UNIVERSIDADE DE BRASÍLIA
INSTITUTO DE CIÊNCIAS BIOLÓGICAS
PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Otimizando os resultados da restauração no Cerrado brasileiro: Uma abordagem de planejamento espacial que integra biodiversidade de lagartos endêmicos, conectividade e custos

Ana Caroline Cardoso Aragão

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia da Universidade de Brasília como parte dos requisitos para a obtenção do título de Mestre em Ecologia.

Orientador: Dr. Guarino Rinaldi Colli

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Sumário

Resumo em português

Diante da considerável perda e fragmentação das áreas naturais do Cerrado brasileiro, a restauração ecológica de áreas degradadas é essencial para conter o declínio da biodiversidade neste *hotspot* de importância global. Metas ambiciosas de restauração e recursos financeiros limitados exigem estratégias espacialmente explícitas que otimizem os resultados da restauração para a biodiversidade, assegurando ao mesmo tempo a relação custo-benefício. Desenvolvemos uma abordagem inovadora de priorização espacial para identificar áreas prioritárias para restauração no Cerrado, integrando a biodiversidade de lagartos endêmicos, a conectividade funcional e os custos de restauração. Ao combinar a riqueza total de espécies e a riqueza de espécies ameaçadas como indicadores de valor para a biodiversidade, consideramos tanto a urgência de conservação quanto a representatividade. A conectividade funcional foi avaliada com base na contribuição de cada área para a conectividade da paisagem, enquanto os custos foram estimados com base no potencial de regeneração natural. A otimização realizada com o pacote *prioritizr* no R resultou em uma solução eficiente que identificou quatro regiões focais para a restauração — Cerrado central, sudeste, oeste e norte — equilibrando valor ecológico e viabilidade de implementação. Os resultados ressaltam a necessidade de restauração estratégica em regiões sob intensa pressão agrícola e fragmentação de habitat. Essa abordagem replicável oferece uma estrutura robusta para orientar ações de restauração ecológica em larga escala em contextos com dados limitados, podendo também subsidiar esforços de planejamento em outros ecossistemas tropicais que enfrentam desafios socioeconômicos e de conservação semelhantes.

Palavras-chave: Metas de biodiversidade; Conectividade funcional; *prioritizr*; Planejamento da restauração; Espécies ameaçadas; Savana tropical.

Introdução geral

A perda e fragmentação de hábitats naturais têm impactos diretos sobre a biodiversidade, causando declínios de espécies, reduzindo a diversidade genética de regiões e comprometendo a capacidade dos organismos de ajustarem suas áreas de distribuição frente às mudanças ambientais globais (Fahrig, 2003; IPBES, 2019). Além disso, a degradação de áreas naturais representa ameaças aos serviços ecossistêmicos, incluindo água e ar limpos, solos saudáveis e outros benefícios essenciais para o bem-estar humano (Gann et al., 2019). Nesse cenário, as regiões tropicais, que abrigam a maior parte da biodiversidade global, são particularmente impactadas pela conversão acelerada de áreas nativas (Arroyo-Rodríguez et al., 2017), de forma que estratégias de conservação de tais regiões vêm sendo amplamente discutidas.

A restauração de ecossistemas degradados tem se consolidado como uma estratégia fundamental para a conservação da biodiversidade, atuando como uma importante aliada da conservação de ecossistemas naturais remanescentes (Dobson et al., 1997; Wiens & Hobbs, 2015). De acordo com a Sociedade para a Restauração Ecológica (2004), a restauração é uma atividade que inicia ou acelera o processo de recuperação de uma área degradada por consequência de atividades antrópicas. Com a recente valorização e avanços no campo da Ecologia da Restauração, entende-se também que ações eficazes de restauração devem equilibrar benefícios ecológicos, sociais e econômicos, como forma de alinhar a prática da restauração às demandas do mundo real (Martin, 2017; Suding et al., 2015). Além disso, como a restauração de áreas degradadas é um compromisso global assumido por diversos países — por meio de iniciativas como o Marco Global de Biodiversidade de Kunming-Montreal, que estabelece a meta de restaurar 30% dos ecossistemas degradados até 2030 (CBD, 2022) — é fundamental que as ações sejam planejadas de forma a atender a urgência e aos objetivos dessas metas.

A definição de áreas prioritárias para restauração surge como uma estratégia essencial para maximizar os benefícios e subsidiar a tomada de decisões. Uma pesquisa recente que estabelece prioridades globais de restauração demonstrou que a restauração de 30% das áreas críticas distribuídas pelo globo pode evitar a extinção de 71% das espécies ameaçadas pelo cenário atual de degradação (Strassburg et al., 2020). Dessa forma, o planejamento espacial para a restauração, seguindo princípios já consolidados pelo campo do planejamento sistemático da conservação (Margules & Pressey, 2000), permite potencializar os benefícios da restauração por meio de uma metodologia objetiva, eficiente e replicável (Crossman & Bryan, 2006).

O Brasil, país mais biodiverso do mundo e que abriga dois hotspots de biodiversidade (Floresta Atlântica e Cerrado) (Myers et al., 2000), está em uma posição oportuna para atingir o protagonismo no cumprimento das metas ambientais globais e conter a crise de biodiversidade (de Figueiredo Machado et al., 2024). Por meio do Plano Nacional de Recuperação da Vegetação Nativa (PLANAVEG), o Brasil firma o compromisso de restaurar 12 Mha até 2030, reconhecendo a priorização de áreas como uma ação essencial para a implementação desse compromisso (Ministério do Meio Ambiente, 2024). A maior parte da literatura sobre planejamento espacial para a restauração em larga escala no Brasil utiliza a Floresta Atlântica como caso de estudo (Crouzeilles et al., 2015; Guerra et al., 2020; Strassburg et al., 2019; Tambosi et al., 2014). Assim, considerando o seu status de *hotspot* global de biodiversidade, o Cerrado se torna uma área de estudo com oportunidades para avanço desse campo.

O Cerrado é a savana neotropical mais rica do planeta, abrigando um número expressivo de espécies endêmicas e importantes áreas de recarga hídrica e de estoque de carbono (Strassburg et al., 2017). Ao mesmo tempo, o bioma enfrenta uma crescente pressão antrópica, impulsionada principalmente pela expansão do agronegócio e destruição de hábitats naturais, resultando em uma crise de biodiversidade (Colli et al., 2020; da Conceição Bispo et al., 2023). Em 2024, pelo segundo ano seguido, o bioma seguiu liderando o desmatamento no Brasil (MapBiomas, 2025). De acordo com os dados de uso e cobertura do MapBiomas, o Cerrado possui aproximadamente metade da sua vegetação nativa original convertida em agropecuária, sendo que 54% das áreas convertidas se enquadram em áreas de pastagens, 28% em áreas agrícolas e o restante em mosaicos de uso e outras áreas não vegetadas (MapBiomas, 2024). No que diz respeito ao grau de proteção do Cerrado, somente cerca de 8,3% da área total do bioma encontra-se oficialmente protegida por Unidades de Conservação (Colli et al., 2020). Essa situação é ainda mais agravada pela legislação ambiental brasileira, uma vez que a maior parte dos remanescentes de vegetação nativa do Cerrado estão localizados dentro de propriedades privadas, que possuem a obrigação legal de manter apenas 20% a 35% de sua vegetação nativa (Brasil, 2012).

Considerando o alto grau de endemismo no Cerrado, os répteis se destacam por apresentarem o maior número de espécies endêmicas se comparados aos demais vertebrados terrestres (Vieira-Alencar et al., 2025). Entre eles, os lagartos são caracterizados por serem um grupo bem representado em estudos no Cerrado e apresentam um endemismo estimado em 42% (Nogueira et al., 2011; Silva et al., 2014). Além disso, trata-se de um grupo ameaçado no bioma, sobretudo devido à perda e degradação do hábitat e às mudanças climáticas (Pontes-da-Silva et al., 2018; Silva et al., 2014). Por sua vez, estratégias de planejamento voltadas à conservação de lagartos endêmicos no Cerrado podem não apenas identificar áreas de valor único para lagartos, mas também beneficiar a conservação de outros táxons. Estudos demonstram uma notável sobreposição entre áreas de endemismo de diferentes grupos no bioma, especialmente entre vertebrados terrestres (Azevedo et al., 2016; Vieira-Alencar et al., 2024), havendo também evidências de coincidência com áreas de endemismo de plantas (Lewis et al., 2023).

A restauração de áreas degradadas no Cerrado torna-se essencial para reverter o cenário de perda de biodiversidade e permitir que o Brasil avance no cumprimento de suas metas ambientais. Estudos que se propõem a priorizar áreas para a restauração no Cerrado consideram diferentes escalas, do nível estadual à escala de bioma. Stefanes et al. (2016) desenvolveram uma proposta para o Cerrado do Mato Grosso do Sul, baseada na resiliência da paisagem e custos de oportunidade, de forma a equilibrar aspectos ecológicos e econômicos no processo da priorização. Nunes et al. (2017) desenvolveram um modelo espacial para estimar custos e benefícios da restauração do Cerrado em Minas Gerais, destacando a utilização do potencial da regeneração natural para a redução de custos. Schüler e Bustamante (2022) priorizaram pastagens do Cerrado visando maximizar biodiversidade e serviços ecossistêmicos e diminuir conflitos com a agricultura. Mais recentemente, Liévano-Latorre et al. (2025) também aplicaram uma abordagem multicritério para planejar a restauração em larga escala nos biomas brasileiros, incluindo o Cerrado.

Com o objetivo de selecionar áreas prioritárias de restauração no Cerrado, com ênfase na conservação da biodiversidade, esta dissertação explora abordagens inovadoras no campo do planejamento espacial para a restauração do bioma. Em primeiro lugar, este estudo é pioneiro ao utilizar o pacote *prioritizr* (Hanson et al., 2024), que emprega algoritmos baseados em programação linear inteira mista (PLIM), para otimizar a seleção das áreas. Essa abordagem representa um avanço em relação aos métodos tradicionalmente empregados na maioria dos estudos no Cerrado, oferecendo a perspectiva de encontrar soluções mais eficientes em menos tempo (Beyer et al., 2016). Além disso, o trabalho propõe a utilização da riqueza de lagartos endêmicos do Cerrado e da riqueza de lagartos endêmicos ameaçados como métricas de biodiversidade para orientar a priorização das áreas passíveis de restauração. A riqueza de espécies foi estimada por meio da sobreposição de modelos de distribuição. Para as espécies com poucos registros de ocorrência, que são, em geral, espécies mais vulneráveis, foi aplicada uma abordagem alternativa e inovadora de modelagem, baseada em imputação filogenética. Essa abordagem permitiu superar uma das principais limitações dos modelos tradicionais e gerou modelos acurados para as espécies menos observadas, capazes de informar o planejamento da restauração de uma forma mais robusta e inclusiva. Foi incorporada também à análise a contribuição de cada área candidata à restauração para a conectividade funcional da paisagem, além de uma camada de custo de restauração baseada no potencial de regeneração natural das áreas elegíveis. Ao combinar essas técnicas, foi desenvolvida uma metodologia que oferece uma contribuição original para o planejamento da restauração no Cerrado e que pode servir de modelo para aplicação em outros contextos e regiões marcados por alta biodiversidade, limitações de dados e restrições de recursos.

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Optimizing restoration outcomes in the Brazilian Cerrado: A spatial planning framework integrating endemic lizard biodiversity, connectivity, and costs

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Abstract

Given the extensive loss and fragmentation of natural areas in the Brazilian Cerrado, ecological restoration of degraded lands is essential to halt biodiversity decline in this globally significant hotspot. Ambitious restoration targets and limited financial resources necessitate spatially explicit strategies that optimize biodiversity outcomes while ensuring cost-effectiveness. We developed an innovative spatial prioritization framework to identify priority areas for restoration in the Cerrado, integrating endemic lizard biodiversity, functional connectivity, and restoration costs. By combining total species richness and the richness of threatened species as proxies for biodiversity value, we accounted for both conservation urgency and representativeness. Functional connectivity was assessed by evaluating the contribution of each area to landscape connectivity, while cost was estimated based on the natural regeneration potential. Optimization using the *prioritizr* package in R produced an efficient solution that identified four focal regions for restoration—central, southeastern, western, and northern Cerrado—balancing ecological value with implementation feasibility. The results underscore the need for strategic restoration in regions under heavy agricultural pressure and habitat fragmentation. This replicable approach offers a robust framework for guiding large-scale ecological restoration in data-limited contexts and can inform biodiversity planning efforts in other tropical ecosystems facing similar conservation and socio-economic challenges.

Keywords: Biodiversity targets; Functional connectivity; *prioritizr*; Restoration planning; Threatened species; Tropical savanna.

Introduction

The rapid degradation of tropical ecosystems, driven primarily by land-use changes, is one of the greatest threats to global biodiversity (IPBES, 2019). In response, the UN Decade on Ecosystem Restoration (2021-2030) has placed the recovery of degraded landscapes at the center of international conservation agendas (Sewell et al., 2020). Restoration is further endorsed by global agreements such as the Sustainable Development Goals (IRP, 2019) and the Kunming-Montreal Global Biodiversity Framework, which aims to restore 30% of degraded ecosystems by 2030 to promote biodiversity, ecosystem services, and connectivity (CBD, 2022). Achieving these ambitious targets requires strong political will and robust planning tools that ensure ecological effectiveness and economic feasibility. Spatial planning for restoration, which builds upon principles of Systematic Conservation Planning (Margules & Pressey, 2000), offers a strategic means to prioritize where and how restoration should occur to maximize ecological return under real-world constraints (Crossman & Bryan, 2006).

A key step in restoration planning is defining spatially explicit biodiversity metrics. Species distribution data are widely used for this purpose, often estimated through correlative Species Distribution Models (SDMs) (Liévano-Latorre et al., 2025; Miranda et al., 2021). However, SDMs require relatively large sample sizes, limiting their effectiveness for rare or poorly known species (Grittz et al., 2024; Radomski et al., 2022). Ironically, these are often the species most in need of conservation attention, as they are disproportionately represented among narrow-ranged, endemic, or threatened taxa (Lomba et al., 2010; Meiri et al., 2018). To address this gap, novel modeling techniques such as ENphylo have been developed. ENphylo utilizes phylogenetic information from closely related taxa to infer distributions for species with limited occurrence data (Mondanaro et al., 2023), enabling more inclusive and comprehensive biodiversity representation in planning exercises. Incorporating such approaches into restoration frameworks offers a timely opportunity to better account for data-deficient species, especially in high-diversity tropical systems.

Connectivity is another critical factor in spatial restoration planning, ensuring the long-term persistence of biodiversity in fragmented landscapes (Antongiovanni et al., 2022; Crouzeilles et al., 2015; Tambosi et al., 2014). Functional connectivity, which integrates landscape configuration with organism-specific dispersal capacities (Auffret et al., 2015), enhances population viability by facilitating movement and gene flow across habitat patches. Strategically restored areas can act as stepping stones or corridors, particularly when designed to reconnect isolated remnants of native vegetation (Manes et al., 2025). At the same time, cost considerations—such as opportunity costs, implementation needs, and natural regeneration potential—must be integrated to maximize return on investment and ensure that restoration strategies remain viable at scale (Barros et al., 2023; Brancalion et al., 2019; Strassburg et al., 2020). Including cost surfaces alongside biodiversity and connectivity layers has become standard practice in restoration prioritization.

Beyond data inputs, the efficiency and scalability of prioritization outcomes depend on the optimization algorithms used. Traditional tools, such as Marxan and Zonation, rely on heuristic or simulated annealing algorithms, which may not guarantee optimal solutions (Moilanen et al., 2022; Watts et al., 2009). In contrast, integer linear programming (ILP) algorithms, such as those implemented in the *prioritizr* R package, offer demonstrably optimal solutions with reduced computational demand (Beyer et al., 2016; Hanson et al., 2024). Their integration into restoration planning represents an important methodological advancement, enabling more transparent, reproducible, and scalable prioritization exercises.

These tools are particularly needed in the Brazilian Cerrado, a global biodiversity hotspot that has lost roughly half its original vegetation cover to agricultural expansion (Colli et al., 2020; Myers et al., 2000). Despite harboring exceptionally high levels of species endemism, particularly among reptiles, the Cerrado remains under-protected and poorly studied in many areas (Strassburg et al., 2017; Vieira-Alencar et al., 2025). Furthermore, the biome is essential in regulating regional climate and providing freshwater (Borma et al., 2022; Fonseca & Bustamante, 2025). Recognizing the broader importance of restoring native ecosystems, the Brazilian government has committed to restore 12 million hectares of native vegetation nationwide by 2030 through initiatives such as *Plano Nacional de Recuperação da Vegetação Nativa* – PLANAVEG (Ministério do Meio Ambiente, 2024), with the Cerrado identified as one of the priority biomes. Nevertheless, operationalizing these commitments requires prioritization frameworks integrating ecological, spatial, and economic dimensions to identify where interventions will have the most impact.

Recent studies have proposed frameworks for spatially explicit restoration planning in the Cerrado, incorporating diverse cost indicators and biodiversity targets (Lewis et al., 2023; Liévano-Latorre et al., 2025; Nunes et al., 2017; Schüler & Bustamante, 2022; Stefanes et al., 2016). These studies often converge on the importance of transitional zones and central regions, which harbor high biodiversity and endemism. However, none have employed *prioritizr* or similar ILP-based tools, nor have they leveraged ENphylo to model the distribution of species with limited occurrence data. These shortcomings represent a missed opportunity to improve the inclusiveness and computational robustness of restoration planning in one of the world's most imperiled savannas.

Among terrestrial vertebrates, reptiles—particularly lizards—stand out for their high endemism in the Cerrado (Colli et al., 2002; Vieira-Alencar et al., 2025). These species often exhibit restricted distributions associated with particular vegetation types and elevational gradients (Azevedo et al., 2016; Nogueira et al., 2011). The availability of validated occurrence datasets (Costa et al., 2007; Silva et al., 2014; Vieira-Alencar et al., 2024) and a comprehensive phylogeny for Squamata (Title et al., 2024) makes lizards an ideal focal group for implementing novel distribution modeling techniques, such as ENphylo, within a rigorous prioritization framework. Here, we develop a spatial planning framework for restoration prioritization in the Cerrado, integrating endemic lizard richness, functional connectivity, and restoration costs. By combining correlative SDMs with phylogenetically informed modeling (ENphylo) and using ILP-based optimization in *prioritizr*, we aim to identify priority areas that maximize ecological return while minimizing financial costs. Our approach advances restoration planning for the Cerrado and provides a flexible and transferable template for other tropical ecosystems facing similar conservation challenges, where biodiversity is high, data are limited, and resources are constrained.

Methods

(a) Study area

We defined candidate areas for restoration as all converted lands within the Cerrado biome, excluding those classified as urban or mining zones. We used the 2023 land use and land cover map from MapBiomas Collection 9.0 (spatial resolution of approximately 30 meters) for the Cerrado to identify the candidate areas. We resampled the map to a resolution of 15 km due to computational limitations. We reclassified land cover into four categories: native vegetation, non-native/non-vegetated, water, and infrastructure (Fig. 1a). “Native” included forests, savannas, grasslands, and rocky outcrops; “non-native/non-vegetated” included pasture, agriculture, mosaics, and other non-vegetated areas; “infrastructure” covered mining and urban areas; “water” retained the original classification. Then, we extracted a mask of candidate areas for restoration corresponding to cells classified as non-native/ non-vegetated, and used it to constrain all input layers in the prioritization analysis (Fig. 1b). We performed all raster operations reported in this and subsequent sections in the RStudio environment (R Core Team, 2024) using the *terra* R package (Hijmans et al., 2025).

