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Original Article

Modeling the current and projected distribution of Brazilian peppertree *Schinus terebinthifolia* Raddi (Anacardiaceae) in the Americas

Modelando a distribuição atual e projetada da pimenta brasileira *Schinus terebinthifolia* Raddi (Anacardiaceae) nas Américas

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Abstract
Global biodiversity is under substantial threat due to biological invasions, a problem exacerbated by climate change. Such invasions have detrimental effects on the environment, economy, and human health, resulting in significant financial burdens. Recently, understanding these challenges has become a highlighted priority within the scientific community. This study focuses on the evaluation of *Schinus terebinthifolia*, native to South America, and its invasive spread into North and Central America, which has resulted in wide distribution and considerable impact. The primary objectives of this study include analyzing the potential distribution of the species under current and future climate scenarios, identifying the areas where its climatic niche is changing. Data collection encompassed a vast dataset of over 30,000 occurrence records of this species, from the following databases: (1) The Global Biodiversity Information Facility provided 22,163 records (GBIF), (2) The virtual Herbarium Reflora contributed 1,438 records, and NeoTropTree made available 6,591 records. Following a rigorous filtering process, 992 occurrences were considered for modeling. In this process, we utilized climate data and climate projections, employing various algorithms, with an emphasis on the consensus model methodology. The research results reveal a clear trend of reduced habitat suitability for *S. terebinthifolia*, especially under scenarios of high global warming. This accentuates the urgency of implementing emission control measures and mitigation strategies. Additionally, the study underscores the crucial importance of continuous monitoring, as well as actions for controlling and restoring affected ecosystems. The significant role played by *S. terebinthifolia* in both its native and invaded areas highlights the need for comprehensive management approaches. In the face of climate change and biodiversity threats, this study provides insightful observations on the dynamics of biological invasions. Success in addressing these issues relies on close cooperation between the scientific community, policymakers, land managers, and local communities. This collaboration is essential for guiding and conducting conservation and biodiversity management efforts in an ever-evolving world.

Keywords: biodiversity, biological invasions, climate change, conservation, invasive species.

Resumo
A biodiversidade global encontra-se sob ameaça substancial devido às invasões biológicas, um problema agravado pelas mudanças climáticas. Tais invasões têm efeitos prejudiciais sobre o meio ambiente, economia e saúde humana, resultando em encargos financeiros significativos. Recentemente, a compreensão desses desafios se tornou prioridade destacada na comunidade científica. Este estudo se concentra na avaliação do *Schinus terebinthifolia*, nativa da América do Sul, e sua disseminação invasiva para a América do Norte e Central, o que resultou em ampla distribuição e impacto considerável. Os principais objetivos deste estudo consistem em analisar a distribuição potencial da espécie sob cenários climáticos atuais e futuros, identificando as áreas onde seu nicho climático está se alterando. A coleta abrangeu um vasto conjunto de mais de 30.000 registros de ocorrências da espécie, nas bases de bados (1) *Global Biodiversity Information Facility* com 22.163 registros (GBIF), (2) O Herbário virtual Reflora com 1.438 registros e o NeoTropTree com 6.591 registros e após um processo de filtragem, 992 ocorrências foram consideradas para modelagem. Nesse processo, empregamos dados climáticos e projeções climáticas, recorrendo a diversos algoritmos, com destaque para a metodologia do modelo de consenso. Os resultados da pesquisa revelam uma clara tendência de redução na adequação do habitat da *S. terebinthifolia,* especialmente sob cenários de elevado

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aquecimento global. Isso acentua a urgência da implementação de medidas de controle de emissões e estratégias de mitigação. Adicionalmente, o estudo ressalta a importância crucial da vigilância contínua, bem como das ações de controle e restauração de ecossistemas afetados. O papel relevante desempenhado por *S. terebinthifolia* em suas áreas nativas e invadidas chama a atenção para a necessidade de adotar abordagens de manejo abrangentes. Diante do cenário de mudanças climáticas e das ameaças à biodiversidade, este estudo contribui com perspicazes observações sobre a dinâmica das invasões biológicas. O sucesso na abordagem dessas questões depende de uma cooperação estreita entre a comunidade científica, legisladores, gestores de terras e as comunidades locais. Essa colaboração é essencial para orientar e conduzir os esforços de conservação e gestão da biodiversidade em um mundo em constante evolução.

