environmental variables to generate ecological insights, predict distributions across landscapes, and provide outputs directly useful for practitioners.

In this study, we aim to assess how native tree species in the Brazilian Amazon forest could face climate changes in the next century and how to improve the species selection for large-scale restoration projects in tropical forests.

2. Material and methods

All the processing was made in R-4.3.3 (R Core Team, 2024), with package dismo (Hijmans et al., 2017) being used for SDM.

2.1. Study area

The Brazilian Amazon represents 60% of the total Amazon forest surface area (Fig. 1)(Flores et al., 2024). According to Köppen classification, the area has Tropical climate, mainly monsoon (49.8%) and without a dry season (43.7%), with a small portion with dry-winter, part of the southern border with the Cerrado (5.9%). The predominant soils are Argisols (42.1%) and Latosols (32.9%). The relief is characterized mainly by vast depressions (57.4%), with plateaus (16.5%) (Gerhard et al., 2020). There are various vegetation types, mainly Dense Ombrophilous Forest (46.2%), Open Ombrophilous Forest (22.3%), and contact zones/ecotones (12.5%)(IBGE, 2019).

2.2. Tree species selection and data

In total, 30 species were selected based on the following criteria: 1) use in restoration programs; 2) seeds with orthodox storage behavior; 3) indigenous to Brazil; 4) broad potential distribution; and 5) representation of different ecological succession groups (Fig. 2, Tab. A1). *Psidium guajava* was included because it is considered naturalized in Brazil, though of unknown origin (Arévalo-Marín et al., 2021). *Eschweilera coriacea*, from a genus with recalcitrant seeds (Calvi and Ferraz, 2014), was also included due to its importance for the biome (Ter Steege et al., 2013). The number of presence points ranged from 47 for *Samanea tubulosa* to 307 for *Trema micranthum*, with a mean of 130 observations across the 30 species (Tab. A2).

Figure 1: Study area location. Red = Brazilian Amazon biome (IBGE, 2019), blue = Amazonia boundary (Eva and Huber, 2005).

2.3. Environmental data

Aiming at and improved prediction of plant distribution and migration, two types of environmental variables were considered: pedological and bioclimatic (Fig. 2)(Zuquim et al., 2020).

Pedological variable was analyzed at six soil depth levels: 05, 515, 1530, 3060, 60100, and 100200 cm. Bulk density at 05 cm was further divided into "upper" and "lower" layers. Soil variables were assumed to remain con-

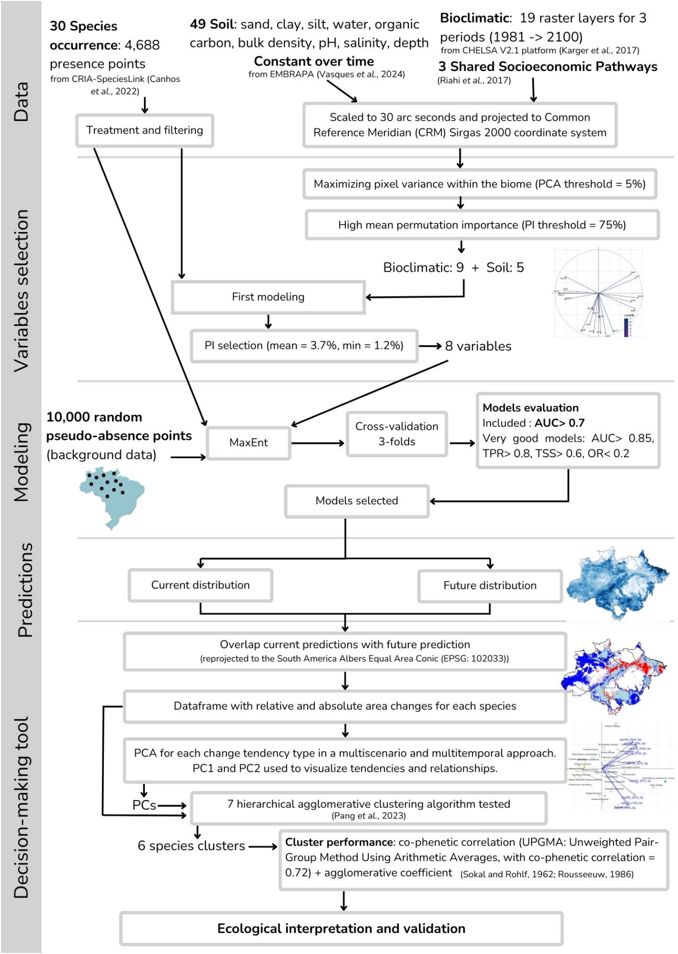

Figure 2: Overview of the framework used for model development. AUC : area under the ROC curve, TPR : True Positive Rate, TSS: True Skill Statistics, OR: Omission Rates, TNR: True Negative Rate (TNR).