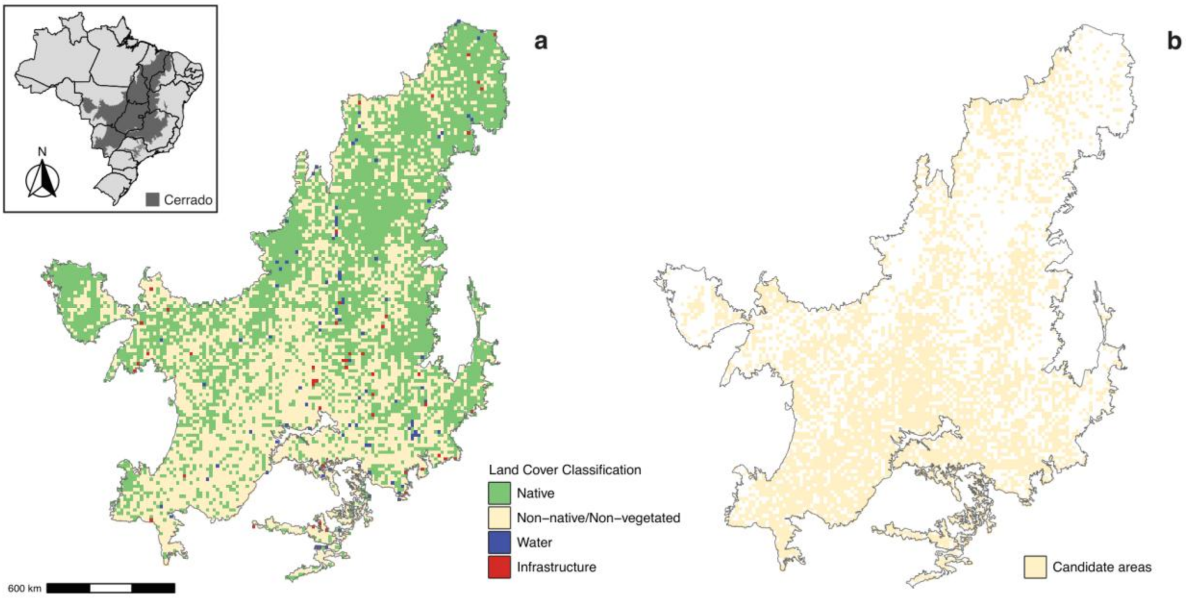

Figure 1. Land cover classification and candidate areas for ecological restoration in the Brazilian Cerrado. (a) Reclassified land cover map from MapBiomas Collection 9.0, aggregated into four major categories: native vegetation (green), non-native/non-vegetated areas (yellow), water bodies (blue), and infrastructure (red). (b) Binary raster mask of candidate areas for restoration, representing all pixels

classified as non-native/non-vegetated. These areas were used as spatial units for prioritization. Inset: location of the Cerrado within South America.

(b) Species Distribution Models (SDMs)

We fit correlative Species Distribution Models (SDMs), which relate species occurrence records to environmental variables. We used the binary predictions from the SDMs to characterize the presence area and calculate richness values for the spatial planning framework to identify priority areas for restoration in the Cerrado.

i. Environmental predictors

We downloaded historical climate (1970–2000) and elevation data from the WorldClim 2.1 database (Fick & Hijmans, 2017) at a spatial resolution of 2.5 arc-minutes. The environmental layers used to represent current conditions include elevation and 19 derived bioclimatic variables. Further details on the organization of these layers are provided in Supporting Information 1.

ii. Occurrence records

We used expert-validated occurrence records for 43 endemic lizard species from the Cerrado. Initially, we had 2950 reliable occurrence records for these species. We removed duplicate records for each species to minimize spatial autocorrelation and avoid model overfitting (Boria et al., 2014), retaining only one record per pixel. After this process, we obtained a final dataset of 1241 records (Table 1).

iii. Modeling Approach

We used the Random Forest (RF) machine learning algorithm to fit the Species Distribution Models for 18 species with more than 20 records (Table 1). RF shows the best predictive performance compared to other algorithms with relatively low computational cost (Valavi et al., 2022). For the 25 species with 20 or fewer records (Table 1), we used the ENphylo algorithm. ENphylo is an innovative approach designed to model the distribution of rare species through phylogenetic imputation and outperform other algorithms' predictive performance under these conditions

(Mondanaro et al., 2023). Further details on the methodology used to build the species distribution models are available in Supporting Information 1.

(c) Richness

We generated a raster layer representing the total richness of endemic lizard species per pixel in the Cerrado by overlaying the binary distribution maps of the 43 species. Recognizing that threatened species require more urgent conservation efforts, we also produced a raster layer representing the richness of threatened endemic lizards, weighted by their respective threat levels. We adopted this approach to treat threatened species as a distinct biodiversity feature, giving greater importance during the prioritization process to candidate restoration cells that overlap with the distribution of these threatened species.

We used a proportional scheme based on each species' threat category according to the Official List of Threatened Species of Brazilian Fauna to assign weights (Ministério do Meio Ambiente, 2022). Among the 43 endemic species, six are classified under a threat category (Table 1): we assigned a weight of 1 to two Vulnerable (VU) species; a weight of 2 to three Endangered (EN) species; and a weight of 3 to one Critically Endangered (CR) species. We multiplied the binary distribution map of each threatened species by its corresponding weight, and then overlaid these weighted maps to produce the final raster layer representing the threat-weighted richness of endemic lizard species in the Cerrado. We resampled all richness layers to ensure they shared the same spatial properties as the raster of candidate restoration areas.

(d) Connectivity

We used the Integral Index of Connectivity (IIC), a metric based on graph theory, to assess the contribution of each restorable pixel to the functional connectivity (Pascual-Hortal & Saura, 2006). In graph theory, the landscape is represented as a network of habitat patches (nodes) connected by links. The IIC is particularly suitable for evaluating connectivity changes due to landscape modification, including ecological restoration (Manes et al., 2025; Pascual-Hortal & Saura, 2006).

We implemented this approach using the R package *Makurhini* (Godínez-Gómez et al., 2025), which enables the simulation of new nodes through restoration and the quantification of their connectivity contribution. We constructed two distinct scenarios of connectivity, based on different criteria for node definition. The first considered only native vegetation within strictly protected areas, identified by intersecting shapefiles from the Brazilian National Registry of Protected Areas (CNUC) with current native cover (Supporting Information 2, Fig. S45). The second included all native vegetation as nodes (Supporting Information 2, Fig. S46). Constructing these two scenarios allowed us to treat connectivity based exclusively on strictly protected areas as a distinct biodiversity value in the prioritization process, highlighting the strategic importance of these areas for Cerrado biodiversity conservation (Françoso et al., 2015).

We adopted Makurhini's default approach to define the dispersal distance used in the functional connectivity assessment. Thus, the dispersal distance was automatically estimated for each scenario as the median Euclidean distance between node pairs. This avoids imposing a fixed threshold, which would be unrealistic given the varied dispersal capacities among lizard species. Additionally, considering the study scale and the limited dispersal ability of lizards, it is more plausible that the resulting patterns reflect the contribution of each restorable pixel to the maintenance of gene flow across generations, rather than to short-term individual movement.

Finally, for each scenario, we performed a dynamic analysis in which each restorable pixel was individually added to the landscape, following the approach proposed by Manes et al. (2025). The contribution of each pixel to functional connectivity was quantified using the *dIIC*, which represents the change in the landscape connectivity index resulting from the addition of that pixel.

(e) Costs

We used a continuous surface of natural regeneration potential of Cerrado pastures, produced by Silva et al. (2023), as a proxy for restoration costs. We assume that areas with higher regeneration potential demand less investment, while areas with lower potential require more active techniques and thus higher costs (Barros et al., 2023; Brancalion et al., 2019). Since our candidate restoration cells included pastures and other non-native land-use classes, estimating the regeneration potential for pixels without original values was necessary. We applied the universal kriging method as a geostatistical spatial interpolation technique, using the R package *gstat* (Gräler et al., 2016). This accurate approach captures deterministic and stochastic components of spatial variation to estimate values for unsampled locations (Fortin & Dale, 2005; Mukhopadhyay et al., 2017). We then inverted the regeneration surface so that high-potential areas reflected lower costs and low-potential areas corresponded to higher costs.

(f) Prioritization

We used the R package *prioritizr* to formulate and solve the spatial prioritization problem. This tool allows the incorporation of multiple parameters, such as objectives, targets, and penalties, to tailor solutions to specific conservation or restoration goals. We adopted the *minimum set objective*, identifying the minimum-cost set of planning units (candidate restoration areas) required to achieve representation targets for each biodiversity feature. The *minimum set objective*, applied to a set of planning units (I) and a set of conservation value features (J), where i represents each specific planning unit and j represents each specific conservation feature, can be expressed by the mathematical equation:

$$Minimize \sum_{i=1}^{I} x_i \, c_i$$

$$subject$$

$$\sum_{i=1}^{I} x_i \, r_{ij} \geq T_j \forall j \in J$$

In the equation, x_i is the decision variable indicating whether planning unit i was selected (x_i = 1) or not (x_i = 0). $c_i$represents the cost associated with planning unit i, r_{ij} denotes the amount of feature j present in unit i and $T_j$is the target set for feature j.

We considered four biodiversity features in our prioritization: the richness of endemic lizard species in the Cerrado, the richness of threatened endemic species weighted by threat level, and two scenarios of pixel-level contribution to functional connectivity. We set a 30% representation target per feature, based on the Kunming-Montreal Global Biodiversity Framework. Since *prioritizr* requires feature-based targets, we adapted the global area-based target to ensure selection of planning units that collectively hold 30% of each feature's total value, emphasizing the most relevant areas. In addition, we set the decision type to binary and assigned an optimality gap of 0%.

Results

(a) Species Distribution Models (SDMs)

Table 1 shows summary results for the Species Distribution Models (SDMs) from the 43 lizard species endemic to the Cerrado. TSS values ranged from 0.3 to 1.0. For each species, we generated a continuous habitat suitability map for the Cerrado, ranging from zero to one (Supporting Information 2, Fig. S2a - S44a) and a binary distribution map (Supporting Information 2, Fig. S2b - S44b).

(b) Prioritization input data: richness, connectivity, and costs

Regions with the highest richness of endemic lizard species are concentrated in the central, southeastern (transition to the Atlantic Forest), and western portions of the Cerrado (western Mato Grosso) (Fig. 2a). For threatened endemic lizards, the highest weighted richness values are scattered throughout the central, southeastern, and western areas (Fig. 2b).

In both connectivity scenarios, candidate pixels that most contribute to the functional connectivity of the biome, if restored, are concentrated in the central portion of the Cerrado, extending into the northern areas (Fig. 2c; Fig. 2d).

The resulting pattern for the restoration cost map is spatially heterogeneous but reveals lower-cost restoration opportunities in the biome's northeast, east, west, southeast, and southwest (Fig. 2e).

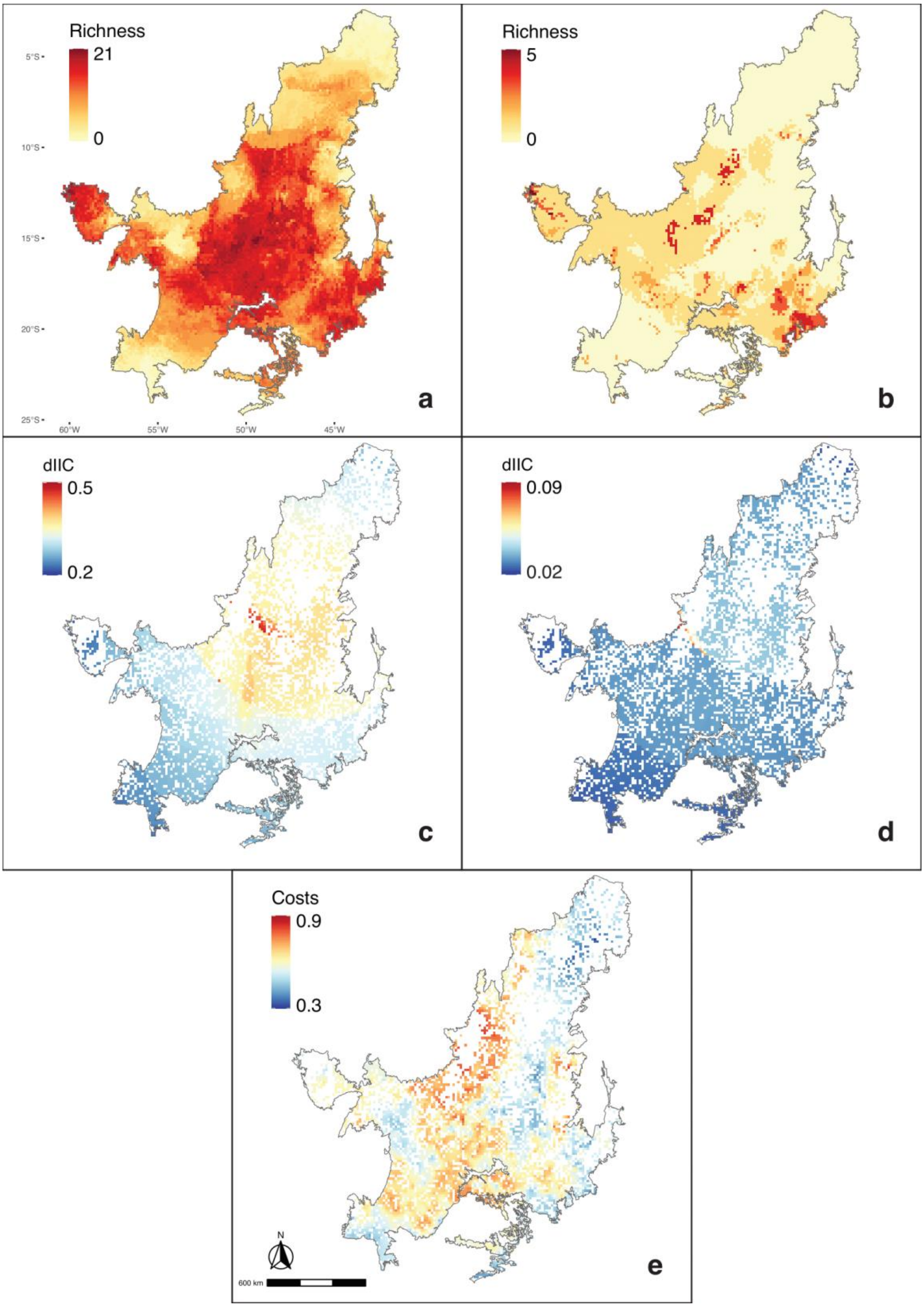

Figure 2. Spatial distribution of biodiversity features and restoration costs used in the prioritization framework for the Cerrado. (a) Total species richness of endemic lizards, estimated by stacking binary species distribution models (range: 0–21 species per pixel); (b) weighted richness of threatened endemic lizards, with weights assigned according to threat status (VU = 1, EN = 2, CR = 3); (c) contribution of each restorable pixel to functional connectivity (*dIIC*), considering only native vegetation inside strictly

protected areas as graph nodes; (d) contribution to connectivity (*dIIC*), considering all native vegetation as nodes; (e) restoration costs, inversely proportional to the potential for natural regeneration; darker red indicates higher projected cost. For (a) and (b), the gradient from dark red to light yellow represents a range from high to low values, respectively, while for (c), (d), and (e), red indicates higher values, orange and yellow represents intermediate values and blue represents lower values.

(c) Prioritization

A total of 4,411 planning units or candidate areas for restoration in the Cerrado were evaluated, of which 1,233 were selected. The optimization process reached an optimality gap of 0%, ensuring the solution obtained is optimal within the defined parameters. The spatial distribution of the selected areas reveals four focal regions for restoration, located in the central, southeastern, western, and northern portions of the Cerrado (Fig. 3).

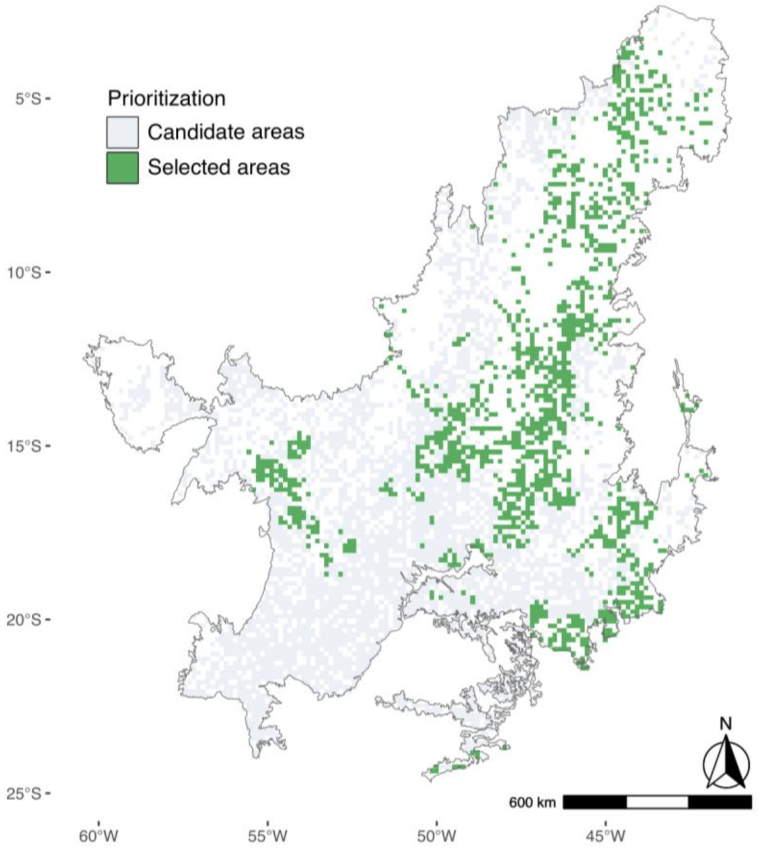

Figure 3. Spatial distribution of selected priority areas for ecological restoration in the Brazilian Cerrado. Map shows planning units (15 × 15 km cells) identified through mixed-integer linear programming optimization using the *prioritizr* R package. Candidate restoration units (gray) were filtered from land

cover classifications (Figure 1), and selected priority units (green) meet representation targets (30%) for four biodiversity features while minimizing total restoration costs. The map highlights four focal restoration regions in the central, southeastern, western, and northern Cerrado.

Discussion

Brazil has made global commitments to protect natural ecosystems and biodiversity, many of which involve restoring degraded areas (de Figueiredo Machado et al., 2024; MMA, 2024). In this context, our study offers a novel and integrative approach to prioritize restoration areas in the Cerrado, aiming to optimize biodiversity gains, minimize costs, and support public policies such as the PLANAVEG. Beyond advancing restoration planning in Brazil's most biodiverse savanna, our framework contributes to achieving global ecosystem restoration targets and offers a scalable model for application in other tropical regions facing similar conservation challenges.