Palavras-chave: biodiversidade, invasão biológica, mudanças climáticas, conservação, espécies invasoras.

1. Introduction

Global biodiversity faces threats from biological invasions exacerbated by climate change. These invasions harm the environment, economy, and human health (Early et al., 2016). Over the past five decades, 60% of global extinctions are attributed to invasive species, resulting in an estimated annual cost of $423 billion (Roy et al., 2023). While the economic benefits of ecosystem services in the Americas total $24.3 billion, human activity and global climate change continue to drive the introduction and spread of non-native species (Andersen et al., 2004), with potential synergistic effects resulting in different regional patterns (Bai et al., 2013; Hulme, 2021).

In general, several studies have projected future trends in habitat suitability and range expansion of destructive invasive species under climate change (Wang et al., 2017; Ahmad et al., 2019; Cruz et al., 2023). By 2050, a 36% increase in the number of exotic invasive species across all taxa is expected (Seebens et al., 2021). However, international legislation aimed at preventing or controlling these invasions does not yet provide effective responses, creating a disparity between the threats posed by invasive exotic species and often poorly quantified response capabilities (Early et al., 2016).

The required period to control these invasions is largely determined by prior taxon understanding and the categorization assessment of these species as non-endemic or invasive (see Shackleton et al., 2019). Moreover, it is crucial to have knowledge of areas with climatic potential for the occurrence of these species. This emphasize the importance of identifying areas that may be affected to avoid the exclusion of native species and mitigate the impact on the ecological dynamics of these environments.

Among the various species of exotic invasive plants worldwide, *Schinus terebinthifolia* Raddi is found in eight regions, including North America, the Middle East, Pacific islands, Australia, Africa, and the Neotropical region (Richardson and Rejmánek, 2011). Native from Argentina (east and northeast), Paraguay (east), Uruguay and Brazil (Carvalho, 2003) this invasive tree stands out among the 191 plants related to food production in Brazil due to its use as a spice, wide distribution, and high annual flowering performance (Neves et al., 2016). When introduced into new regions, *S. terebinthifolia* colonizes disturbed environments such as pastures, open fields, road margins, and forest clearings, leading to reduced diversity of native plant species due to resource competition.

Although widely distributed in the Southeast and Northeast regions of Brazil, research on *S. terebinthifolia* has primarily focused on its floral biology, investigating the reproductive and vegetative phenology of the plant, which includes detailed analyses of seasonal patterns of flowering, fruiting, and vegetative growth (Césario and Gaglianone, 2008; Milani et al., 2013). Additionally, ethnobotany has also been a target of investigation, given the importance of the plant's traditional use for different purposes, including medicinal and culinary properties (Santos et al., 2009; Nocchi et al., 2022). However, the ecology of the plant also sparks significant interest among researchers, who explore its interaction with the surrounding environment through secondary metabolites (Pilatti et al., 2019), as well as its preference for specific types of soil and its adaptation to different water conditions (Santos et al., 2023). Furthermore, the commercialization of *S. terebinthifolia* is a relevant aspect to be considered, especially due to the growing interest in phytotherapy and the natural products industry, which has driven the demand for medicinal plants like this one (Nocchi et al., 2022), as well as in gastronomy (Camillo, 2018; Nocchi et al., 2022). However, the scarcity of studies on distribution modeling and the impacts of climate change on this species remain a limitation. Therefore, the aim of this study is to address the following research questions: (1) What is the potential distribution of *S. terebinthifolia* under current and future climate scenarios? and (2) In which areas of the Neotropical region is this species experiencing displacement in its climatic niche between native and introduced regions?