stant over 100 years to serve as limiting factors in future species distribution estimations.

Bioclimatic data were high-resolution climatologies for Earth's terrestrial surfaces, with a 30 arc seconds resolution. Nineteen raster layers were acquired for the periods 1981-2010 (influencing current species distribution), 2011-2040, 2041-2070, and 2071-2100. These future periods were analyzed under three different Shared Socioeconomic Pathways (Riahi et al., 2017) (SSP1-2.6, SSP3-7.0, SSP5-8.5 Fig. A1 here considered as "optimistic", "medium" and "pessimistic" scenarios, respectively). Future estimates are based on the GFDL-ESM 4 model Geophysical Fluid Dynamics Laboratory Earth System Model version 4, NOAA National Oceanic and Atmospheric Administration (Dunne et al., 2020).

To minimize spatial distortions, all layers were clipped to the respective biome extent, rescaled to 30 arc seconds when necessary, and reprojected to the CRM (Common Reference Meridian) Sirgas 2000 coordinate system.

2.3.1. Variables selection

The selection of variables for the model followed two steps in order to select those surpassing a 5% contribution threshold (PCA) and to minimize collinearity biases (PI, for more details see Fig. 2) (Smith and Santos, 2020). The 9 bioclimatic and 5 soil Principal Components (PCs) were selected and included in the first model run based on PCA and PI analysis (Fig. A2, A3 and Tab. A3). For the final models, eight variables were chosen based on their PI values (Tab. A4) (Altmann et al., 2010).

2.4. MaxEnt model

MaxEnt (Maximum Entropy) is a machine learning method that predicts species' potential distributions using presence data, background data, and environmental variables and is adaptable to small sample size. It creates species probability distribution as uniform as possible within environmental constraints by overlapping observed presence data with environmental predictors Phillips et al. (2006); Pearson et al. (2007); Elith et al. (2011). Ten thousands random background data points, pseudo-absence points, were generated randomly for areas lacking presence data (Renner et al., 2015; Elith and Leathwick, 2009).

We used 3-fold cross-validation, suitable for small samples, because it performs better than the usually used 5-fold (James et al., 2013; van Tiel et al., 2024; Guisan et al., 2017) (Fig. A4).

The models were evaluated using multiple metrics (Fig. 2).Models evaluation is detailed in Appendix B. Models with an AUC >0.7 were accepted for the binary predictions of species' potential distributions, using the threshold that maximizes the sum of TPR and TNR. Models with TPR <0.6, TSS <0.4, or OR >0.6, but maintaining AUC >0.7, were considered to have fair performance and were used in the analysis.

2.5. Decision-making tools

To serve as practical tools, our models generated binary predicted distribution maps using estimated climatic conditions for present and future periods, highlighting areas of increase, decrease, and stability relative to the current distribution.

2.5.1. Overlap maps principal component analysis

As knowledge on tropical species grows (Reategui-Betancourt et al., 2025), multivariate analyses are increasingly valuable for identifying patterns and synthesizing information (Perelman and Puhl, 2023). Overlap map results were used to calculate relative and absolute area changes per species for each period and scenario. Values were categorized as "Loss" (L), "Gain" (G), "Stability" (S), and "Net Change" (NC increase minus decrease), both as percentages (e.g., Gp = Gain percentage area) and absolutes (e.g., NCa = Net change absolute area). PCA was performed on each subset, with biplots of the first two PCs visualizing species impacts under climate change, showing tendencies and relationships. This method offers restoration practitioners an unified, multi-scenario approach for quickly comparing species tendencies before consulting detailed maps.