By using mixed-integer linear programming via *prioritizr*, we achieved computationally optimal solutions (0% gap), offering a clear advantage over traditional tools like Marxan and Zonation, which rely on algorithms that do not guarantee optimality (Beyer et al., 2016). This represents a methodological advance in restoration planning for the Cerrado, improving efficiency and robustness. Additionally, we addressed the challenge of modeling species with limited occurrence data, a major limitation in conventional SDMs. By applying ENphylo, we successfully modeled distributions for species with as few as one record, improving the inclusiveness of biodiversity metrics and demonstrating the potential of our framework in data-limited contexts worldwide.

The spatial patterns of total richness and threat-weighted richness of endemic lizards reveal regions of high species concentration within the Cerrado, particularly in the biome's central, southeastern, and western parts. These results align with previous studies on reptile endemism in the Cerrado, which point to a higher concentration of endemic species in elevated regions, including the Espinhaço Range (southeast), the Parecis Plateau and areas near Chapada dos Guimarães (west), as well as the Central Plateau (center) (Azevedo et al., 2016; Nogueira et al., 2009; Nogueira et al., 2011).

While our analysis focused on endemic lizards, previous research suggests that patterns of endemism in well-studied groups can serve as valuable proxies for broader biodiversity, helping to guide conservation decisions and identify areas of unique conservation value (Antongiovanni et al., 2022; Lamoreux et al., 2006). Moreover, there is evidence that endemism patterns of other terrestrial vertebrates in the Cerrado may overlap with those observed for lizards (Azevedo et al., 2016; Vieira-Alencar et al., 2024; Vieira-Alencar et al., 2025). Thus, although our taxonomic focus imposes some limitations and does not represent the entire biological diversity of the biome, our results may offer useful insights for guiding restoration efforts that benefit multiple taxa.

Restoring individual pixels in the central and northern Cerrado would most effectively enhance functional connectivity. These regions host the largest strictly protected areas and the most extensive native vegetation remnants (Sano et al., 2019), making them strategic for linking key habitats. Connectivity plays a crucial role in sustaining biological flow in landscapes with intermediate levels of native vegetation cover (Villard & Metzger, 2014), as is the case in the Cerrado. However, the current state of fragmentation in the biome is concerning—an estimated 78% of connector fragments were lost between 2000 and 2017 (Grande et al., 2020). This fact highlights the importance of considering functional connectivity as a key biodiversity feature in restoration planning and prioritizing the recovery of landscape connectors.

Integrating cost into spatial restoration planning is crucial for optimizing efficiency and prioritizing areas with higher ecological returns at lower investment. We used natural regeneration potential as a proxy for restoration cost, since areas with higher potential require fewer interventions and, consequently, lower financial input. Limited funding is one of the main barriers to large-scale restoration, especially given its high implementation costs—for example, in the Cerrado, direct seeding can cost USD 797–1656/ha per year ((Raupp et al., 2020). Despite this, comprehensive and reliable cost estimates for large-scale restoration remain scarce (Brancalion et al., 2019), hindering informed decision-making and highlighting important knowledge gaps for future research. Given these limitations, our approach represents a feasible method to incorporate cost into restoration planning, though it remains an approximation that can be refined as better data emerge.

The spatial distribution of areas selected through prioritization reflects the balance achieved by the algorithm in minimizing costs while meeting the targets established for biodiversity features. The innovative methodological approach in this study found spatial patterns consistent with the existing literature. This study highlighted high-priority areas concentrated in the central portion of the biome and in transition zones, especially those adjacent to the Atlantic Forest, similar to other large-scale restoration planning studies in the Cerrado (Lewis et al., 2023; Liévano-Latorre et al., 2025; Schüler & Bustamante, 2022).

The areas selected in the central Cerrado stand out for their high total richness of endemic lizards and are also known for hosting altitudinal gradients that support the formation of endemism centers for flora and fauna (Azevedo et al., 2016; Lewis et al., 2023). Additionally, this region functions as a strategic link between major protected areas, offering opportunities for connectivity between them. Despite their ecological importance, these areas face intense agricultural pressure, with many already nearing legal limits for expansion (Sano et al., 2019), heightening the urgency for restoration and conservation actions.

The areas selected in the southeast, at the transition to the Atlantic Forest, also stand out due to their high total richness of endemic lizards, as well as the presence of potentially suitable habitats for threatened endemic lizards, such as *Placosoma cipoense* (Supporting Information 2, Fig. S29) and *Heterodactylus lundii* (Supporting Information 2, Fig. S23). Like the central portion, this region is characterized by areas of high elevation, which create favorable conditions for the emergence of endemism centers (Lewis et al., 2023). Moreover, this region is a transition zone between the Cerrado and the Atlantic Forest— an ecotone— which typically presents high diversity due to the mix of species from different ecosystems (Kark, 2013). Conversely, the southeastern Cerrado has a long history of human occupation, with intense urban and agricultural pressures, making it one of the biome’s most altered and fragmented regions (Sano et al., 2019). Even though restoration of these fragments may contribute little to large-scale connectivity, their recovery is essential for biodiversity maintenance, especially for endemic and threatened taxa.

Despite similarities with previous studies, our results also revealed new focal areas, particularly in the northern portion of the biome. The northern portion of the Cerrado exhibited low values of the total and weighted richness of threatened endemic lizards. This region is characterized by knowledge gaps regarding biodiversity (Colli et al., 2020; Vieira-Alencar et al., 2025) and has a more recent history of land occupation compared to other parts of the biome (Rausch et al., 2019; Sano et al., 2019). It also encompasses a higher proportion of native remnants, inside and outside protected areas. Despite the lower species richness observed, restoring selected pixels in this region could contribute to maintaining biological flow between remnant habitats and protected areas, primarily due to their strategic position in the landscape. However, the region’s prominence in the prioritization is also explained by the presence of areas with lower restoration costs, favoring their selection by the algorithm. The northern Cerrado is increasingly threatened by the expansion of the last agricultural frontier in Brazil, particularly due to the intensification of monocultures in the MATOPIBA region, an acronym for the states of Maranhão, Tocantins, Piauí, and Bahia (Rausch et al., 2019). This context underscores the urgency of advancing strategic conservation and restoration actions in the region, while ecological and economic conditions still favor interventions.

Finally, the areas selected in the western portion of the Cerrado (southern Mato Grosso) include regions potentially suitable for some endemic and threatened lizards, and present relatively low restoration costs. The selected areas are located in a region with a high concentration of annual croplands and cultivated pastures, where many units have already surpassed legal land conversion limits, underscoring the urgency of restoration efforts (Sano et al., 2019).

We recognize that real-world restoration planning involves other factors that were not accounted for in our analysis. For example, restoration within protected areas is often significantly more feasible than in productive agricultural lands. Expanding the set of criteria to include factors such as legal designation, agricultural suitability, and social or political constraints could provide a more realistic basis for guiding restoration efforts. Nonetheless, our framework represents a significant advance in restoration planning in the Cerrado by addressing common limitations in species distribution modeling and delivering optimal solutions through exact algorithms. While further refinements are needed, the framework presented here lays a strong foundation for more informed and efficient restoration strategies in the Cerrado and other data-limited tropical regions.

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Tables

Table 1. List of endemic lizard species from the Cerrado, including the number of occurrence records (N), modeling approach used to fit the SDMs, TSS values of the models, threat status according to the Official List of Threatened Species of Brazilian Fauna, and the weight assigned to each species based on its threat status.

Species	**N**	**Modeling Approach**	**TSS**	**Threat status**	**Weight**
Alopoglossus collii	5	Enphylo	0.77		
Ameiva jacuba	9	Enphylo	0.50		
Ameiva parecis	5	Enphylo	1.00	Endangered (EN)	2
Ameivula cipoensis	7	Enphylo	0.85		
Ameivula jalapensis	11	Enphylo	0.89		
Ameivula mumbuca	13	Enphylo	0.87		
Ameivula xacriaba	5	Enphylo	0.70		
Anolis meridionalis	70	Random Forest	0.83		
Bachia bresslaui	32	Random Forest	0.79		
Bachia cacerensis	2	Enphylo	1.00		
Bachia didactyla	2	Enphylo	0.90	Endangered (EN)	2
Bachia geralista	5	Enphylo	0.30		
Bachia micromela	1	Enphylo	0.70		
Bachia oxyrhina	5	Enphylo	1.00		
Bachia psamophila	1	Enphylo	0.70	Critically Endangered (CR)	3
Coleodactylus brachystoma	42	Random Forest	0.87		
Colobosaura modesta	106	Random Forest	0.89		
Enyalius capetinga	7	Enphylo	0.88		
Eurolophosaurus nanuzae	23	Random Forest	0.91		

Gymnodactylus amarali	60	Random Forest	0.89		
Gymnodactylus guttulatus	7	Enphylo	1.00		
Heterodactylus lundii	20	Enphylo	0.93	Vulnerable (VU)	1
Hoplocercus spinosus	66	Random Forest	0.83		
Kentropyx paulensis	59	Random Forest	0.85		
Kentropyx vanzoi	32	Random Forest	0.78	Vunerable (VU)	1
Manciola guaporicola	40	Random Forest	0.89		
Micrablepharus atticolus	43	Random Forest	0.89		
Placosoma cipoense	11	Enphylo	0.84	Endangered (EN)	2
Psilops seductus	2	Enphylo	0.70		
Rhachisaurus brachylepis	12	Enphylo	0.96		
Salvator duseni	38	Random Forest	0.85		
Stenocercus albolineatus	13	Enphylo	0.78		
Stenocercus canastra	2	Enphylo	0.90		
Stenocercus quinarius	15	Enphylo	0.91		
Stenocercus sinesaccus	10	Enphylo	0.81		
Tropidurus callathelys	3	Enphylo	0.99		
Tropidurus chromatops	5	Enphylo	0.69		
Tropidurus itambere	155	Random Forest	0.91		
Tropidurus montanus	33	Random Forest	0.86		
Tropidurus oreadicus	160	Random Forest	0.90		
Tupinambis matipu	28	Random Forest	0.87		
Tupinambis quadrilineatus	36	Random Forest	0.82		
Vanzosaura savanicola	40	Random Forest	0.88		

Supporting Information 1: Species Distribution Models

1. Species with more than 20 records

We used the Random Forest algorithm, implemented in the R package *biomod2* (Thuiller et al., 2025), to fit the distribution of 18 species with more than 20 records (Table 1). All analyses described in this section were conducted in the RStudio environment (R Core Team, 2024).

(a) Environmental predictors

We used the R package *terra* (Hijmans et al., 2025) to stack and crop the environmental layers according to the extent of the occurrence records of the 18 species added to a 5-degree buffer, ensuring the inclusion of relevant information for the calibration of the models. To reduce uncertainties in the estimates of the model parameters, we identified and removed highly correlated environmental variables by performing an analysis of the variance inflation factor (VIF) with the R package *usdm* (Naimi et al., 2014), considering as collinear those with VIF > 4. We maintained six predictors: Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean Temperature of Wettest Quarter (BIO8), Precipitation Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18), and Precipitation of Coldest Quarter (BIO19). For each species, the six environmental layers were cropped again according to the minimum convex polygon (MCP) encompassing all occurrence points of the species, expanded by a 5° buffer. This new environmental extent was used to define the modeling area for each species, ensuring the representation of an accessible area for the species of interest (Jarnevich et al., 2015).

(a) Continuous suitability and binary distribution models

Using *biomod2*, we generated 20 sets of pseudo-absences within the boundaries of each species' modeling area, each set containing the same number of presences. By doing so, we are considering that the performance of the model improves with the increase of replicates of pseudoabsences, but reaches the asymptote at 20 (Barbet-Massin et al., 2012). To generate the pseudo-absences, we used the Surface Range Envelope approach, which selects the pseudo-absences in environmental conditions that differ in a defined proportion from the conditions of the presence points (Thuiller et al., 2025). We used the six environmental layers, cropped by the minimum convex polygon (MCP) plus buffer, as predictor variables, and the occurrence records and pseudo-absences as the response variable to build habitat suitability models for each species. We implemented cross-validation using a k-fold approach with 10 repetitions, splitting the data into five equal parts per repetition. After generating individual models for each pseudo-absence set, we combined the best-performing models into a single ensemble model. Model selection was based on the True Skill Statistic (TSS) evaluation metric (Allouche et al., 2006), retaining those with TSS > 0.7. Next, we projected the habitat suitability model of each species for the area of the Cerrado biome. Finally, we applied the TSS threshold to binarize the continuous suitability predictions and generate a binary distribution map for each species.

2. Species with up to 20 records

We used the ENphylo algorithm, available in the R package *RRdtn* (Mondanaro et al., 2025) to fit the distribution of 25 species with up to 20 records (Table 1). The algorithm combines Environmental Niche Factor Analysis (ENFA) — which estimates the environmental suitability of species with a minimum number of occurrence records — with phylogenetic imputation, allowing to estimate the environmental suitability of related species that have insufficient records (Mondanaro et al., 2023). This methodology is based on the principle that related species tend to share environmental preferences and tolerance limits. Thus, the information obtained for the species modeled by ENFA, which have more robust data, is used to infer the environmental suitability of the species with fewer records. ENphylo requires three input data: a phylogenetic tree that includes species with few records and related species with robust data, an environmental layer covering the available background area for all species, and occurrence records and background points for each species present in the tree.

(a) Phylogenetic tree

We used the time-calibrated phylogeny of Title et al. (2024) which represents the most recent dated phylogeny of scaled reptiles (Squamata). When crossing the 25 species of interest with the phylogeny, we found that some were missing. To impute the absent taxa in the reference phylogeny, we employed Taxonomic Addition for Complete Trees (TACT), a stochastic method for resolving polytomies (Chang et al., 2020). The method uses estimates of species birth and death from a reference phylogeny and taxonomic information from all species of interest, deposited in a guide taxonomic tree, to place the missing taxa in the incomplete phylogeny. Following the procedure described by Chang et al. (2020), we generated the guide taxonomic tree and imputed the missing species into the reference phylogeny using codes executed in the Docker Desktop software (Merkel, 2014). After generating the complete phylogeny, we created a subset of the phylogeny with the aid of the R package *ape* (Paradis & Schliep, 2019) containing the 25 endemic species of interest and 94 related species with robust data. The related species were selected based on the following criteria: species that belonged to the same families as the 25 target species and have more than 20 occurrence records. This final set allowed the construction of a subtree with 119 species in total (Supporting Information 2, Fig. S1), which was used by the algorithm to model the distribution of the 25 endemic lizard species with up to 20 occurrence records.

(b) Environmental predictors

We repeated the steps described in item 1a: preparation of environmental layers, including stacking and cropping them according to the extent of the occurrence records of the 119 species, expanded by a 5-degree buffer; and variance inflation factor (VIF) analysis, removing variables with VIF > 4. In the end, we retained eight predictors: Elevation, Mean Diurnal Range (BIO2), Isothermality (BIO3), Mean Temperature of Wettest Quarter (BIO8), Precipitation of Driest Month (BIO14), Precipitation Seasonality (BIO15), Precipitation of Warmest Quarter (BIO18), and Precipitation of Coldest Quarter (BIO19).

(c) Occurrence records and background points

Since ENphylo is unable to convert results into suitability values for species with fewer than five known presences, we adopted the strategy described by Mondanaro et al. (2024) to include these cases in the analysis. Using functions from the *terra* R package, we generated n pseudo-presences for each species with fewer than five original records (Table 1), where $n = 5 -$ the number of known presences for that species.

To do this, we identified cells adjacent to presence cells using the knight's move criterion, extracted the values of the environmental predictors for both the presence and adjacent cells, and selected the adjacent cells most similar to the presence cells in terms of environmental conditions, based on Euclidean distance. The adjacent cells with the lowest Euclidean distances were added to the original dataset as pseudo-presences for the species with fewer than five records. As the final step in preparing ENphylo input data, we randomly generated 10,000 background points for each species within the extent of the environmental layer.

(d) Continuous suitability and binary distribution models

Using the *RRdtn* package, we evaluated the models through bootstrap cross-validation, splitting the data into 80% for training and 20% for testing, and repeating the procedure 10 times. Model predictive performance was assessed using the True Skill Statistic (TSS). To account for phylogenetic uncertainty, we repeated the entire process with 100 alternative phylogenies, randomly generated by modifying the topology and branch lengths of the original phylogeny. For each species, we selected the model with the highest TSS value among the 100 replications. As the focus of the analysis is on the 25 endemic lizard species of the Cerrado modeled with phylogenetic imputation, we projected the environmental suitability and binary distribution of these species onto a new environmental raster bounded by the limits of the Cerrado biome.

3. References

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Supporting Information 2: Supplementary Figures

Figure S1. Phylogenetic tree used to fit the distribution of 25 lizard species with up to 20 occurrence records using the ENphylo algorithm. The tree includes the 25 target species and 94 closely related species with robust data.

Figure S2. (a) Continuous habitat suitability and (b) binary presence–absence map of *Alopoglossus collii* across the Cerrado.

Figure S3. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameiva jacuba* across the Cerrado.

Figure S4. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameiva parecis* across the Cerrado.

Figure S5. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameivula cipoensis* across the Cerrado.

Figure S6. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameivula jalapensis* across the Cerrado.

Figure S7. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameivula mumbuca* across the Cerrado.

Figure S8. (a) Continuous habitat suitability and (b) binary presence–absence map of *Ameivula xacriaba* across the Cerrado.

Figure S9. (a) Continuous habitat suitability and (b) binary presence–absence map of *Anolis meridionalis* across the Cerrado.

Figure S10. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia bresslaui* across the Cerrado.

Figure S11. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia cacerensis* across the Cerrado.

Figure S12. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia didactyla* across the Cerrado.

Figure S13. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia geralista* across the Cerrado.

Figure S14. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia micromela* across the Cerrado.

Figure S15. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia oxyrhina* across the Cerrado.

Figure S16. (a) Continuous habitat suitability and (b) binary presence–absence map of *Bachia psamophila* across the Cerrado.

Figure S17. (a) Continuous habitat suitability and (b) binary presence–absence map of *Coleodactylus brachystoma* across the Cerrado.

Figure S18. (a) Continuous habitat suitability and (b) binary presence–absence map of *Colobosaura modesta* across the Cerrado.

Figure S19. (a) Continuous habitat suitability and (b) binary presence–absence map of *Enyalius capetinga* across the Cerrado.

Figure S20. (a) Continuous habitat suitability and (b) binary presence–absence map of *Eurolophosaurus nanuzae* across the Cerrado.

Figure S21. (a) Continuous habitat suitability and (b) binary presence–absence map of *Gymnodactylus amarali* across the Cerrado.

Figure S22. (a) Continuous habitat suitability and (b) binary presence–absence map of *Gymnodactylus guttulatus* across the Cerrado.

Figure S23. (a) Continuous habitat suitability and (b) binary presence–absence map of *Heterodactylus lundii* across the Cerrado.

Figure S24. (a) Continuous habitat suitability and (b) binary presence–absence map of *Hoplocercus spinosus* across the Cerrado.

Figure S25. (a) Continuous habitat suitability and (b) binary presence–absence map of *Kentropyx paulensis* across the Cerrado.