2. Material and Methods

2.1. Occurrence records and data cleaning

We obtained 30,192 occurrence records of *S. terebinthifolia* from three primary sources: (1) The Global Biodiversity Information Facility provided 22,163 records (GBIF, 2023); (2) Herbário virtual Reflora contributed 1,438 records (JBRJ, 2023); (3) NeoTropTree provided 6,591 records (NeoTropTree, 2023). These records underwent rigorous manual verification. Duplicate records and those with questionable identification were removed. Only records within forest fragments and those with geographic coordinates compatible with the resolution used in our models (5 arc-minutes) were considered. After this manual filtering, 1,009 occurrences of *S. terebinthifolia* remained (Figure 1).

We employed the CELLSIZE occurrence thinning method, as described by Fourcade et al. (2014), to counteract sampling bias. From the last step filtering

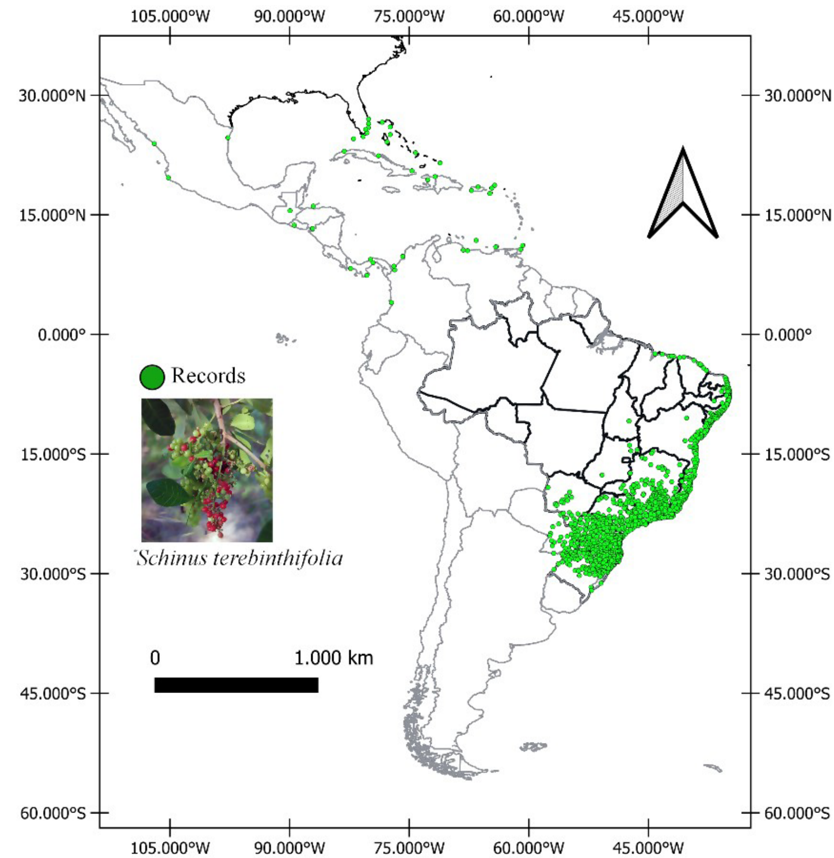

Figure 1. Compilation of known occurrences of *Schinus terebinthifolia* from America.

1,009 occurrences, the number was further reduced to 992 filtered occurrences. This method operates by randomly selecting a single occurrence within each grid cell, which is sized at twice the resolution of the associated environmental variables. For our study, the resolution was set at 5 arc-minutes, equivalent to approximately 9.0 km at the equator (Fourcade et al., 2014; Velazco et al., 2019).