2.5.2. Overlap maps cluster analysis

To simplify species selection, groups based on climate change effects on species distribution were identified through Cluster Analysis using PCs from the previous PCA (Fig. 2). Among the tested methods, the UPGMA (Unweighted Pair-Group Method Using Arithmetic Averages) algorithm was selected, as it achieved the highest co-phenetic correlation (0.72). The cluster analysis offers a quick overview of species tendencies by integrating uncertainties for an initial global overview.

3. Results

3.1. Models evaluation

The 30 developed models achieve high performance, as all evaluation metrics are far better than the thresholds (section 2.4, Appendix B). The mean AUC, TPR, TSS, and OR were 0.83 (ś 0.05), 0.78 (ś 0.12), 0.55 (ś 0.10), and 0.22 (ś 0.12), respectively. The species exhibiting the highest model performance was *Chloroleucon acacioides* (AUC = 0.94, TSS = 0.75, OR = 0), while the lowest performance model was for *Trema micranthum* (AUC = 0.75, TSS = 0.68, OR = 0.32).

3.2. Environmental variables

The selected variables (Fig. 3) represent clear limiting factors in species distribution. The variable with the greater average permutation importance (PI) was Bio8 Mean air temperatures of the wettest quarter (31.8%) with the period from 1981 to 2010 presenting a mean max. of 27.5 řC in the Brazilian Amazon.

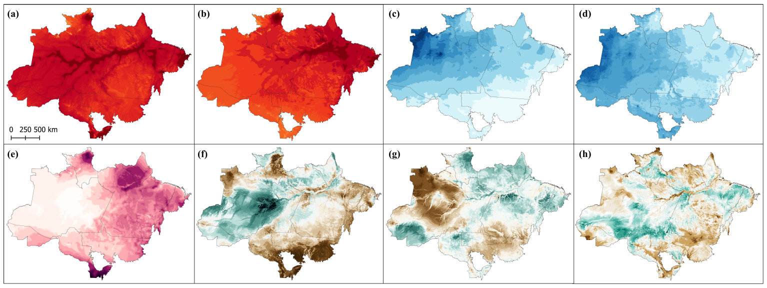

Figure 3: Environmental variables used in the models. (a) Bio8: mean daily air temperatures of the wettest quarter over one year, ranging from 11řC (yellow) to 30řC (dark red); (b) Bio9: mean daily air temperatures of the driest quarter over one year, from 11řC (yellow) to 30řC (dark red); (c) Bio17: mean precipitation of the driest quarter over one year, from 8 (light) to >800 m^3/month (dark); (d) Bio18: mean precipitation of the warmest quarter over one year, from 8 (light) to >800 m^3/month (dark); (e) Bio4: standard deviation of the monthly mean temperatures -seasonality-, from 0.2řC (light pink) to 1.7řC (dark purple). Panels (f), (g), and (h) represent PCA-derived variables summarizing soil property variations: (f) PC1: higher sand content and bulk density (brown) vs. higher water capacity and silt content (blue); (g) PC3: higher clay content (brown) vs. higher organic carbon (blue); (h) PC4: pH lower and less organic carbon (brown) vs higher pH and organic carbon (blue).

3.3. Principal component and cluster analysis

Analyzing the biplots (Fig. 4) provides an overview of species' response tendencies to climatic and soil conditions and highlights the scenarios where these responses are most pronounced. Although these results do not account for geographical coordinates, ecological interactions, or genetics of population, they offer a general perspective on the impacts of climate change on species.

PC1 and PC2 in each PCA accounted for over 95% of the variance among species for each tendency type. Strong correlations were observed between later periods (2070, 2100) under medium and pessimistic scenarios (SSP370, SSP585), as well as between optimistic scenario (SSP126) and 2040 (Fig. A5 for PCA correlation graphs). Thereby, the impact of climate change seems to increase over time, highlighting the need to include scenarios where actions to reduce climate change are unsuccessful.