Figure S26. (a) Continuous habitat suitability and (b) binary presence–absence map of *Kentropyx vanzoi* across the Cerrado.

Figure S27. (a) Continuous habitat suitability and (b) binary presence–absence map of *Manciola guaporicola* across the Cerrado.

Figure S28. (a) Continuous habitat suitability and (b) binary presence–absence map of *Micrablepharus atticolus* across the Cerrado.

Figure S29. (a) Continuous habitat suitability and (b) binary presence–absence map of *Placosoma cipoense* across the Cerrado.

Figure S30. (a) Continuous habitat suitability and (b) binary presence–absence map of *Psilops seductus* across the Cerrado.

Figure S31. (a) Continuous habitat suitability and (b) binary presence–absence map of *Rhachisaurus brachylepis* across the Cerrado.

Figure S32. (a) Continuous habitat suitability and (b) binary presence–absence map of *Salvator duseni* across the Cerrado.

Figure S33. (a) Continuous habitat suitability and (b) binary presence–absence map of *Stenocercus albolineatus* across the Cerrado.

Figure S34. (a) Continuous habitat suitability and (b) binary presence–absence map of *Stenocercus canastra* across the Cerrado.

Figure S35. (a) Continuous habitat suitability and (b) binary presence–absence map of *Stenocercus quinarius* across the Cerrado.

Figure S36. (a) Continuous habitat suitability and (b) binary presence–absence map of *Stenocercus sinesaccus* across the Cerrado.

Figure S37. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tropidurus callathelys* across the Cerrado.

Figure S38. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tropidurus chromatops* across the Cerrado.

Figure S39. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tropidurus itambere* across the Cerrado.

Figure S40. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tropidurus montanus* across the Cerrado.

Figure S41. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tropidurus oreadicus* across the Cerrado.

Figure S42. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tupinambis matipu* across the Cerrado.

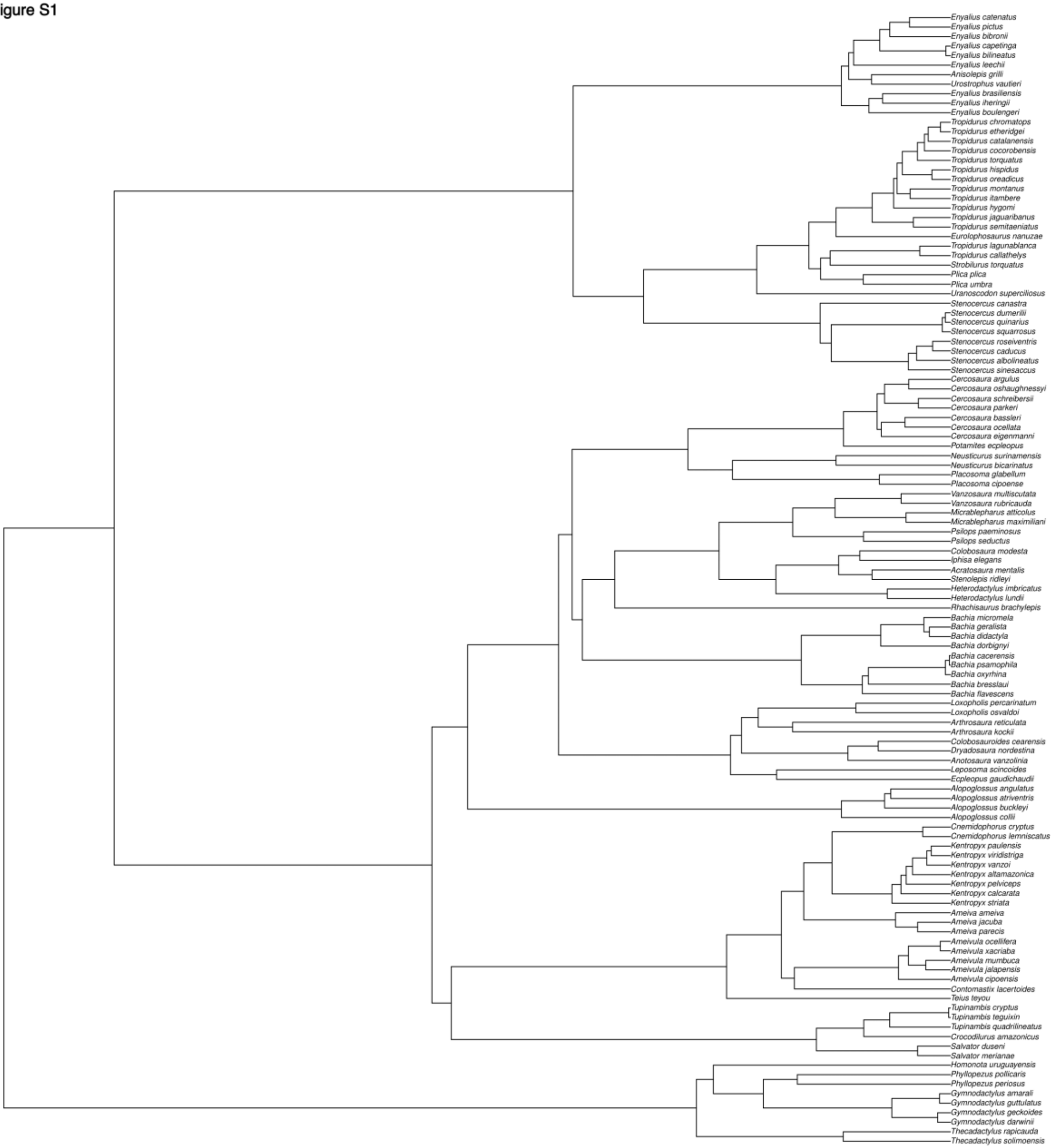
Figure S43. (a) Continuous habitat suitability and (b) binary presence–absence map of *Tupinambis quadrilineatus* across the Cerrado.

Figure S44. (a) Continuous habitat suitability and (b) binary presence–absence map of *Vanzosaura savanicola* across the Cerrado.

Figure S45. Native vegetation patches within strict protected areas considered in the first connectivity scenario.

Figure S46. Native vegetation patches considered in the second connectivity scenario, including all native areas.

Figure S1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Enyalius brasiliensis
Enyalius iheringii
Enyalius boulengeri
Tropidurus chromatops
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Tropidurus cocorobensis
Tropidurus torquatus
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Tropidurus hygomi
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Tropidurus semitaeniatus
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Tropidurus lagunablanca
Tropidurus callathelys
Strobilurus torquatus
Plica plica
Plica umbra
Uranoscodon superciliosus
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Stenocercus dumerilii
Stenocercus quinarius
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Stenocercus albolineatus
Stenocercus sinesaccus
Cercosaura argulus
Cercosaura oshaughnessyi
Cercosaura schreibersii
Cercosaura parkeri
Cercosaura bassleri
Cercosaura ocellata
Cercosaura eigenmanni
Potamites ecpleopus
Neusticurus surinamensis
Neusticurus bicarinatus
Placosoma glabellum
Placosoma cipoense
Vanzosaura multiscutata
Vanzosaura rubricauda
Micrablepharus atticolus
Micrablepharus maximiliani
Psilops paeminosus
Psilops seductus
Colobosaura modesta
Iphisa elegans
Acratosaura mentalis
Stenolepis ridleyi
Heterodactylus imbricatus
Heterodactylus lundii
Rhachisaurus brachylepis
Bachia micromela
Bachia geralista
Bachia didactyla
Bachia dorbignyi
Bachia cacerensis
Bachia psamophila
Bachia oxyrhina
Bachia bresslaui
Bachia flavescens
Loxopholis percarinatum
Loxopholis osvaldoi
Arthrosaura reticulata
Arthrosaura kockii
Colobosauroides cearensis
Dryadosaura nordestina
Anotosaura vanzolinia
Leposoma scincoides
Ecpleopus gaudichaudii
Alopoglossus angulatus
Alopoglossus atriventris
Alopoglossus buckleyi
Alopoglossus collii
Cnemidophorus cryptus
Cnemidophorus lemniscatus
Kentropyx paulensis
Kentropyx viridistriga
Kentropyx vanzoi
Kentropyx altamazonica
Kentropyx pelviceps
Kentropyx calcarata
Kentropyx striata
Ameiva ameiva
Ameiva jacuba
Ameiva parecis
Ameivula ocellifera
Ameivula xacriaba
Ameivula mumbuca
Ameivula jalapensis
Ameivula cipoensis
Contomastix lacertoides
Teius teyou
Tupinambis cryptus
Tupinambis teguixin
Tupinambis quadrilineatus
Crocodilurus amazonicus
Salvator duseni
Salvator merianae
Homonota uruguayensis
Phyllopezus pollicaris
Phyllopezus periosus
Gymnodactylus amarali
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Thecadactylus rapicauda
Thecadactylus solimoensis

Figure S2

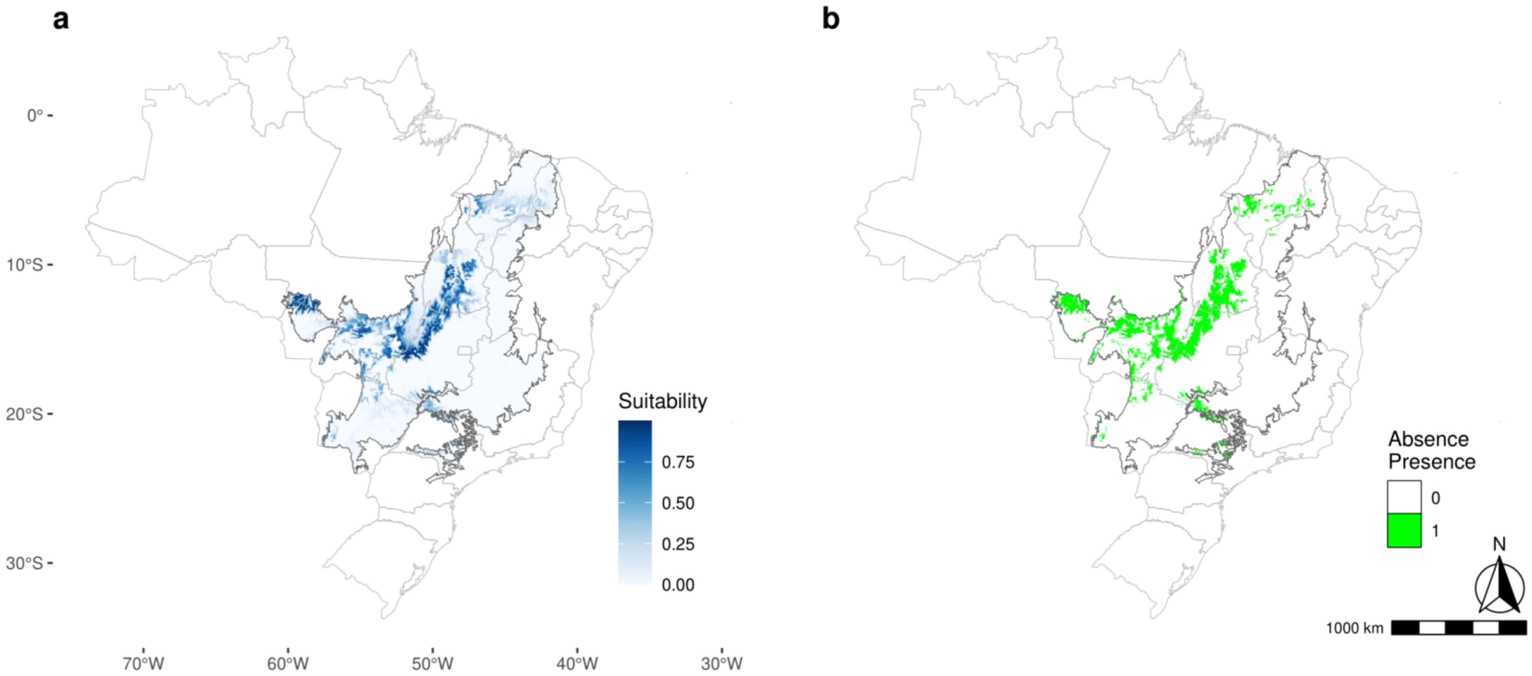
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Figure S3

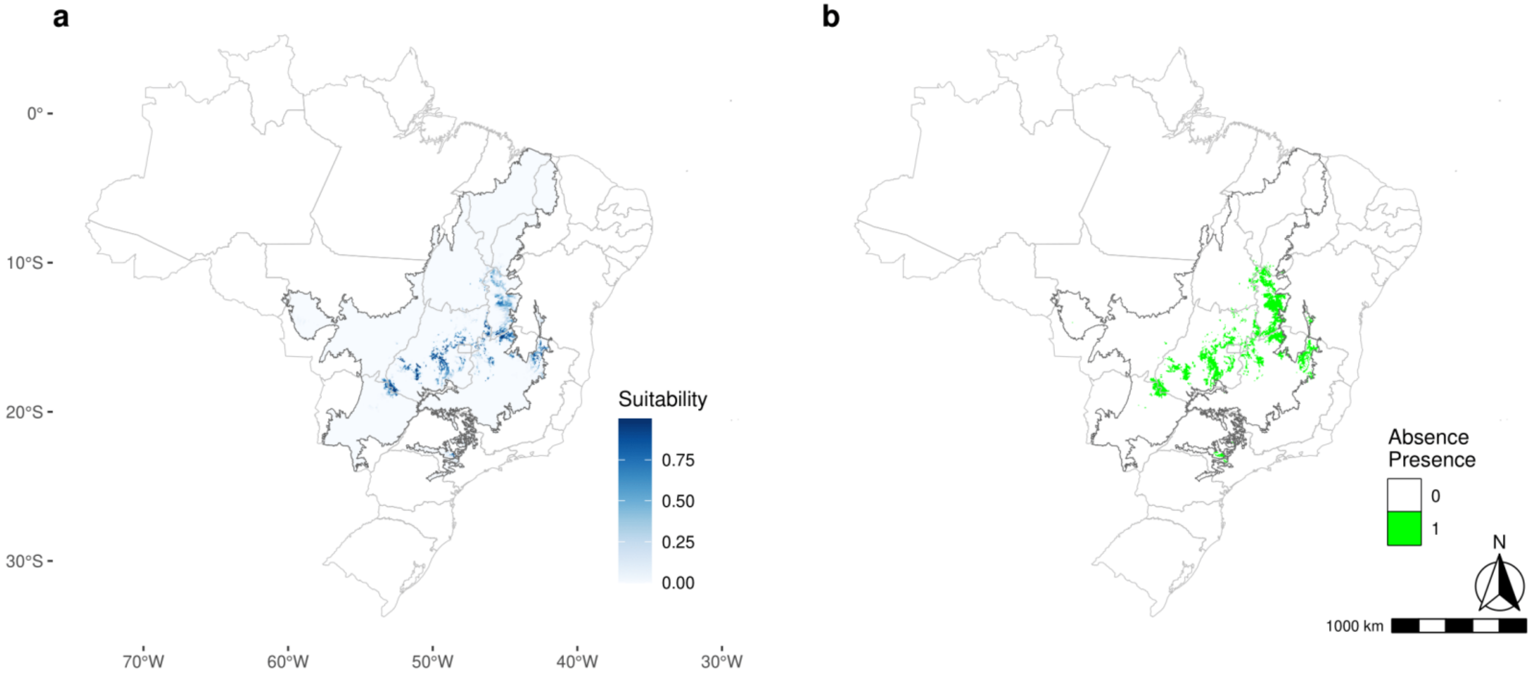
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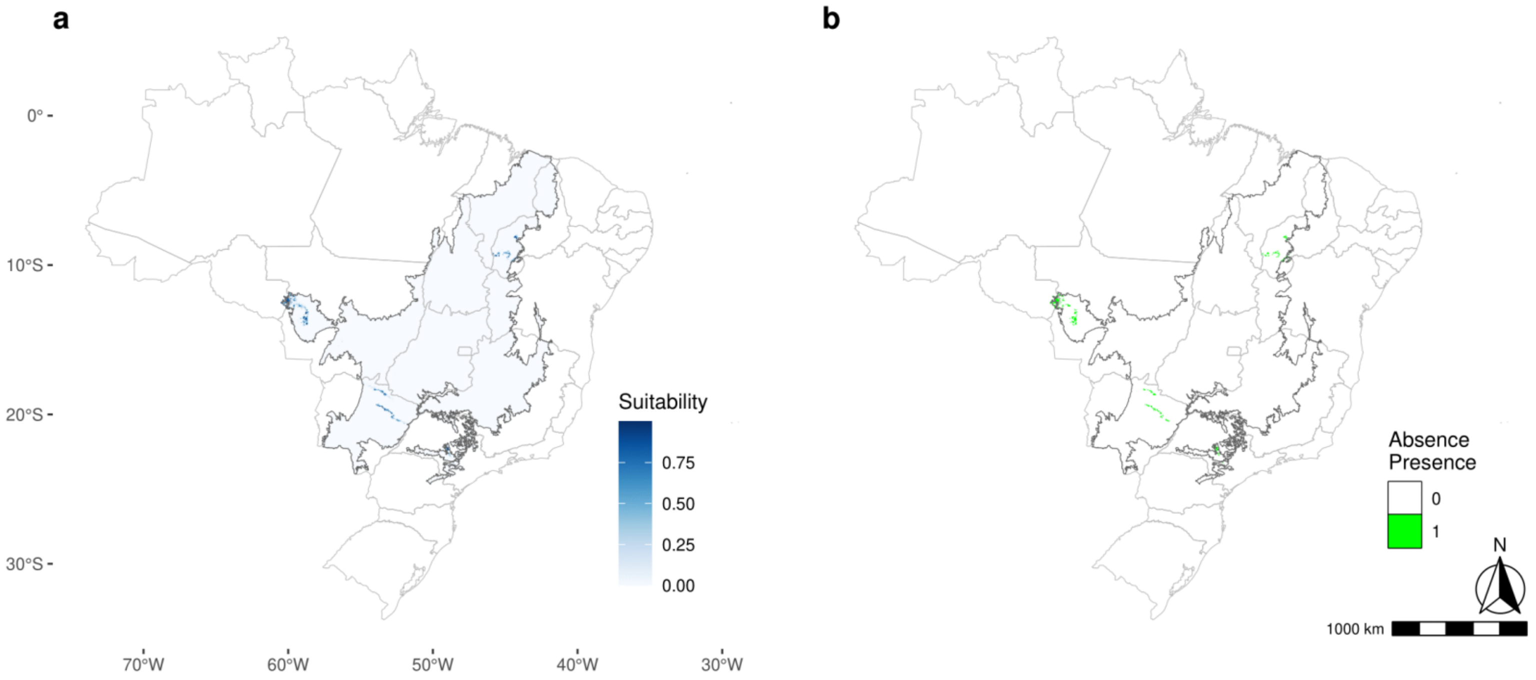
Figure S4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N
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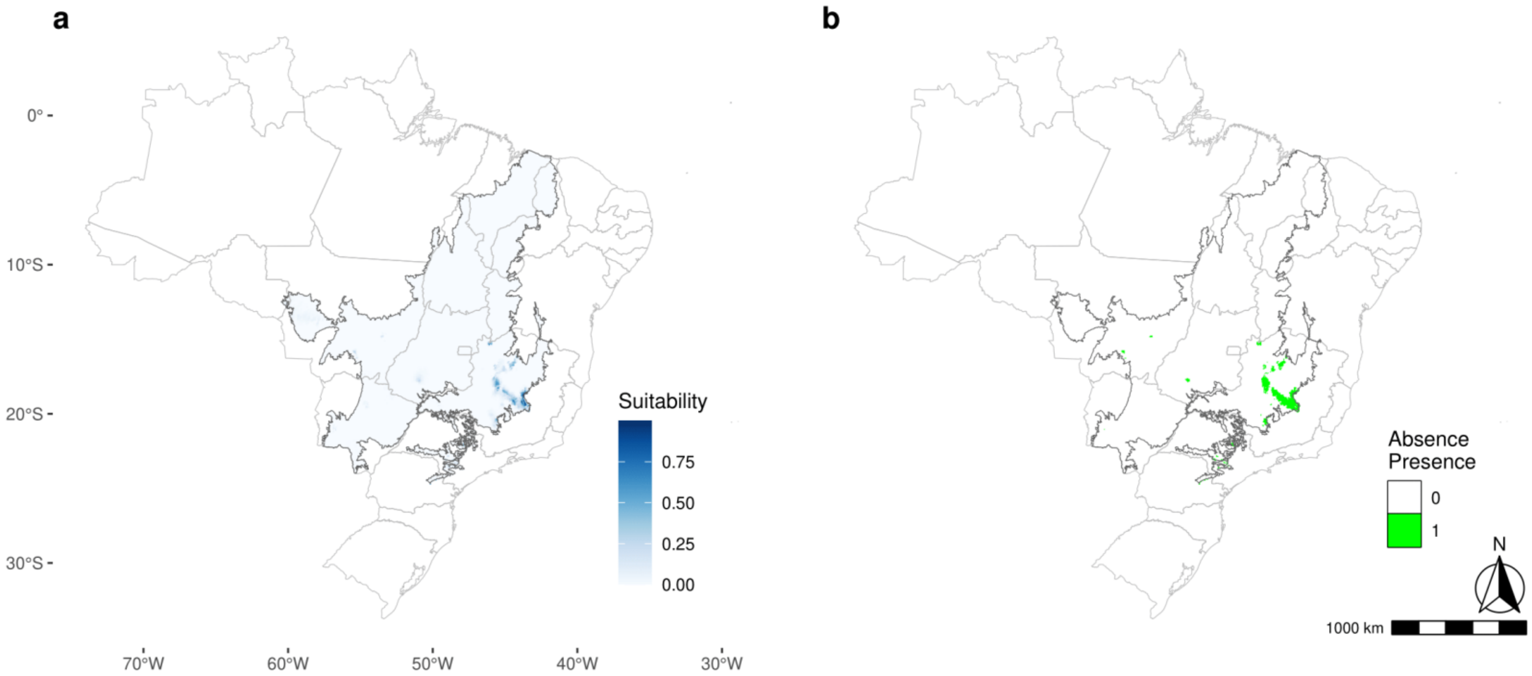
Figure S5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1000 km