2.2. Environmental data

Climate factors are primary determinants of a species' overall distribution (Guisan and Thuiller, 2005). We incorporated 19 bioclimatic macroscale variables from WorldClim 2.1 (WorldClim, 2023) that reflect both current and projected future conditions. All spatial data were standardized to a 5 arc-min resolution (Fick and Hijmans, 2017). At large scales, abiotic conditions are pivotal, dictating the size and shape of species distributions on continental or regional scales. Such scales also minimize the effects of biological interactions (Hortal et al., 2010). Additionally, this resolution diminishes the spatial autocorrelation inherent in the original variables (Pimenta et al., 2022).

Using the MIROC6 model from the General Circulation Models (CMIP6), we projected geographical distributions under two scenarios: (1) SSP2-4.5 (moderate, with temperature rise of ~2.1-4.3 °C and 26.84 CO_2 gigatons by 2100) and (2) SSP5-8.5 (business-as-usual, with a temperature rise of ~3.8-7.4 °C and 129.85 CO_2 gigatons by 2100). These scenarios cover four periods from 2021 to 2100, allowing for tracking niche shifts over time. To address concerns of multicollinearity and reduce the number of variables, we created a set of non-redundant variables, excluding predictors with strong correlations using the Variance Inflation Factor (VIF >10) (Table 1) (Marquaridt, 1970).

2.3. Ecological niche models

The "M area" (as defined by Soberón and Peterson, 2005) was delineated using a BUFFER area designed for model fitting. This BUFFER was defined by a 300 km radius around the occurrence data (Barve et al., 2011). This area is essential as it includes the spectrum of environmental conditions under which the species has been known or is anticipated to exist throughout its evolutionary history (Soberon and Peterson, 2005). Pseudoabsences and background data were set at a 1:1 ratio to the presence data and were supplemented with 10,000 random points. These points were primarily focused on predicted low suitability zones as determined by the Bioclim model (Engler et al., 2004).

Table 1. Classification of bioclimatic predictors based on the Variance Inflation Factor (VIF) for niche characterization of *S. terebinthifolia*.

Predictor	Description	VIF	Status
BIO1	Annual Mean Temperature	>10	Not Used
BIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))	>10	Not Used
BIO3	Isothermality (BIO2/BIO7) (×100)	>10	Not Used
BIO4	Temperature Seasonality (standard deviation ×100)	>10	Not Used
BIO5	Max Temperature of Warmest Month	<10	Used
BIO6	Min Temperature of Coldest Month	<10	Used
BIO7	Temperature Annual Range (BIO5-BIO6)	<10	Used
BIO8	Mean Temperature of Wettest Quarter	>10	Not Used
BIO9	Mean Temperature of Driest Quarter	>10	Not Used
BIO10	Mean Temperature of Warmest Quarter	<10	Used
BIO11	Mean Temperature of Coldest Quarter	<10	Used
BIO12	Annual Precipitation	<10	Used
BIO13	Precipitation of Wettest Month	<10	Used
BIO14	Precipitation of Driest Month	>10	Not Used
BIO15	Precipitation Seasonality (Coefficient of Variation)	>10	Not Used
BIO16	Precipitation of Wettest Quarter	>10	Not Used
BIO17	Precipitation of Driest Quarter	>10	Not Used
BIO18	Precipitation of Warmest Quarter	<10	Used
BIO19	Precipitation of Coldest Quarter	<10	Used

Multiple algorithms, such as maximum entropy, MXS, MXD, SVM, and GLM, were used for potential distribution area predictions. The consensus model averaged the top algorithms' predictions, incorporating only those with above-average TSS (Allouche et al., 2006; Velazco et al., 2019). This model, further refined by the Jaccard metric, provided a reliable species distribution estimate, benefiting from ensemble modeling's enhanced accuracy (Araújo and New, 2007; Norberg et al., 2019; Thuiller et al., 2019).

Our models underwent k-fold cross-validation with five folds (Fielding and Bell, 1997). We assessed performance using AUC, TSS, and the Jaccard index (Leroy et al., 2018), introducing the latter to offset potential biases. A score over 0.7 in any metric indicated satisfactory performance.

The entire modeling procedure, including adjustments, was executed using the ENMTML R package (Andrade et al., 2020). Finally, distribution maps were generated with QGIS version 3.22.14.