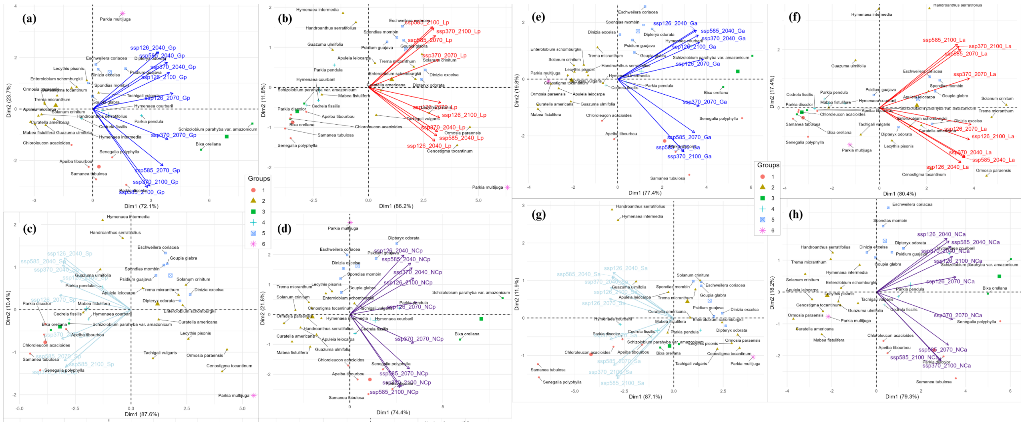

Figure 4: (a)(d): absolute area change biplots, (e)(h) relative change biplots. PC1 is positively correlated with tendency type, except for Stability (S) (c, g). For Gain (G) (a, e), Net Change (NC) (d, h), and S, PC2 is negatively correlated with later periods and high-emission scenarios, but positively correlated for Loss (L) (b, f). In NC (d, h), positive PC1 indicates net gain, while negative PC1 indicates net loss.

First, we'll present species clustering based on the model results. Using PCs 1 and 2 of Gp, Ga, Lp, La, NCp, and NCa as variables, this method integrates a multi-scenario perspective, facilitated by PCAs dimensionality reduction. While requiring careful interpretation, it reduces the risk of relying on a misleading single scenariocrucial given the complexity of climate change and its multifaceted influence on species distribution.

In our case study, six species clusters were identified, with three particularly relevant for restoration in the Brazilian Amazon due to their high success probability across all scenarios (Tab. 1). Cluster 1 and 3 showed the greatest potential for range expansion, comprising seven pioneer species likely to thrive across the Amazon, despite the limited current distribution of two species in cluster 3. Cluster 4 grouped three species with minimal gains or losses, maintaining stable areas and resulting in near-zero net change.

Clusters 2 and 5, which included 14 species, exhibited a general decline in distribution. Higher emission scenarios exacerbated range loss, with cluster 5 showing a risk of extinction for some species by 2100 under the pessimistic scenario. Although *Mabea fistulifera* was classified in cluster 2, 63% of its current distribution is projected to remain stable by 2100. Finally, cluster 6, composed of only *Parkia multijuga*, had a smaller current distribution and tends to lose area or even face extinction.

3.4. Overlap maps

For a more refined species selection tailored to specific regions, overlap maps offered a clear visualization of species distribution dynamics for each scenario and period (Fig. A6). Figure 5 shows the evolution of spacial distribution over time in the two opposite scenarios for two species with opposite conduct: *Samanea tubulosa*, which tended to highly increase its distribution, and *Solanum crinitum*, a species that may be extinct from the Amazon in a pessimistic scenario (SSP585).

The results for 2040 suggest that short-term restoration efforts could benefit from an increase in suitable areas for most species, a trend observed consistently across all periods under a positive climate change scenario. This observation is further supported by the variable correlations identified in the

Table 1: Species clusters description

Clusters	**Cluster description**	**Species**
1	Large stable area and great increase in distribution	*Apeiba tibourbou*
		Chloroleucon aracioides
		Parkia discolor
		Senegalia polyphylla
		Samanea tubulosa
2	Great decrease in area	*Apuleia leiocarpa*
		Curatella americana
		Guazuma ulmifolia
		Mabea fistulifera
		Enterolobium schomburgkii
		Lecythis pisonis
		Cenostigma tocantinum
		Solanum crinitum
		Ormosia paraensis
		Tachigali vulgaris
		Trema micranthum
		Handroanthus serratifolius
		Hymenaea intermedia
3	Extreme increase and small current distribution	*Bixa orellana*
		Schizolobium parahyba var. am.