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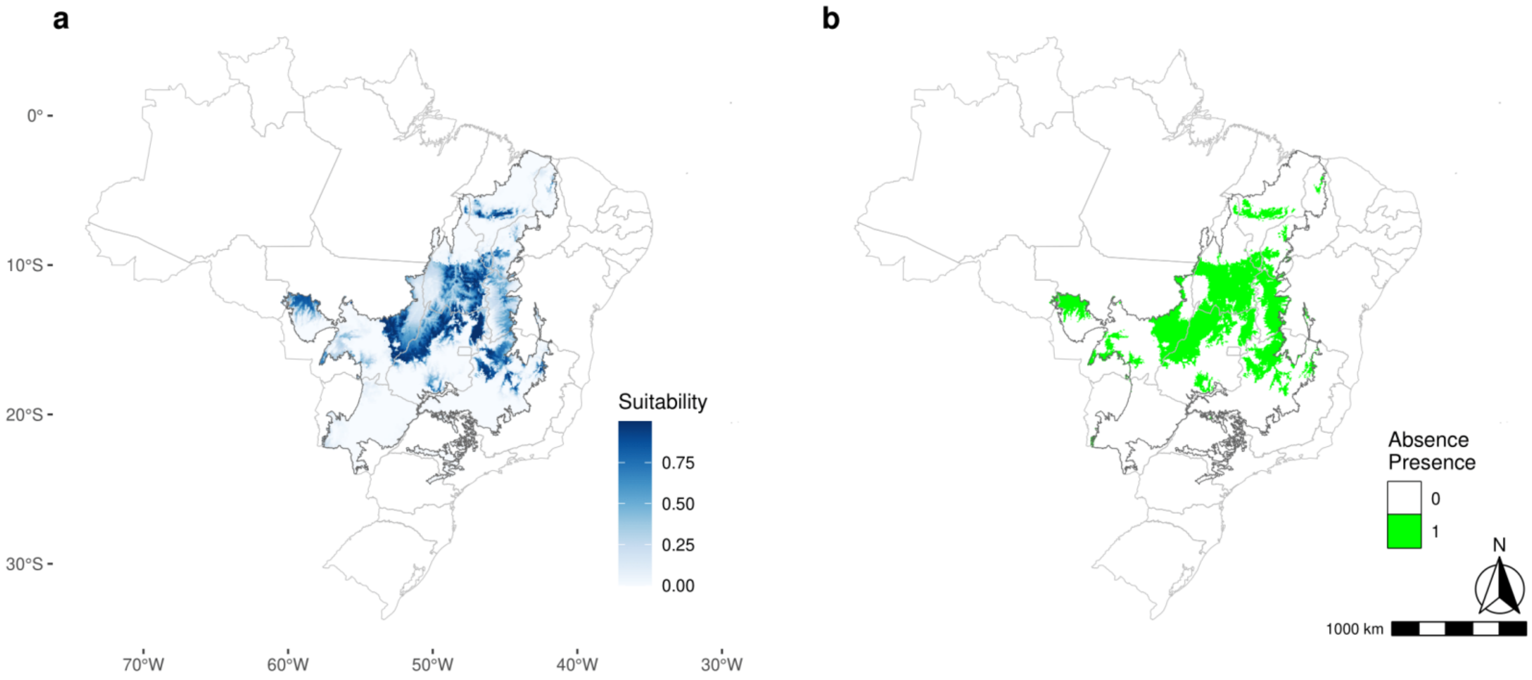
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Suitability
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Figure S7

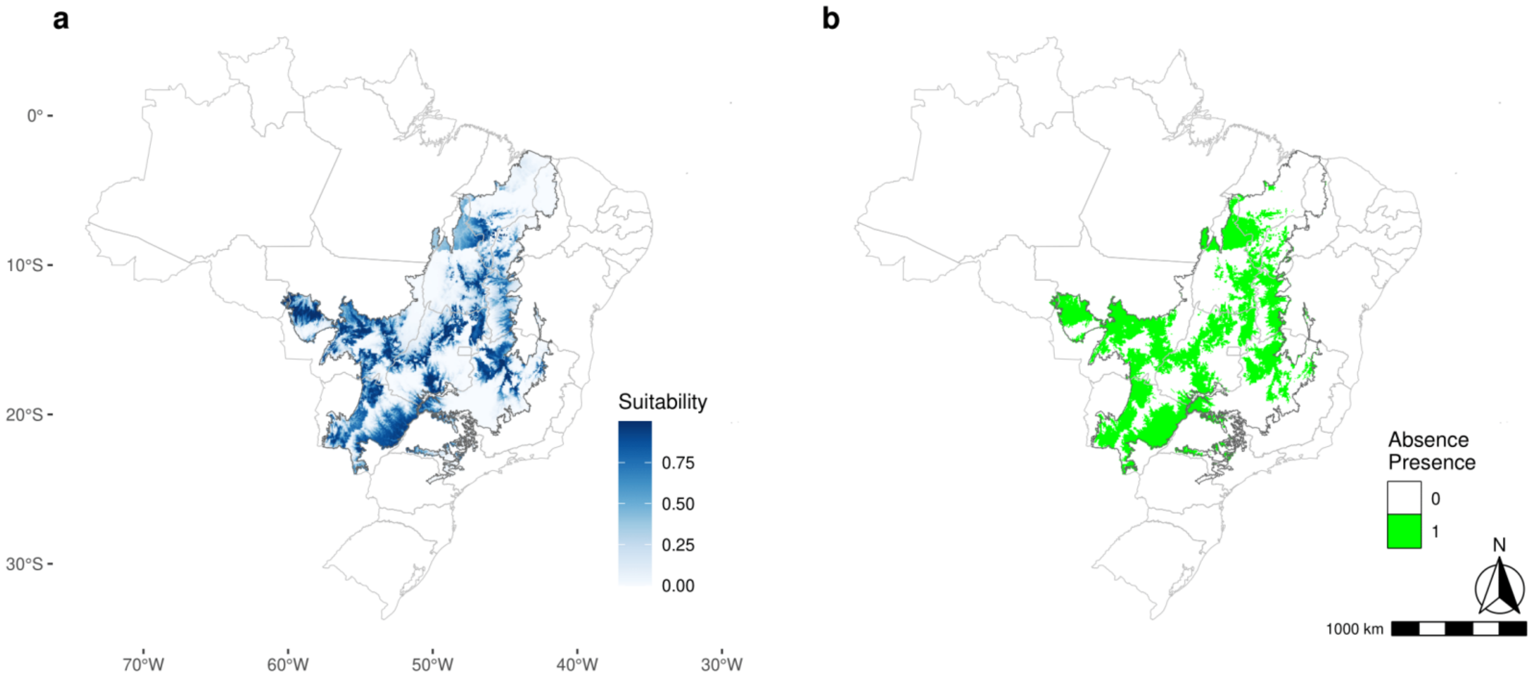
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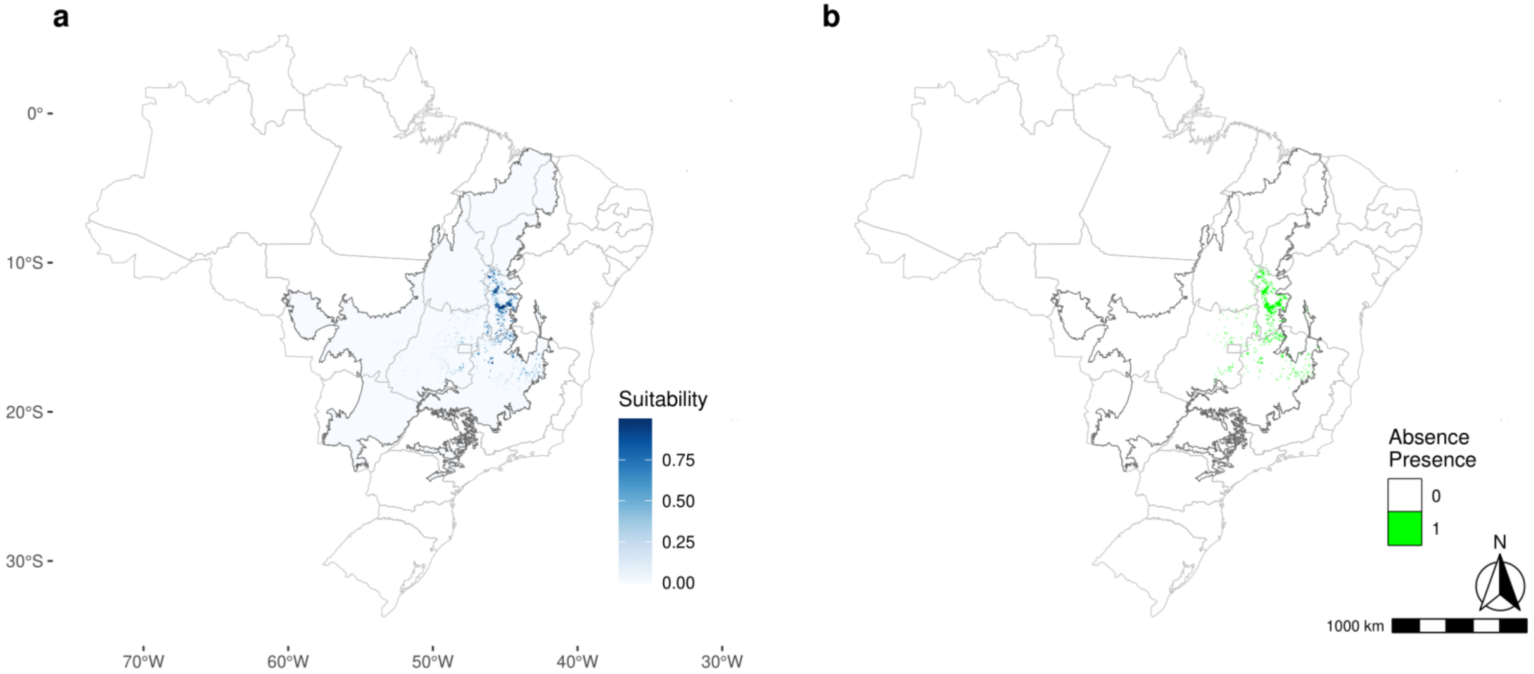
Figure S8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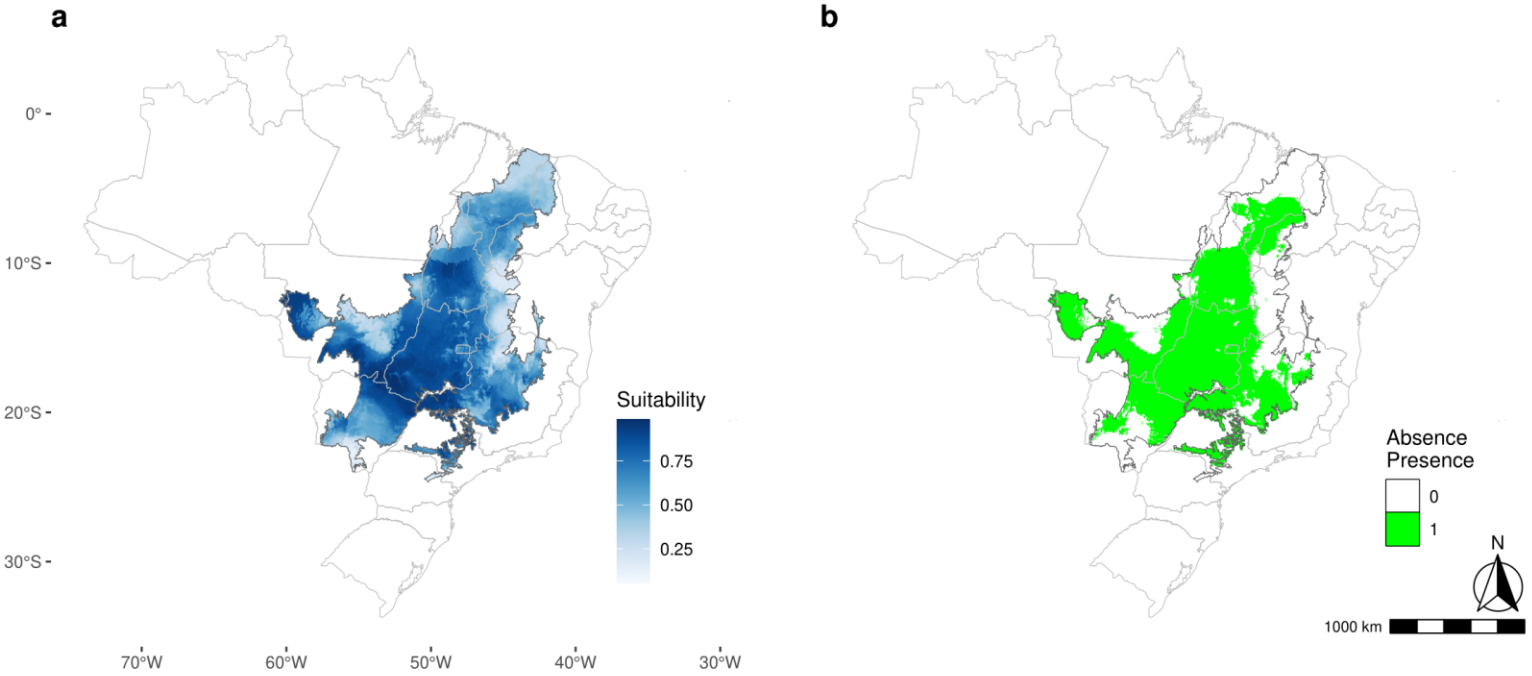
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Figure S10

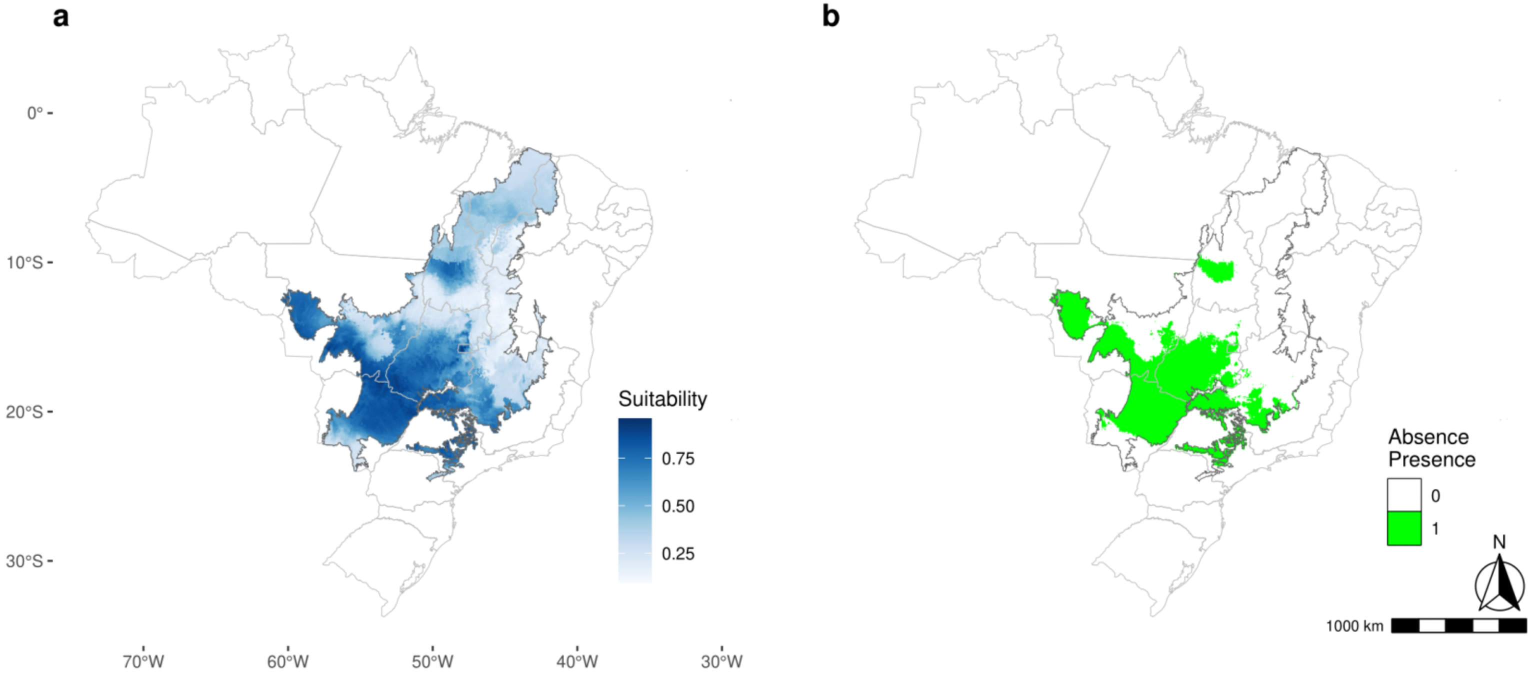
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Figure S11