3. Results

In determining the niche characterization of *S. terebinthifolia*, various bioclimatic predictors were evaluated based on the Variance Inflation Factor (VIF). As shown in Table 1, out of the 19 bioclimatic variables considered, nine predictors were selected for inclusion in the model, while the others were excluded due to high collinearity (VIF > 10). Specifically, the model utilized predictors capturing temperature extremes and variations, such as the "Max Temperature of Warmest Month" and the "Temperature Annual Range". Additionally, the predictors describing annual precipitation patterns and those of specific quarters were also incorporated. These selections ensure a more robust and accurate model by reducing multicollinearity, thus improving the reliability of the projected niche characterization for *S. terebinthifolia*.

The evaluation of modeling algorithms for *S. terebinthifolia* highlighted the robustness of the consensus model. While individual algorithms like SVM exhibit commendable accuracy, the consensus model consistently outperforms in terms of precision across the evaluated metrics. Specifically, the Area Under the Curve (AUC) values for the consensus model suggest exemplary discrimination capabilities. While the GLM and MXD models yield proficient results, MXS lags slightly, especially in its TSS and Jaccard scores (Table 2).

3.1. Predicted current and future potential distributions

The Figure 2 offers an incisive look at the evolving environmental suitability patterns of the *S. terebinthifolia* from its current to projections leading up to the year 2100. The current potential distribution of *S. terebinthifolia* exhibits a widespread environmental suitability across the Latin American continent, as illustrated by the broader spectrum of suitability evident in the map.

As we progress into future projections, there's a clear and undeniable contraction of habitat suitability

Table 2. Algorithms and consensus model performance for *Schinus terebinthifolia*. Generalized Linear Models (GLM); Maximum Entropy Default (MXD); Maximum Entropy Simple (MXS); Support Vector Machine (SVM); Area Under the Curve (AUC); True Skill Statistic (TSS).

Algorithm	AUC (±SD)	TSS (±SD)	Jaccard (±SD)
GLM	0.987 ± 0.004	0.932 ± 0.017	0.933 ± 0.016
MXD	0.979 ± 0.008	0.910 ± 0.020	0.913 ± 0.019
MXS	0.959 ± 0.005	0.789 ± 0.019	0.816 ± 0.014
SVM	0.993 ± 0.002	0.956 ± 0.003	0.955 ± 0.003
Consensus model	0.991 ± 0.002	0.956 ± 0.010	0.956 ± 0.010