Clusters	Cluster description	Species
4	Gains and losses, with considerable stable area	*Cedrela fissilis* *Hymeneae courbaril* *Parkia pendula*
5	Possible extinction in Amazon in 2100 under pessimistic scenario (SSP5-85)	*Eschweilera coriacea* *Dinizia excelsa* *Dipteryx odorata* *Goupia glabra* *Psidium guajava* *Spondias mombin*
6	Small current distribution, possible extinction in Amazon under mitigate and pessmistic scenario	*Parkia multijuga*

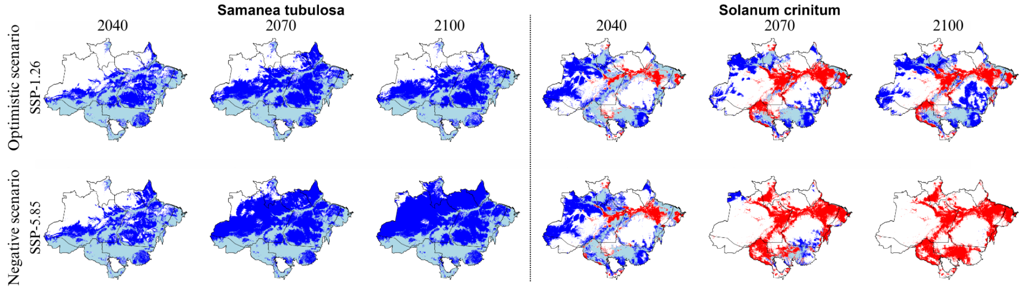

Figure 5: Overlap maps of *S. tubulosa* and *S. crinitum* in 2 climate change scenarios tested (with optimistic prediction above and with pessimist prediction at the bottom) for each prediction time. Light blue: stable distribution area, blue: expansion of distribution area, red: decrease in distribution area. Estimated current distribution is visualized by combining light blue and red areas.

PCA.

For the 2070 medium scenario (SSP370), the early-successional (ES) species predicted to experience the greatest percentage loss of its current distribution is *P. multijuga* (94%). In terms of absolute area, *S. crinitum* faces the largest loss (890,480 kmš). Conversely, *S. parahyba var. amazonicum* may experience the greatest relative expansion, increasing its area by 394.2%, while *S. polyphylla* shows the largest absolute increase, totaling 2,361,756 kmš. Under the negative scenario for 2070, *P. multijuga* continues to show the highest loss percentage (95%), and *S. parahyba var. amazonicum* maintains the greatest gain percentage (305%). In absolute terms, *H. serratifolius* faces the greatest losses (1,085,974 kmš), whereas *S. tubulosa* exhibits the highest gains (1,368,556 kmš).

For 2100, the late-successional (LS) species predicted to have the highest percentage losses under the medium scenario is *E. coriacea* (98.5%), and under the pessimistic scenario is *D. odorata* (99.5%). In terms of absolute area, *H. intermedia* may face the greatest losses under both medium (204,753 kmš) and pessimistic scenario (1,104,860 kmš). On the other hand, *P. pendula* may have the greatest relative gain (125%), and *H. courbaril* the largest absolute area increase (723,417 kmš) in the medium scenario. Under pessimistic, *H. courbaril* presents the greatest relative (69%) and absolute gains (786,303 kmš).

Although individual maps are used for species selection, analyzing the combined distribution maps of all species reveals significant trends, contributing to macroecological studies. The current and future predictions under a negative scenario highlight areas where the probability of persistence of the selected species is high and where only few or none of them may survive (Fig. 6). In our application, persistence probability is highest in the eastern Brazilian Amazon, around the Amazon River delta, and lowest in warmer, highly seasonal regions.