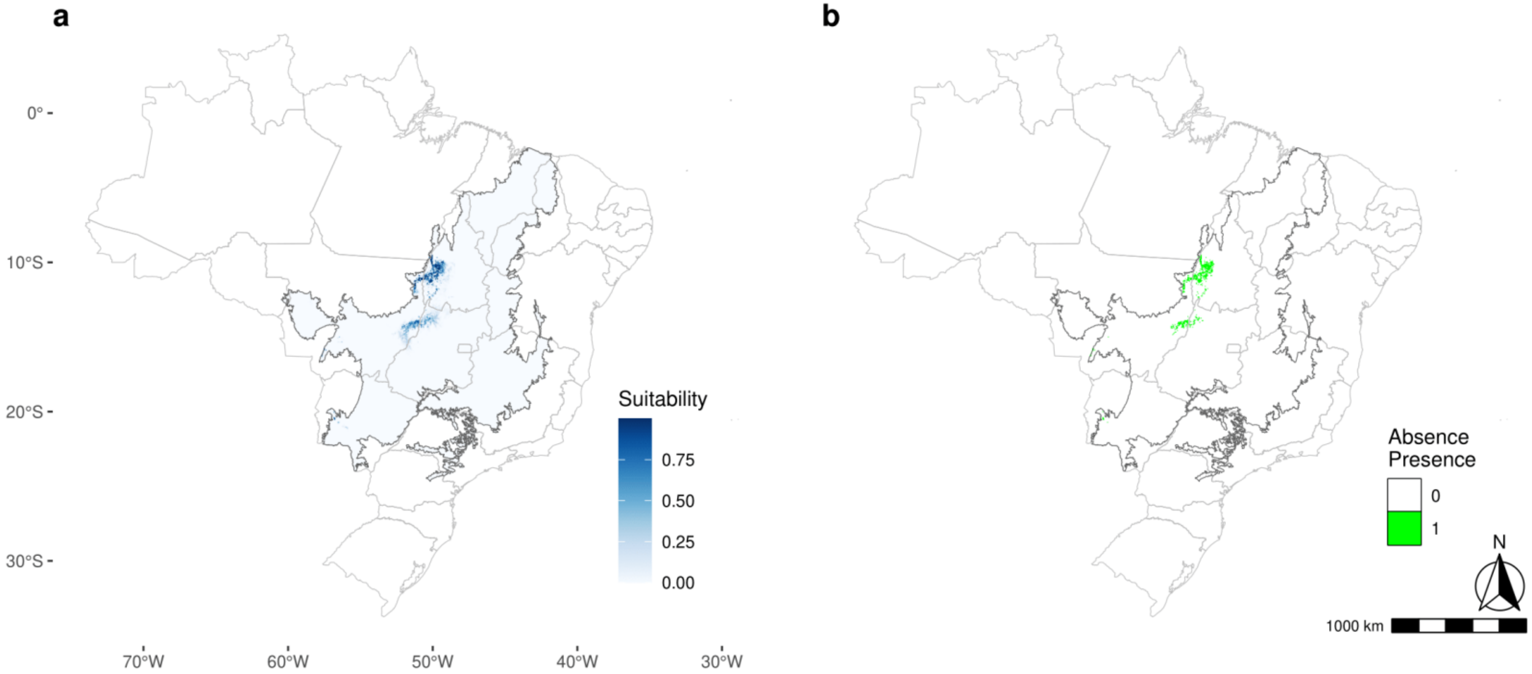
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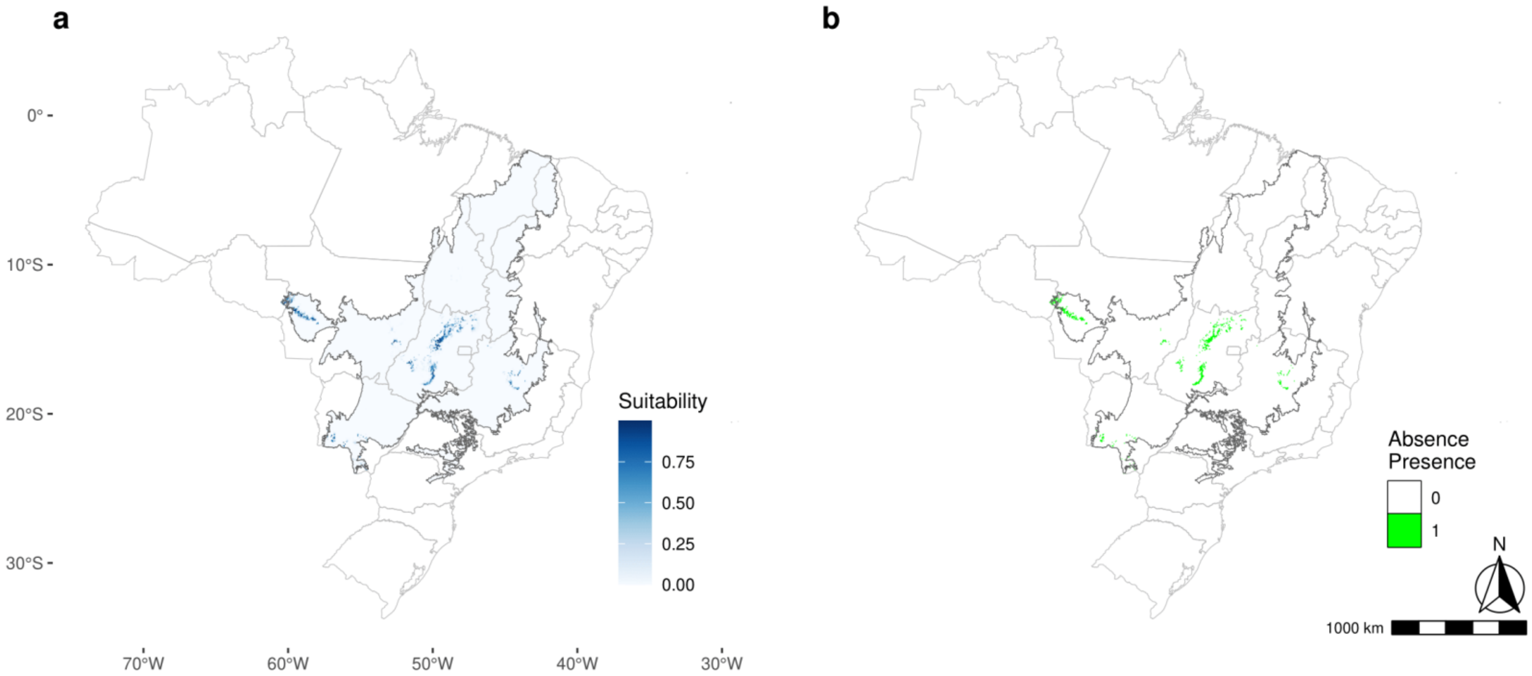
Figure S12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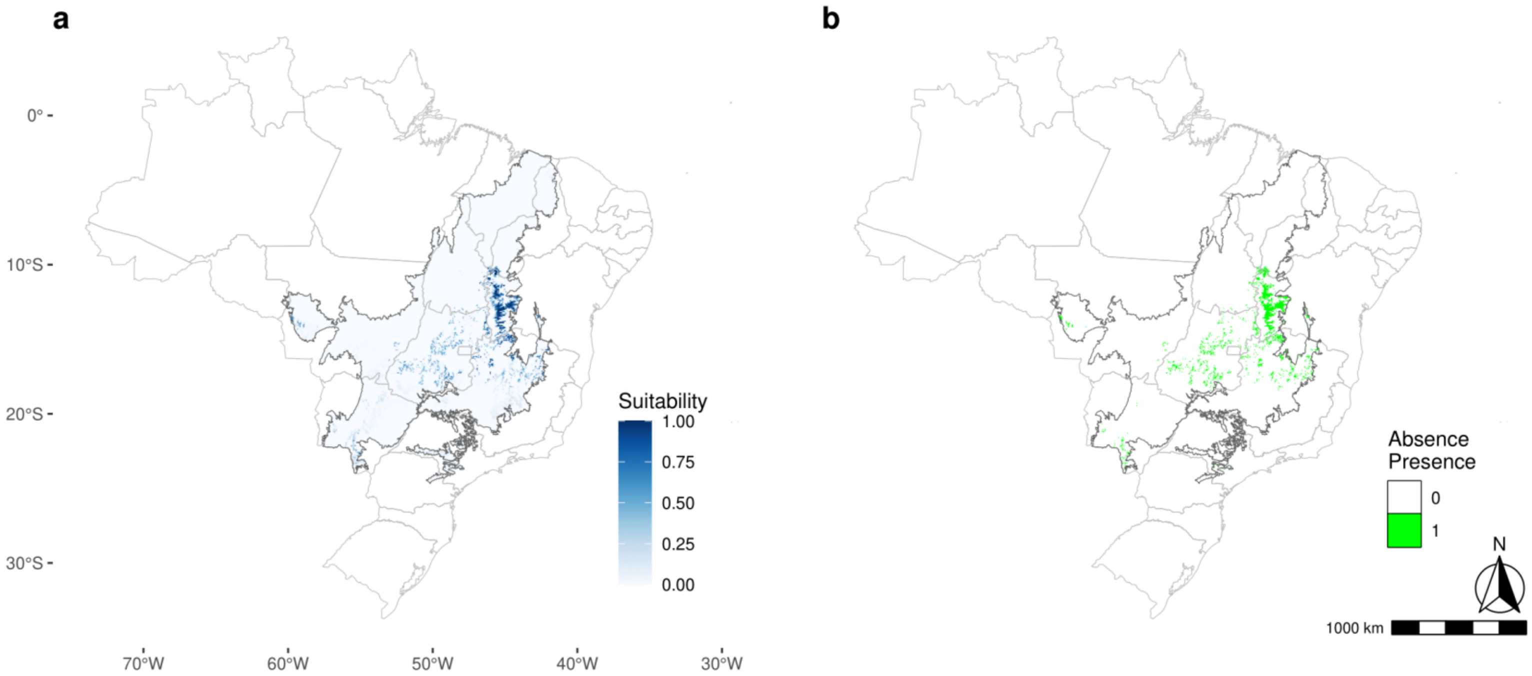
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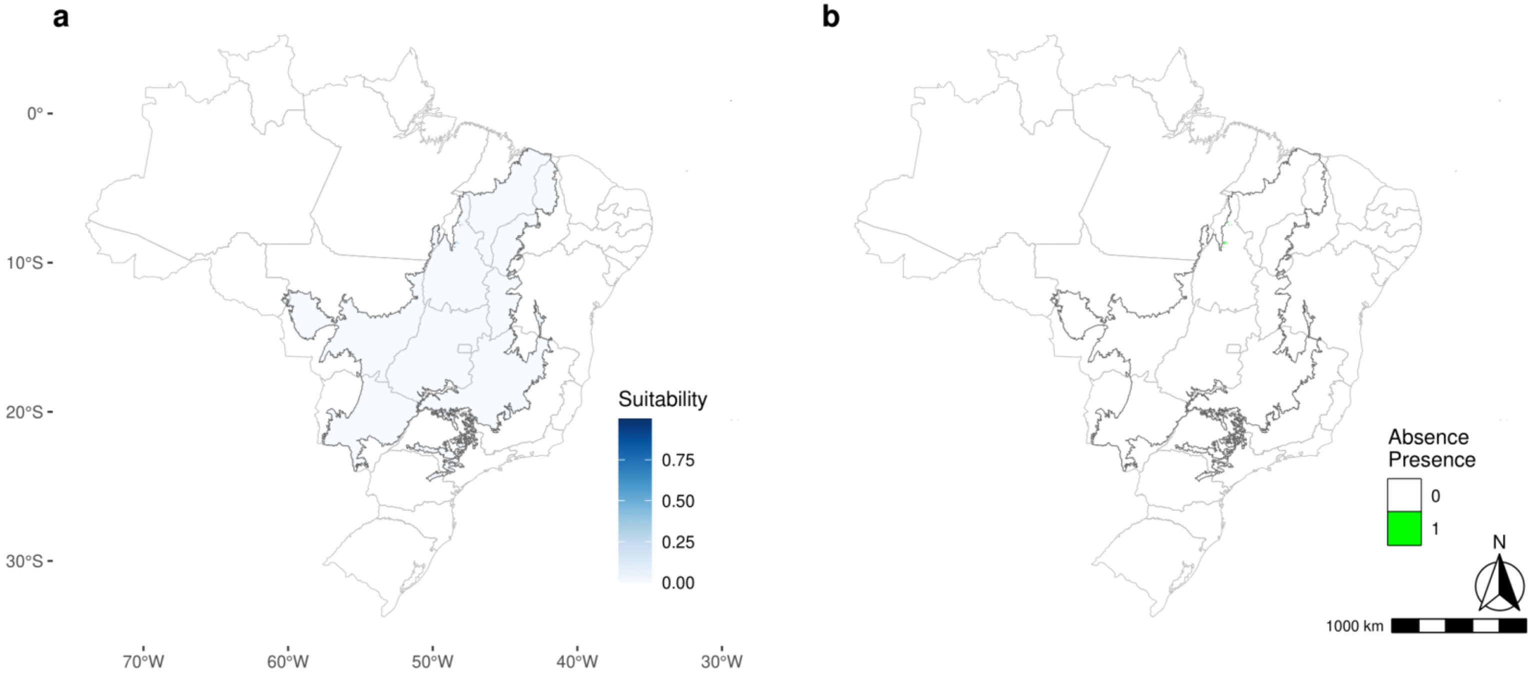
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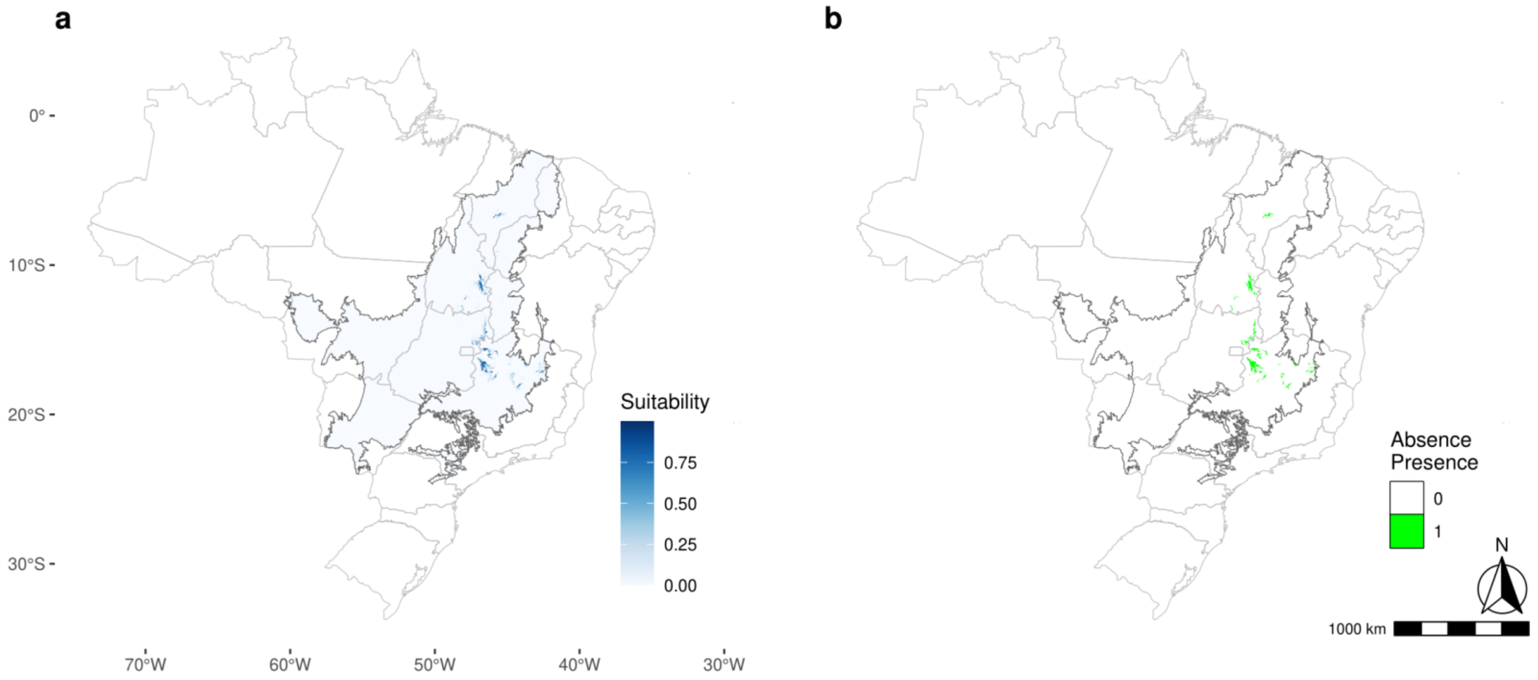
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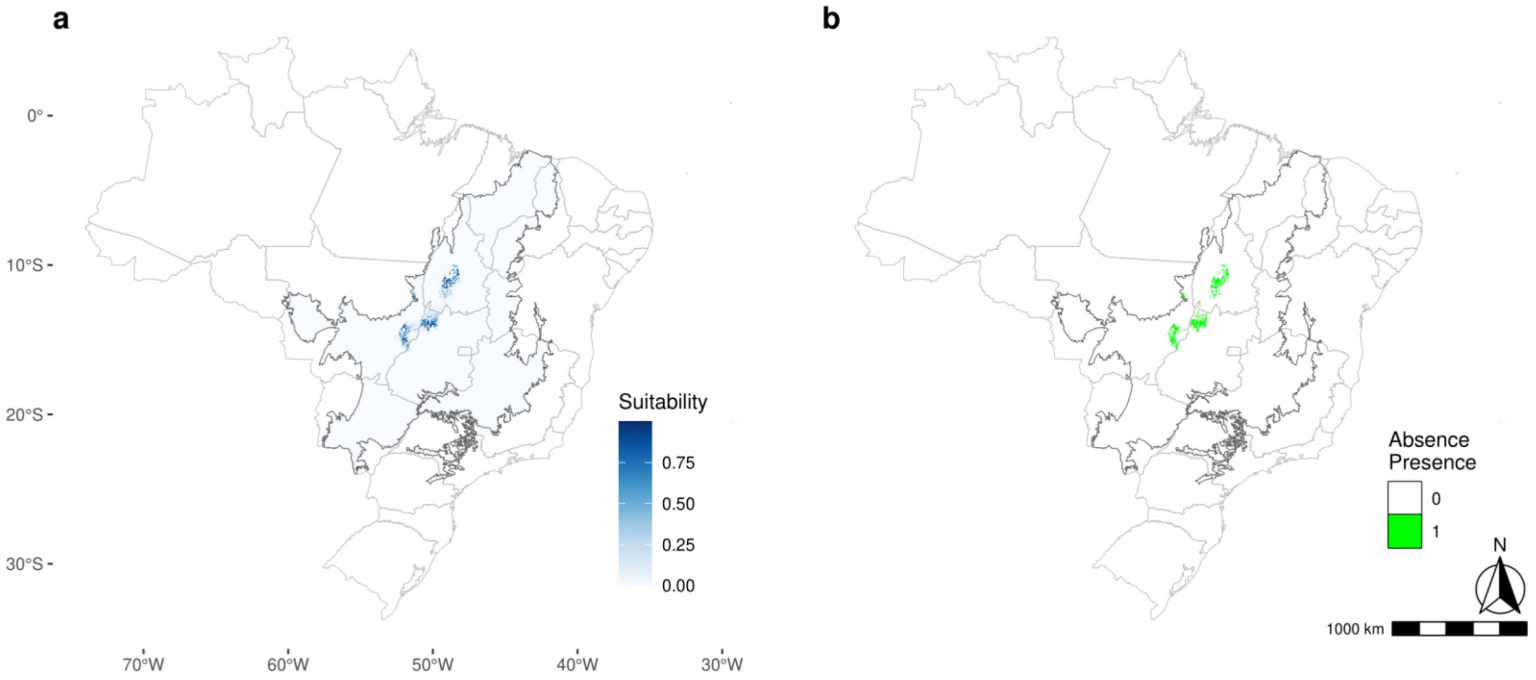
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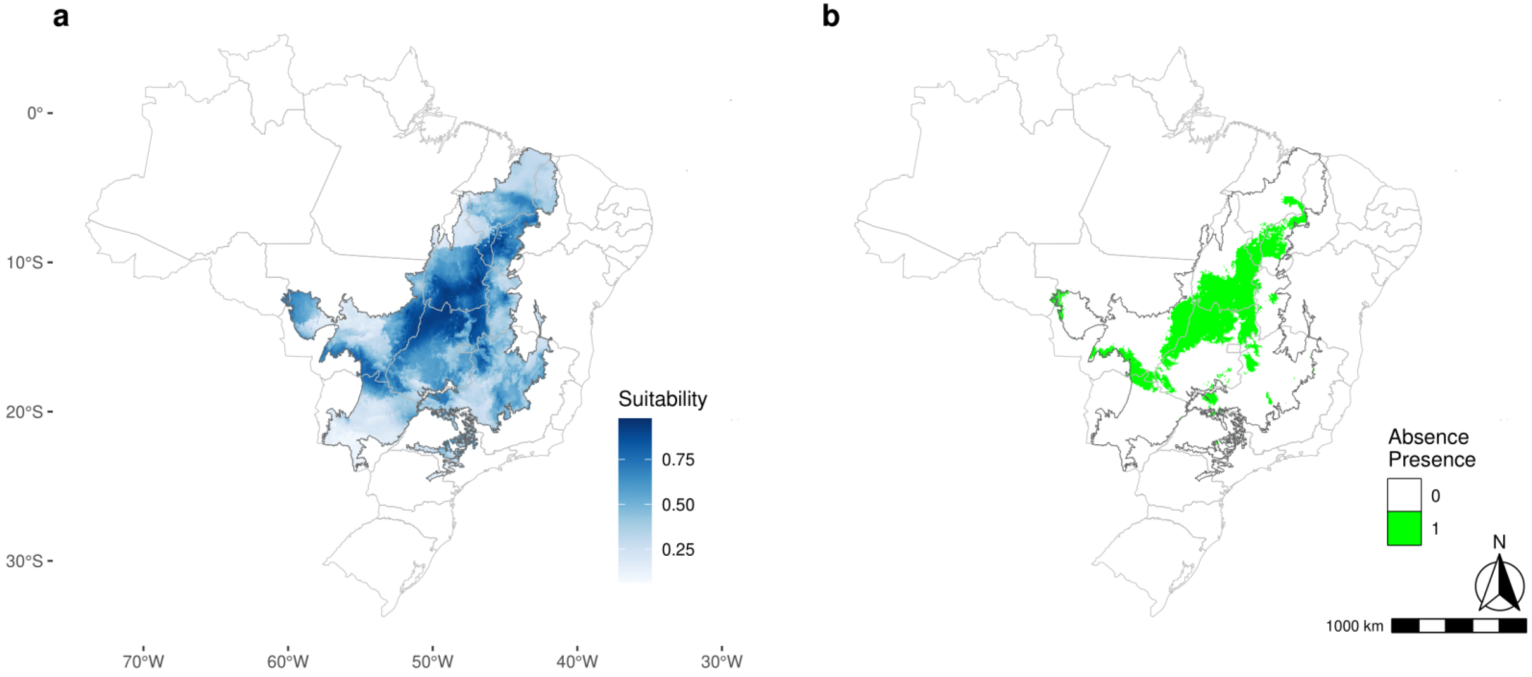
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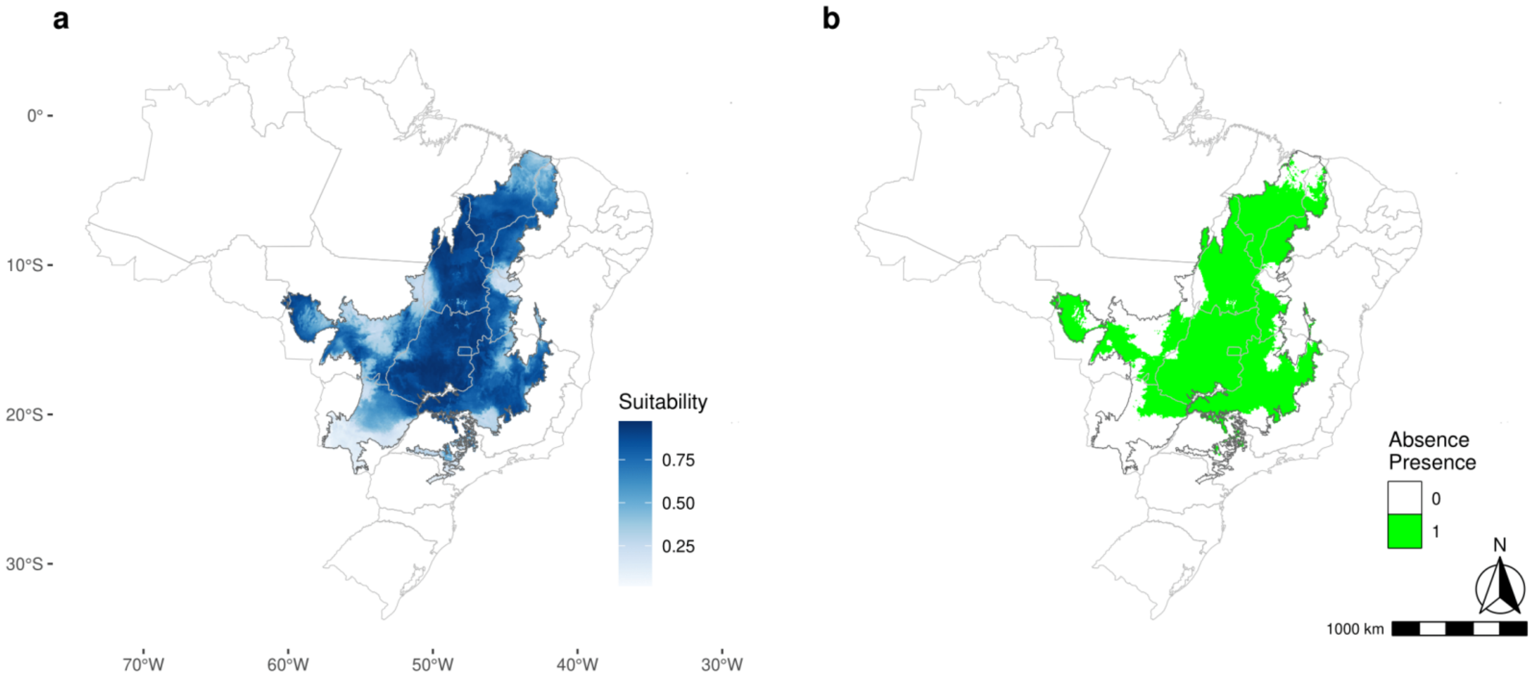
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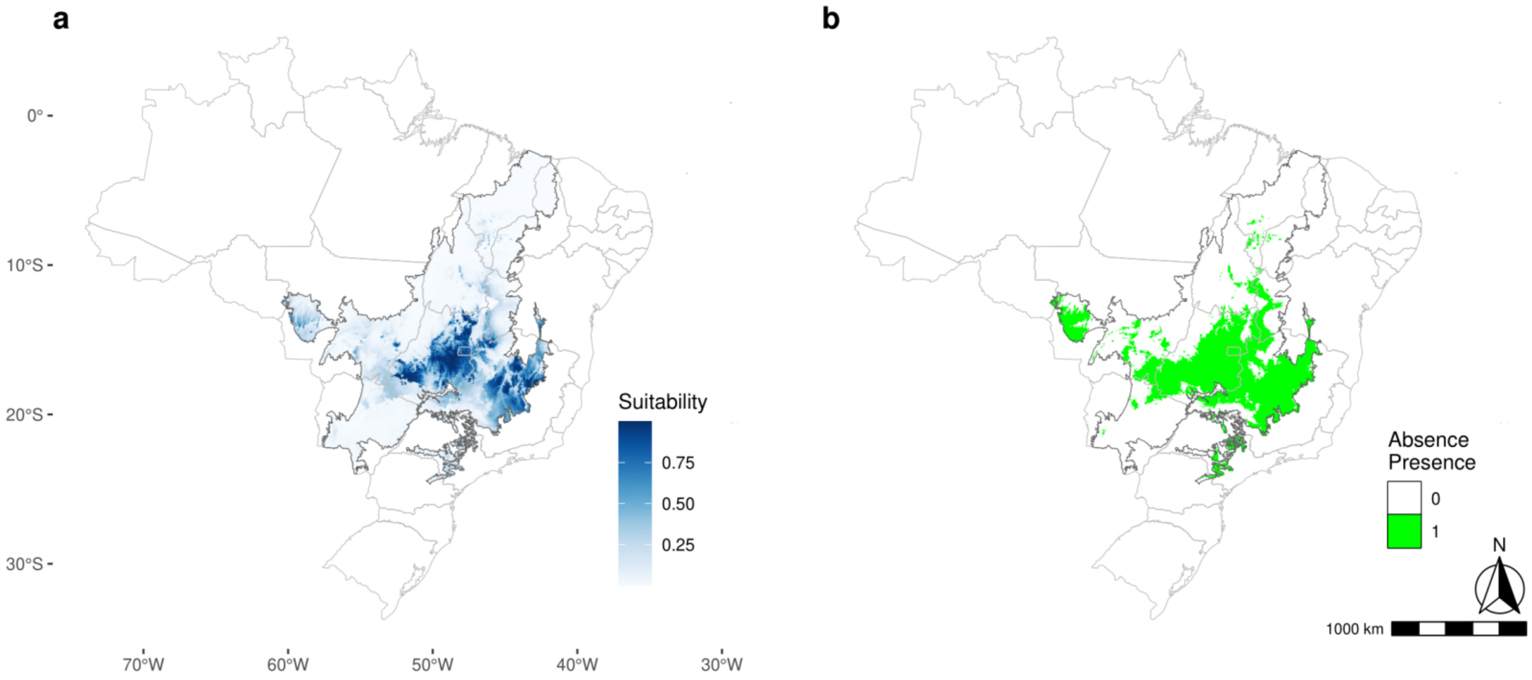