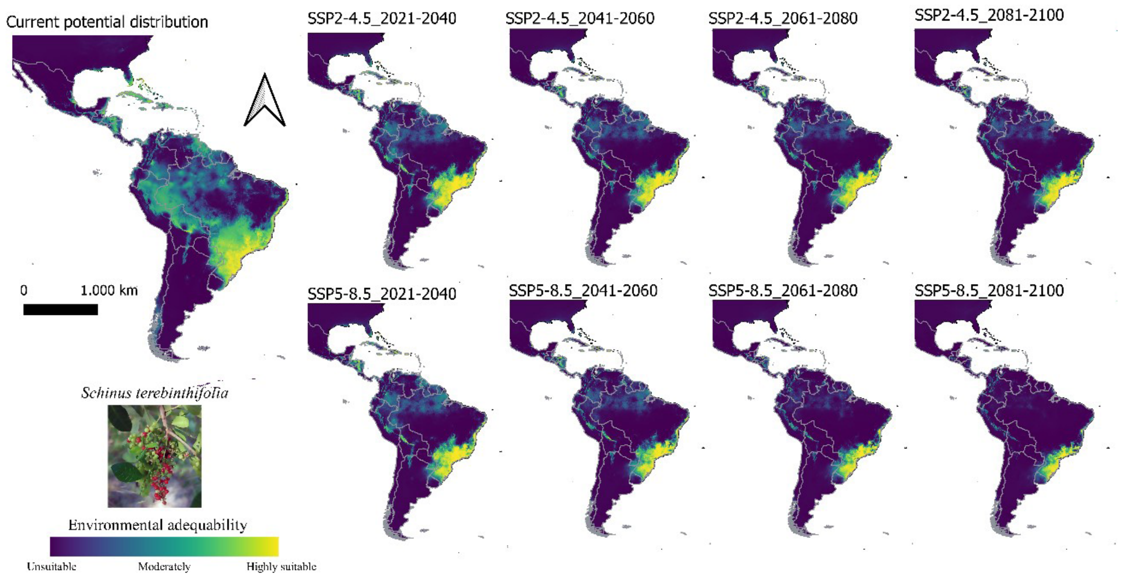

Figure 2. Predicted Distribution of *S. terebinthifolia* from Current Patterns to Projections for 2100. The map showcases current and future habitat suitability under two climate scenarios (SSP2-4.5 & SSP5-8.5) across four-time intervals.

for *S. terebinthifolia*. Under both the SSP2-4.5 and SSP5-8.5 climate scenarios, a decrease in environmental adequability for this species is noticeable, but the contraction is notably more pronounced under the SSP5-8.5 scenario. This more aggressive model, which factors in higher greenhouse gas emissions, showcases a more significant reduction in suitable habitats for the species.

By the end of the century, specifically leading up to 2100, the regions exhibiting the highest habitat suitability are largely concentrated in the south and southeast regions of Brazil. This points to a stark change from its current widespread distribution. Moreover, the areas of the Atlantic Forest along the Brazilian coast also stand out as significant strongholds for the species' habitat suitability.

Another notable observation is that under the high-emission scenario, SSP5-8.5, the species' suitable habitats face a more drastic reduction compared to the moderate scenario. The implications of this could be manifold, but what stands out is the urgency and importance of emission control and mitigation strategies.

4. Discussion

Invasive species, such as *S. terebinthifolia*, are noteworthy for their remarkable ability to adapt to various types of vegetation, enabling them to spread by increasing seed and biomass productivity (Hogg et al., 2020). Modeling studies play a pivotal role in understanding biological invasions and their impact on climate change. These invasions have proven to be responsible for a significant portion of global extinctions, resulting in substantial economic costs (Roy et al., 2023). This underline the necessity of addressing these threats, especially in the context of climate change, which can exacerbate the issue further.

Our findings indicate a trend of reduced habitat suitability for *S. terebinthifolia* under projected climate scenarios (SSP2-4.5 and SSP5-8.5), with this contraction being particularly pronounced in the high-emission scenario (SSP5-8.5). Despite anticipated reductions in environmental suitability under future scenarios, current conditions in South America still reveal large areas of potential habitat where regions like the Andes (Bolivia, Peru, Guyana, Suriname) have no recorded invasions but possess environmental suitability. *S. terebinthifolia* is already present in Mexico, Guatemala, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Brazil, Paraguay, and the Caribbean islands. The moderate emission scenario suggests that the areas in these countries will remain suitable, potentially allowing the species to become well-established by 2100. However, under the high-emission scenario, suitable environmental suitability areas are expected to decrease progressively. Nevertheless, even under the high-emission scenario, models project that suitable areas are expected to remain in Brazil, Paraguay, and Uruguay, with only narrow corridors of suitable habitats persisting in the Andean regions of Bolivia, Peru, and Colombia, as well as smaller patches in Venezuela, certain Caribbean islands, and parts of Central America by 2100. This discovery highlights the invasive species' potential to increase competition for native species both non-native regions and areas without previous records, potentially further destabilize ecosystems, as discussed in previous studies (see Ahmad et al., 2019; Hogg et al., 2020; Alencar et al., 2022, 2024; Aguiar et al., 2023). Therefore, the need to implement control strategies, as previously suggested (Canavan et al., 2021), and applied (see Bowers et al., 2022), becomes increasingly essential. Furthermore, the observation that areas of higher suitability are concentrated in the southern and southeastern regions of Brazil suggests the possibility of distribution pattern changes with regional-scale impacts.