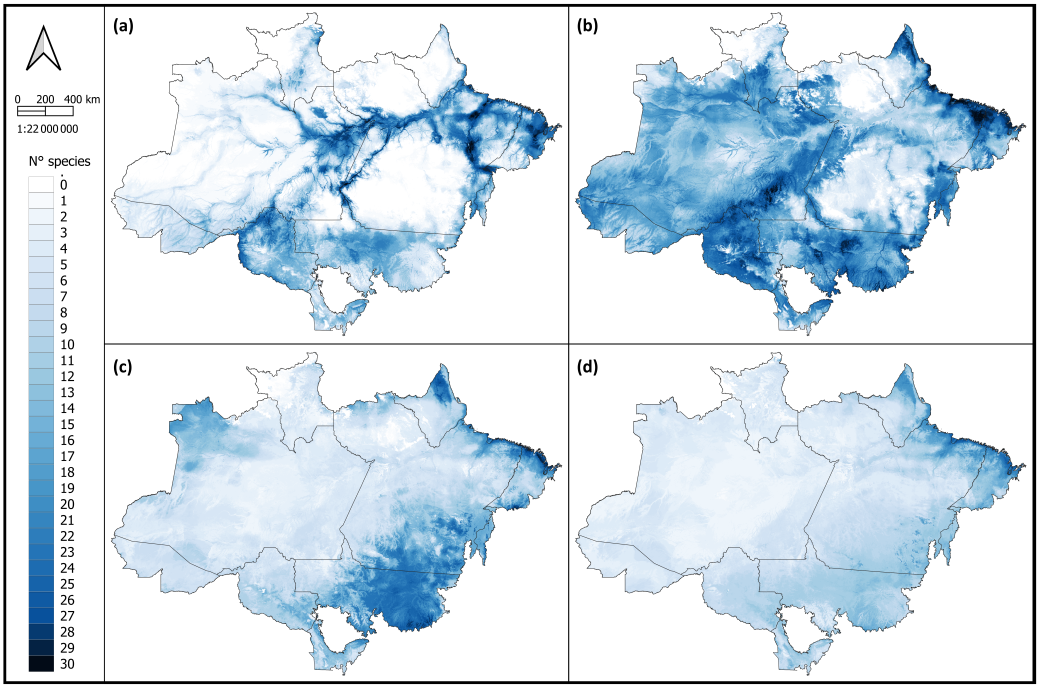

Figure 6: Compilation of 30 selected species distribution in the pessimist scenario (SSP5-8.5) of climate change varying in time. Darker color means more different species are predicted to be present, and white means no species are expected to be present. (a) The present distribution of species, (b) prediction for 2040, (c) prediction for 2070, and (d) prediction for 2100.

Analyzing combined distribution maps highlights critical regions for conservation, like warmer and highly seasonal regions of the Amazon, where targeted efforts could maximize species persistence under varying climate scenarios, especially in areas predicted to face severe biodiversity loss.

4. Discussion

Climate change impacts species unevenly, with some unable to adapt and facing potential extinction. Restoration strategies that disregard future climate scenarios risk failure by contributing to biodiversity loss, facilitating the spread of invasive species, and intensifying climate change impacts, ultimately perpetuating a harmful feedback loop.

4.1. Distribution dynamic

Model projections across three climate scenarios reveal varying species distribution patterns. Initially, even under pessimistic scenarios, all species exhibit greater area expansions than losses; however, most experience significant declines in later years. This suggests an initial resilience that gives way to vulnerability as climate change intensifies. Zuidema et al. (2020) note that tropical species may initially increase their drought resistance with elevated atmospheric CO_2 until a temperature threshold. Then, CO_2 may increase drought sensitivity (Chen et al., 2024). By 2070, species distributions show a clear shift away from drought-prone regions of the Amazon.

In montane forests, such as the Andes and Central America, most species are shifting upslope toward cooler environments (Fadrique et al., 2018; Feeley et al., 2013). While lowland communities tend to remain relatively stable under warming conditions (Freeman et al., 2018), some lowland-submontane species are migrating upslope (Feeley, 2012). In the subtropical Atlantic Forest, unique patterns emerge, including downward migrations driven by biotic interactions (Bergamin et al., 2024). In the Amazon lowlands, drought-tolerant genera are increasing as wet-affiliated taxa decline, although vegetation responses are lagging behind the pace of climate change (Esquivel-Muelbert et al., 2019).

Past climate changes caused species to shift altitudes in tropical forests, allowing time for migration (Bush et al., 2004). However, the long generation times of tropical trees delay their responses to current rapid warming, increasing the risk of mass extinctions (Fadrique et al., 2018; Esquivel-Muelbert et al., 2019). This observation underscores the need for assisted migration experiments in restoration and enrichment projects to support further research (Garcias-Morales et al., 2023).