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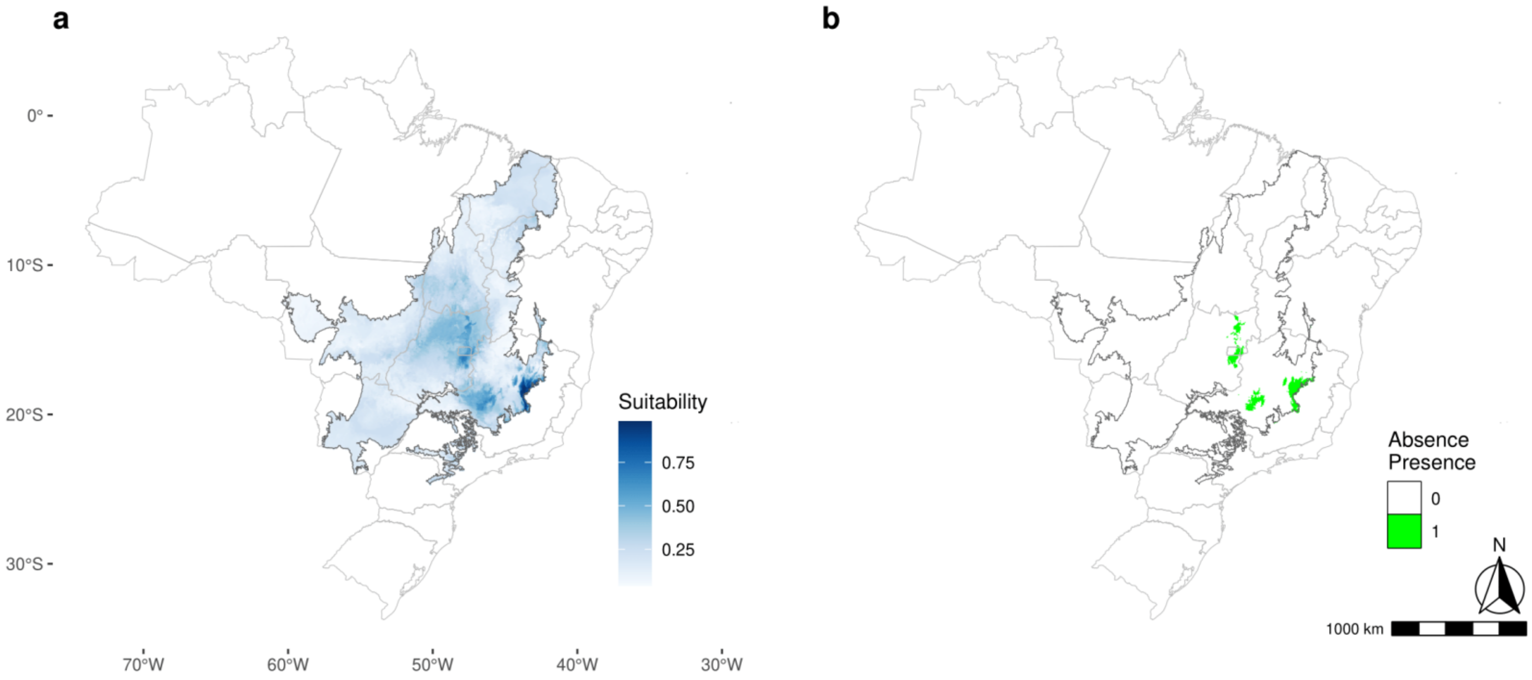
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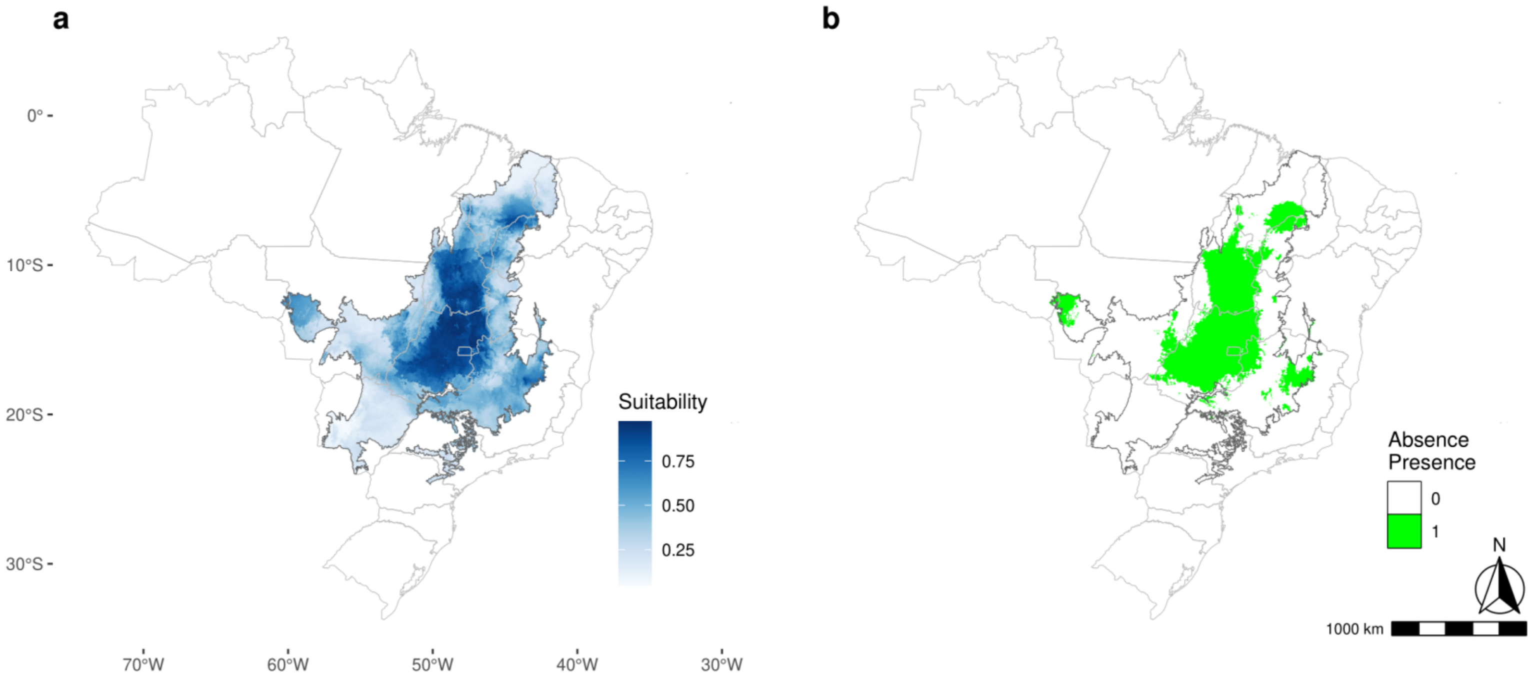
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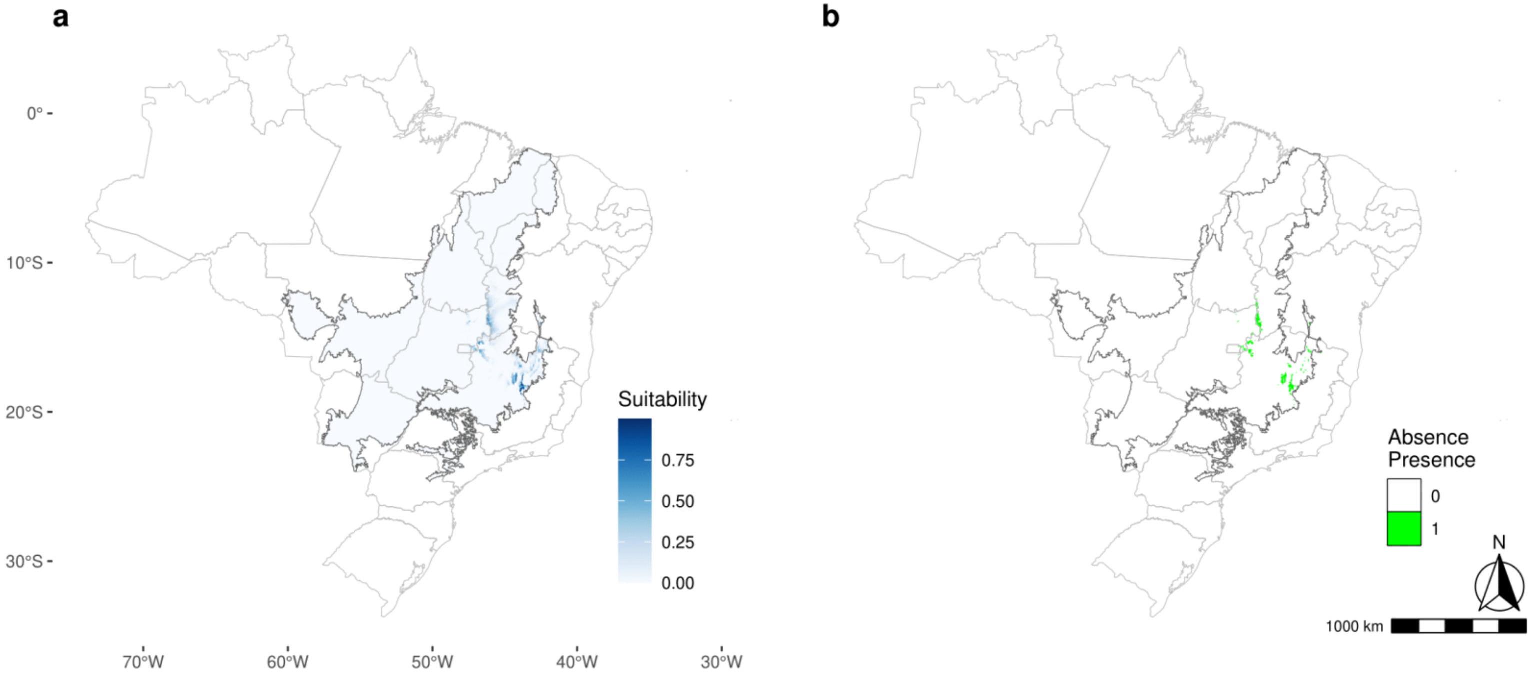
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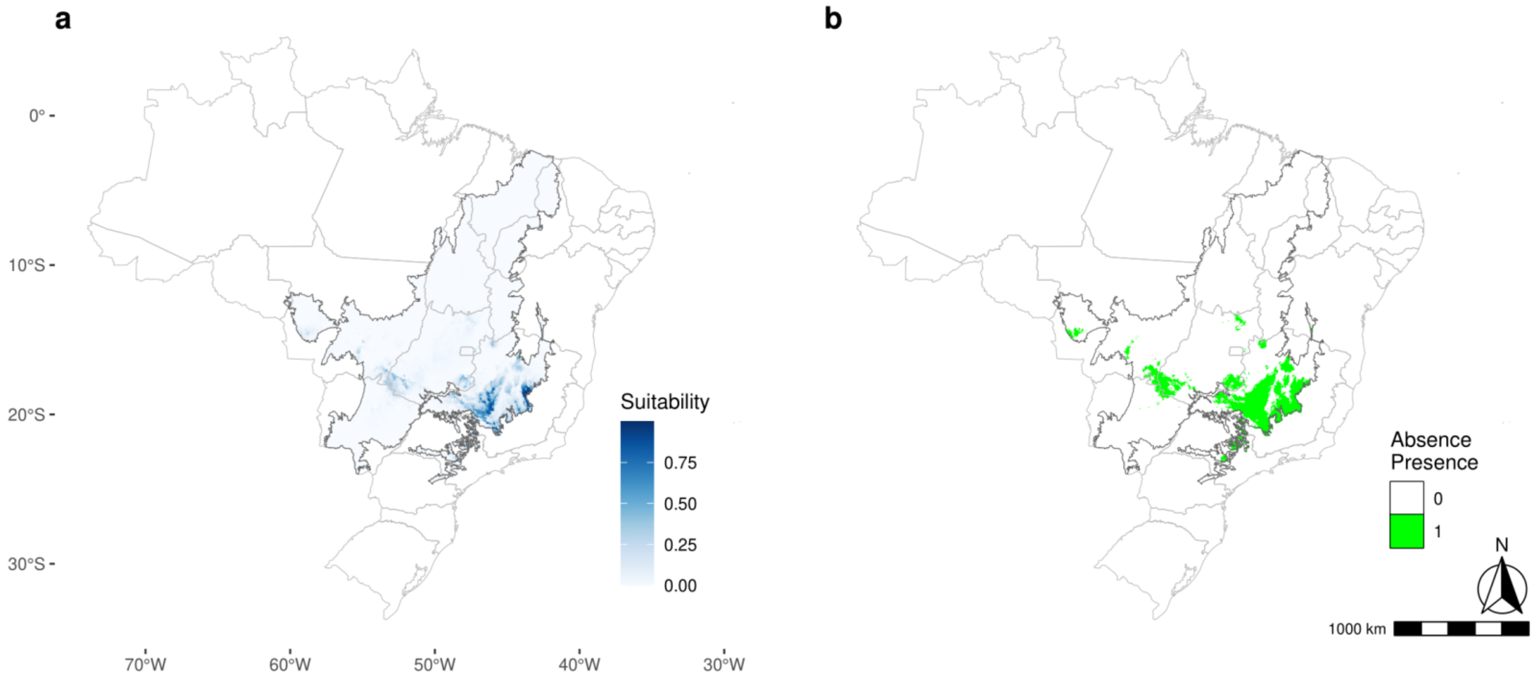
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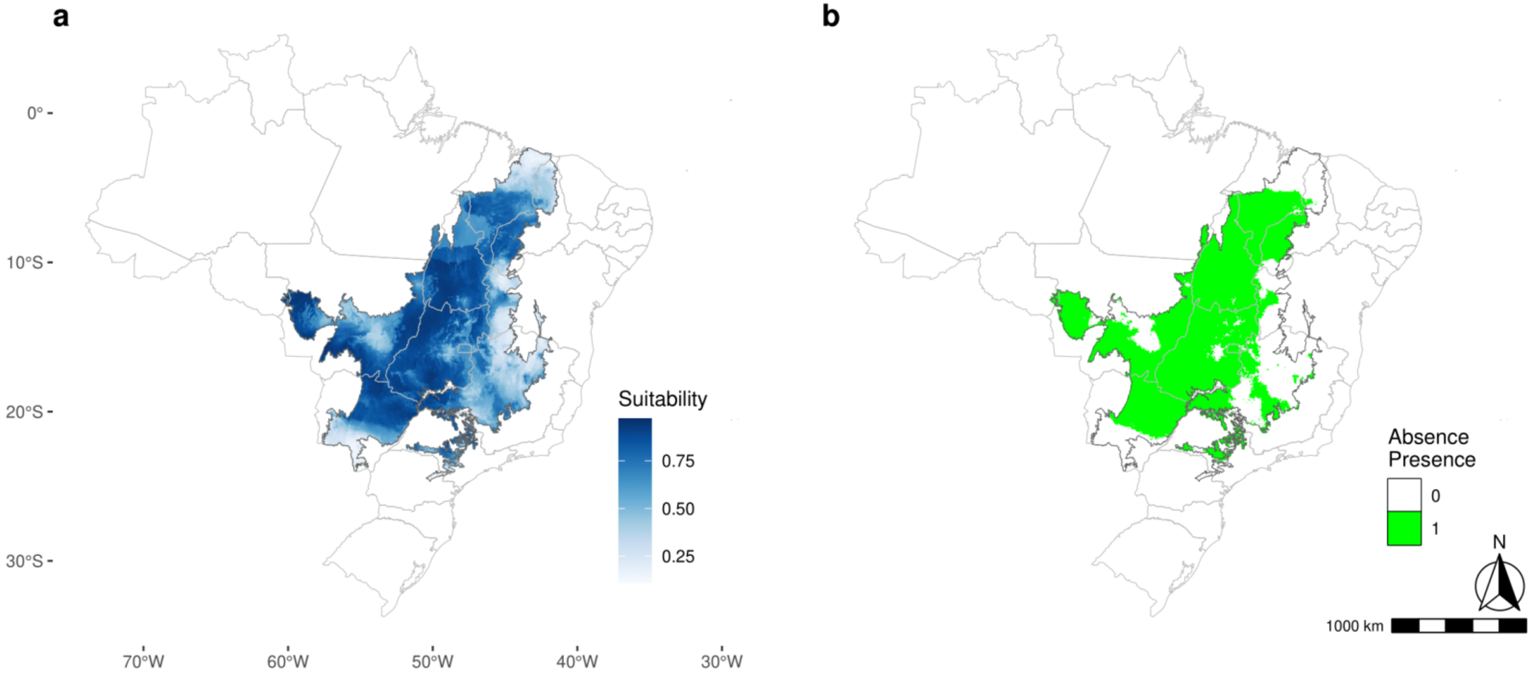
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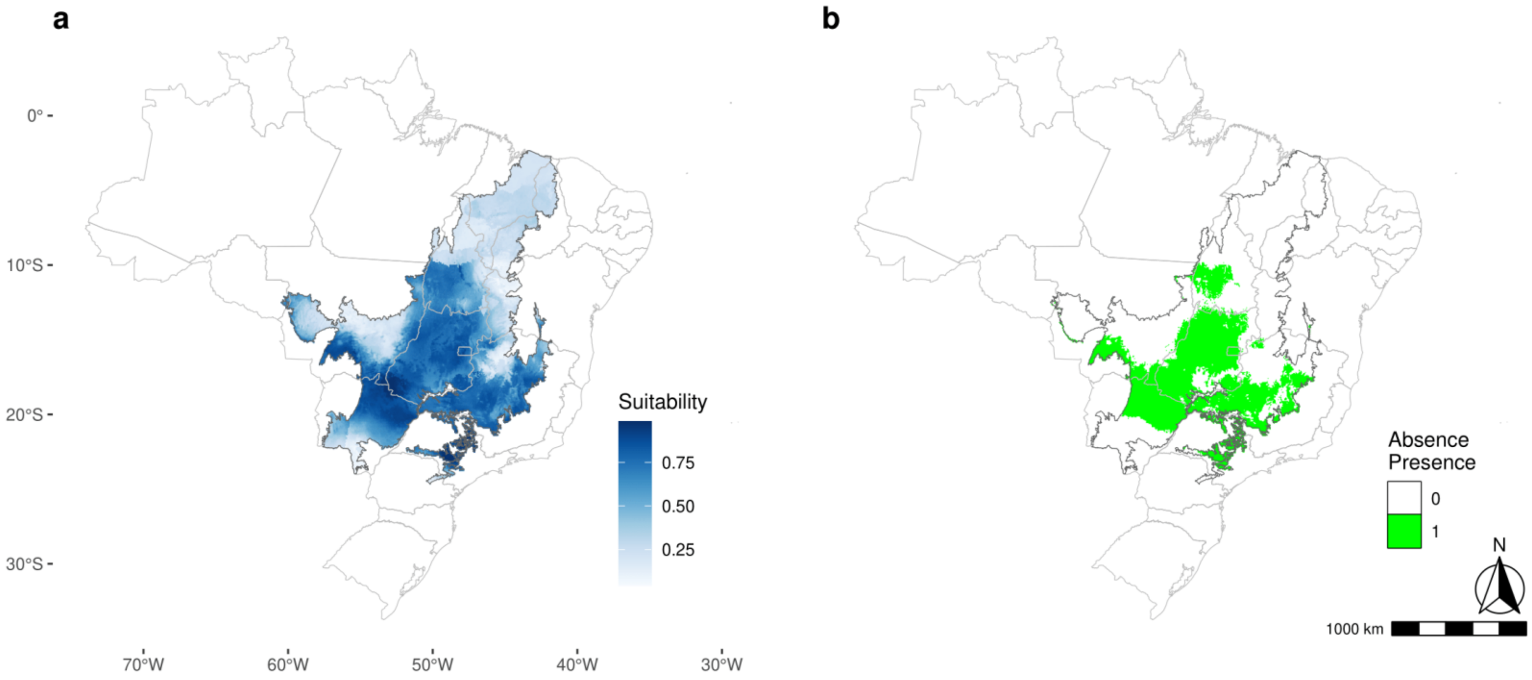
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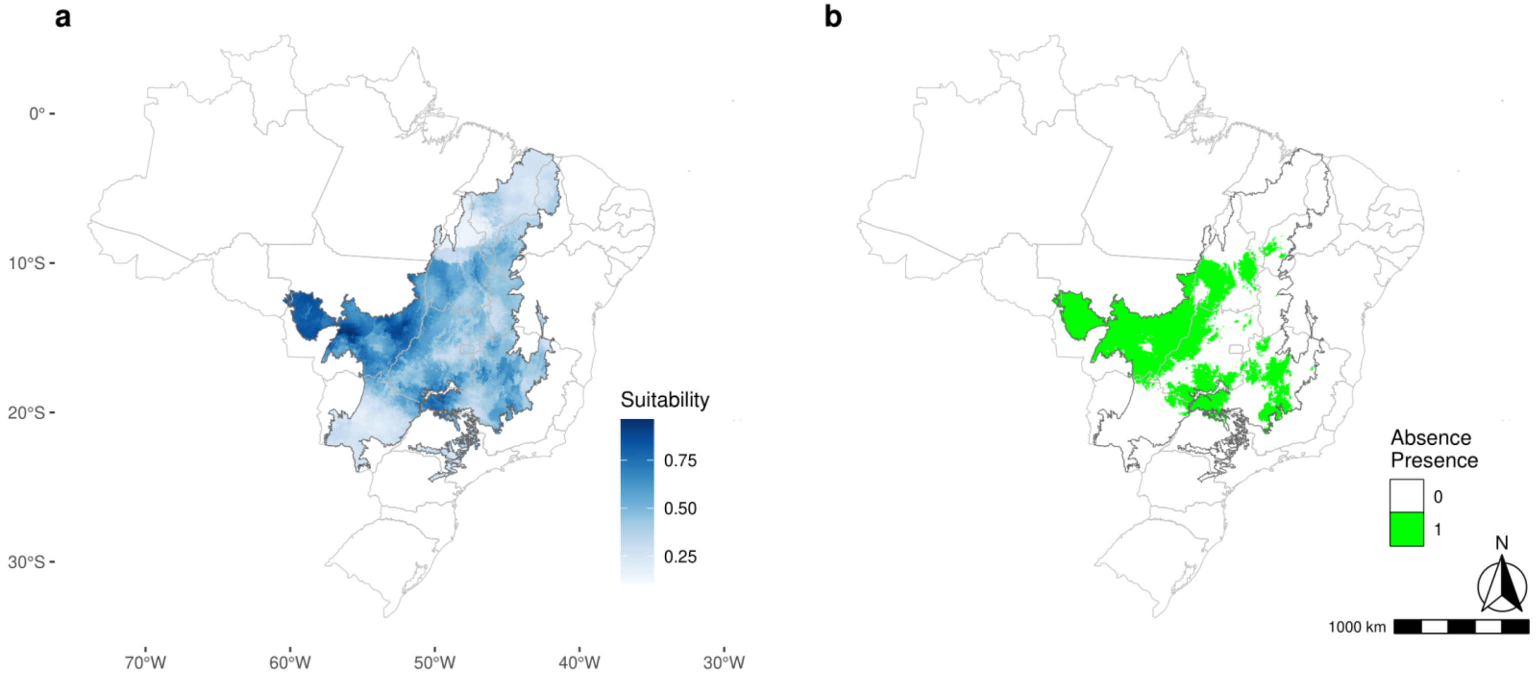
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Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S27