However, it is of utmost importance to highlight that the reduction in habitat suitability in a high-emission scenario brings forth significant challenges, with a substantial increase in the number of invasive species expected by the year 2050 (Seebens et al., 2021). This reinforces the urgency of adopting measures to control greenhouse gas emissions and implement mitigation strategies, as emphasized by Cruz et al. (2023). Nevertheless, it is essential to consider that this study focused on a single species, and the impacts of climate change on biological invasions can vary considerably among different taxonomic groups.

The finding that the consensus model outperforms other algorithms in predicting distribution areas is encouraging, as it suggests a higher accuracy in projecting the impacts of climate change. Models can play a crucial role in contributing to effective management both in and around conservation units and in controlling the introduction of invasive exotic species with notable natural dispersal capacity (Wang et al., 2017). These results highlight challenges that require immediate action, such as the control of greenhouse gas emissions and the development of long-term management strategies (Hulme, 2021; Cruz et al., 2023; Roy et al., 2023). Furthermore, they underscore the ongoing importance of research and monitoring to assess the effects of climate change on biodiversity and biological invasions (Seebens et al., 2021). This continuous monitoring is fundamental to inform decisions and the development of effective management strategies.

Brazilian pepper is valued in some regions for its medicinal properties and culinary use (Ronchi et al., 2022). However, upon introduction into novel ecosystems, such as Florida and South Africa, this species exhibits a pronounced capacity for engendering detrimental effects impacts (see Hogg et al., 2020; Canavan et al., 2021). The adverse impacts on native fauna are extensively recorded, positioning invasive species as the second most significant driver of contemporary extinctions, subsequent only to habitat destruction (Bellard et al., 2016).

The negative impact of *S. terebinthifolia* on invaded ecosystems outside South America is remarkable, especially due to its ability to colonize disturbed habitats, such as pastures, road margins, forest clearings, and mangroves (Enloe et al., 2021; Canavan et al., 2021). This invasion results in resource competition, harming biodiversity and leading to a decline in native plant species (Ahmad et al., 2019). Furthermore, Brazilian pepper can alter the natural fire cycles in ecosystems, increasing their frequency and affecting local vegetation.

To mitigate those impacts, it will be crucial to adopt comprehensive management strategies. This includes monitoring and early detection for a swift response, employing physical and chemical control methods, with manual removal in smaller areas and the use of selective herbicides in larger ones. Furthermore, investing in the restoration of affected ecosystems is essential, promoting the planting of native species and sustainable practices. Awareness along with public policies regarding the impacts of invasive species and the importance of biodiversity is crucial (Early et al., 2016). Ongoing research supports the improvement of these strategies, ensuring an evidence-based approach and effective long-term management.

5. Conclusion

The present study, to the best of our knowledge, is the first to model the current potential distribution and predicted the future distribution of *S. terebinthifolia* under climate change. In the current scenario, despite notable advancements in scientific and technological development related to bioclimatic modeling, the growing threat to global biodiversity resulting from biological invasions exacerbated by climate change makes it essential to understand and mitigate these challenges. Projections of distribution under current and future climate scenarios indicate a significant decline in suitable habitats in North and Central America, especially under high-emission scenarios, leaving only areas previously identified as native. Additionally, this study underlines the need for collaboration among scientists, policymakers, land managers, and local communities to tackle these challenges, particularly in Atlantic Forest areas, a critical biodiversity hotspot on this continent. Strategies such as monitoring, control, restoration, and awareness play crucial roles in the battle against the impacts of biological invasions, as in the case of Brazilian pepper, which threatens vulnerable ecosystems. Therefore, the research has provided valuable insights into the dynamics of invasive species distribution in the face of climate change and highlights the importance of effective policies and actions to mitigate their impacts. These findings are crucial in guiding future conservation and biodiversity management efforts in a constantly changing world.

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