Maps indicate that many studied species, currently found in Dense Ombrophilous Forest, may shift to Evergreen Seasonal Forest regions by 20412070 under warmer scenarios. Despite a seasonal climate, these regions retain high soil moisture, enabling deep-rooted trees to access water during dry periods, avoid water stress, and retain leaves year-round (Ivanauskas et al., 2008).

By 2100, many species may shift to the eastern Amazon, offering higher hydraulic safety margins (Tavares et al., 2023), or to coastal zones under high-emission scenarios, where the GFDL-ESM 4 model projects lower temperature seasonality. Historical migrations during the Last Glacial Maximum similarly favored coastal areas with reduced continentality, suggesting these regions may remain suitable for rainforest species under extreme climate shifts (Pinaya et al., 2024).

Finally, the contraction and expansion of rainforests, dry seasonal forests, and savannas, along with their floristic changes, are key aspects of Neotropical natural history (Pennington et al., 2006). Paleoecology studies reveal potential ecosystem shifts, such as the dominance of drier-affiliated taxa during Holocene dry conditions over current interfluvial wetlands (Spater et al., 2024). These floristic changes may drive interspecific competition in more suitable environments, creating biotic barriers to projected distributions (Webb et al., 2008).

The complexity of species suitability extends beyond current biome boundaries and the abiotic factors considered in this study. Transition zones, such as those between the Amazon and Cerrado biomes, are highly dynamic ecosystems shaped by factors like fire and phosphorus limitation (Dionizio et al., 2018). Climate change and large-scale deforestation are projected to amplify fire disturbances and drought events in the Amazon (Drüke et al., 2023; Bottino et al., 2024). For instance, extreme droughts, once rare, could occur every 1015 years with a 2řC increase in global temperatures (Clarke et al., 2024). Therefore, drought and fires are critical factors to consider in restoration projects. Otherwise, these projects may exacerbate regional water cycle disruptions.

To build climate-resilient restoration strategies, it is essential to consider the intricate impacts of climate change on species distributions, increase species diversity in restoration planning, and prioritize species-specific suitability assessments under changing conditions, supported by field experiments to refine projections.

4.2. Species functional ecology

Reviewing species' biological characteristics in relation to our results is essential for choosing the appropriate species mix for successful restoration efforts.

Comparing models results with ecological traits (Tabs. A1, A5) allowed hypotheses on cluster traits explaining species distribution changes. However, some species (*C. americana, E. schomburgkii, H. courbaril, T. micranthum*) showed variability in reported leaf deciduousness classes, underscoring the need for further studies to characterize ecological traits across populations under diverse environmental conditions. Moreover, we identified ecological evidence within each species cluster that explains distribution shifts and informs the selection of optimal species for long-term restoration in the Amazon.

Species in cluster 1 demonstrated significant expansion of suitable climatic areas while maintaining large stable regions. All are known as pioneers, following a deciduous leaf phenology strategy except *P. discolor* (Tab. A5). Deciduousness is linked to dry tolerance (de Oliveira et al., 2024), hydraulic safety (Oliveira et al., 2021), and CO_2 storage capacity (Rodrigues et al., 2023), while pioneer species exhibit high plasticity in functional traits under environmental changes (Wittemann et al., 2024; Manrique-Ascencio et al., 2022) and strong dispersal and establishment rates that support migration (Laurance et al., 1998). *P. discolor* and *S. tubulosa* stand out in literature for their high wood density (Tab. A5), which correlates negatively with xylem cavitation, enhancing drought resistance (Serra-Maluquer et al., 2022; Marchand, 2022). Their predicted success likely stems from two key factors: pioneer traits enabling the colonization of suitable environments and high wood density and/or a deciduous leaf strategy that improves drought tolerance an important advantage under increasing Amazon drought conditions.

Cluster 3 includes two pioneer species with low wood density, *B. orellana* and *S. parahyba var. amazonicum*, the latter showing significant vertical wood density variations (Romero et al., 2024). Both species, known for their rapid growth (Rosa, 2006; Lorenzi, 2009), currently have limited distributions but are projected to experience substantial expansion in the future. The Amazon-endemic *S. parahyba var. amazonicum* may increase below-ground biomass under water deficit conditions, supporting its future distribution (Tourne et al., 2016). *B. orellana*, with a broad Neotropical range, shows a net gain in suitable restoration areas but may face limitations due to high Amazonian temperatures (Lorençone et al., 2024).

Cluster 4 comprises secondary successional species that, despite regional losses across all scenarios, retained substantial stable areas and expanded into colder regions. These species tolerate various soil conditions, including poor soils, and employ drought survival strategies (Rodríguez-Ramírez et al., 2022; Grogan and Schulze, 2012). For instance, *C. fissilis* mitigates drought by shedding leaves early in the dry season, though drought reduces its growth and wood density (Rodriguez et al., 2023; Mendivelso et al., 2016). Understanding its interpopulation variability is vital, as old-growth *C. fissilis* forests thrive in drought-prone areas (Pereira et al., 2018). Similarly, *H. courbaril* develops superficial roots and tolerates drought through reduced photosynthesis, leaf loss, and high wood density (Da Silva-Pinheiro et al., 2016; Luz et al., 2023).

In conclusion, functional ecology plays a crucial role in identifying species with diverse potential for tropical forest restoration. Among the selected species, we identified three climate-relevant patterns: (1) species with traits that enhance water security, (2) fast-growing species with substantial future area expansion, vital for rapid land cover recovery, and (3) secondary species adapted to poor soils, maintaining stable areas while ecologically complementing the other groups. These findings highlight the importance of selecting species with traits that foster plasticity, resilience, resistance, and adaptation to extreme climate events, ensuring the long-term success of restoration efforts.

4.3. Model and prediction improvements

This study demonstrates the value of statistical modeling as a decision-support tool for climate-resilient restoration, providing the first distribution estimates for 30 species in the Brazilian Amazon under various climate scenarios. While our approach advances evidence-based species selection, opportunities remain to refine accuracy and applicability by addressing challenges such as sampling biases, predictor selection, model validation, and generalizability (Vaughan and Ormerod, 2005; Gelfand, 2020).

Focusing on the Amazon biome, our models minimize biases by limiting analyses to regional populations, although broader ranges for non-endemic species and migration dynamics could enhance future applications. Addressing geographical biases in sampling, such as overrepresentation of accessible areas, remains critical. Although target-group background data is a promising solution (Phillips et al., 2017), we used a random background approach to ensure scalability across species.

Improving generalizability requires more robust validation. While k-fold cross-validation reduces overfitting, limited presence data (47 to 307 records per species) constrained the use of independent test sets, which are essential for validating performance under varied conditions. Tailoring predictors to individual species and incorporating non-linear features like quadratic terms and hinge functions could further enhance accuracy (Phillips et al., 2017).

Climatic models also influence predictions. Future studies could improve robustness by comparing multiple models for each variable rather than relying on a single dataset (Rahman and Pekkat, 2024). Additionally, incorporating biotic interactions through Joint Species Distribution Models (JSDM) would enable better species combinations for restoration (Pollock et al., 2014).

Despite these challenges, the models achieved strong evaluation metrics, highlighting key trends in species behavior under climate change. These insights emphasize the need for continued collaboration between researchers and practitioners to refine tools and techniques, advancing tropical forest restoration in increasingly dynamic and degraded landscapes.

5. Conclusion

This study underscores the complexity of climate change impacts on species distributions and highlights the critical need for adaptive and evidence-based ecological restoration strategies. By combining modeling efforts with functional ecological analyses, we identified three distinct species clusters with unique restoration advantages: drought-resilient pioneers, fast-growing species for rapid land cover recovery, and secondary species adapted to poor soils and adverse conditions. These findings demonstrate the importance of incorporating ecological traits into species selection to enhance restoration outcomes and build climate-resilient forests. By fostering diversity across ecological groups, practitioners can bolster forest resilience to future climate extremes, offering a strategic framework for sustainable restoration. We emphasize the importance of collaboration between scientists and practitioners to refine decision-support tools that address the complex interplay of ecological and climatic factors, ultimately working to preserve and restore these increasingly vulnerable tropical ecosystems.

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8. Authors contribution

- Conceived the ideas and concept: EC, TOGT, RMA
- Data curation and formal analysis: TOGT
- Writing - original draft: TOGT, MV
- Writing - review & editing: MV, TOGT, RMA, LM, EC
- Supervision: EC

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