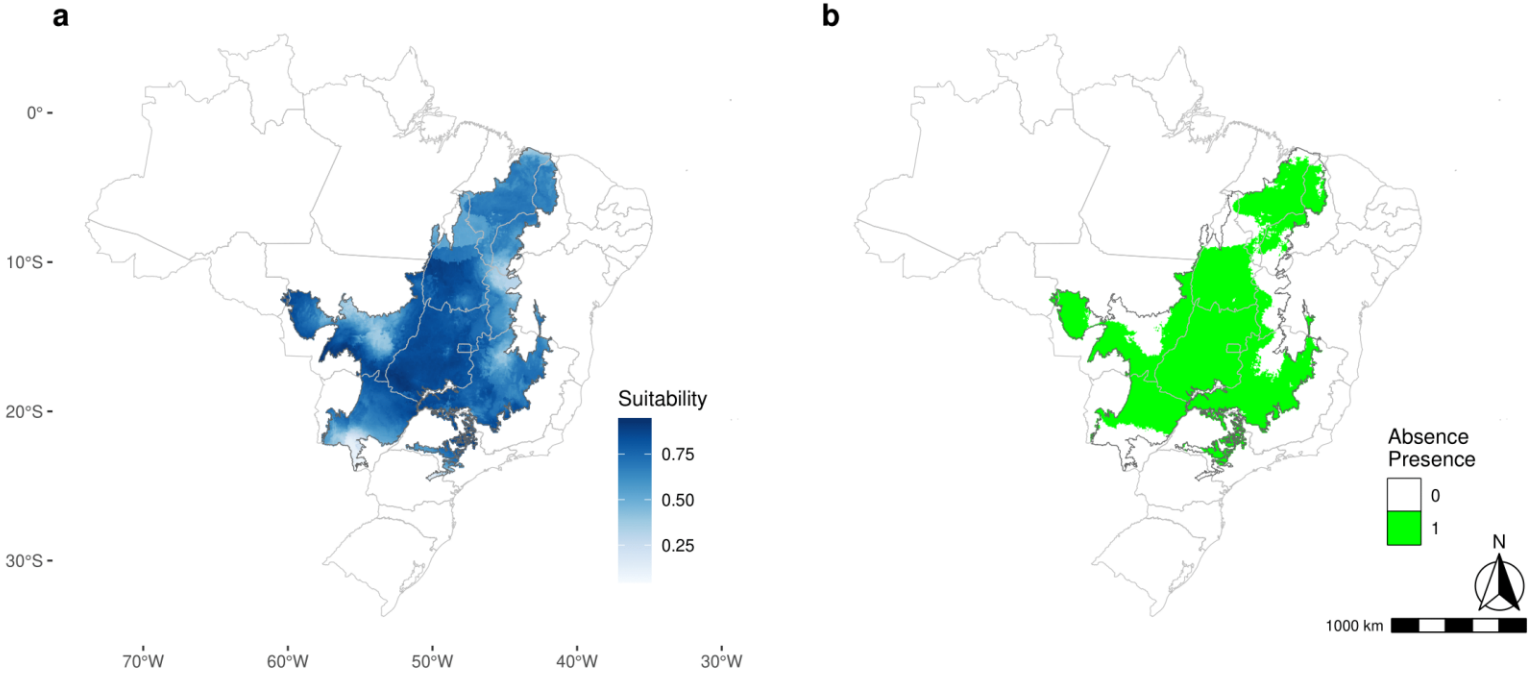

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S28

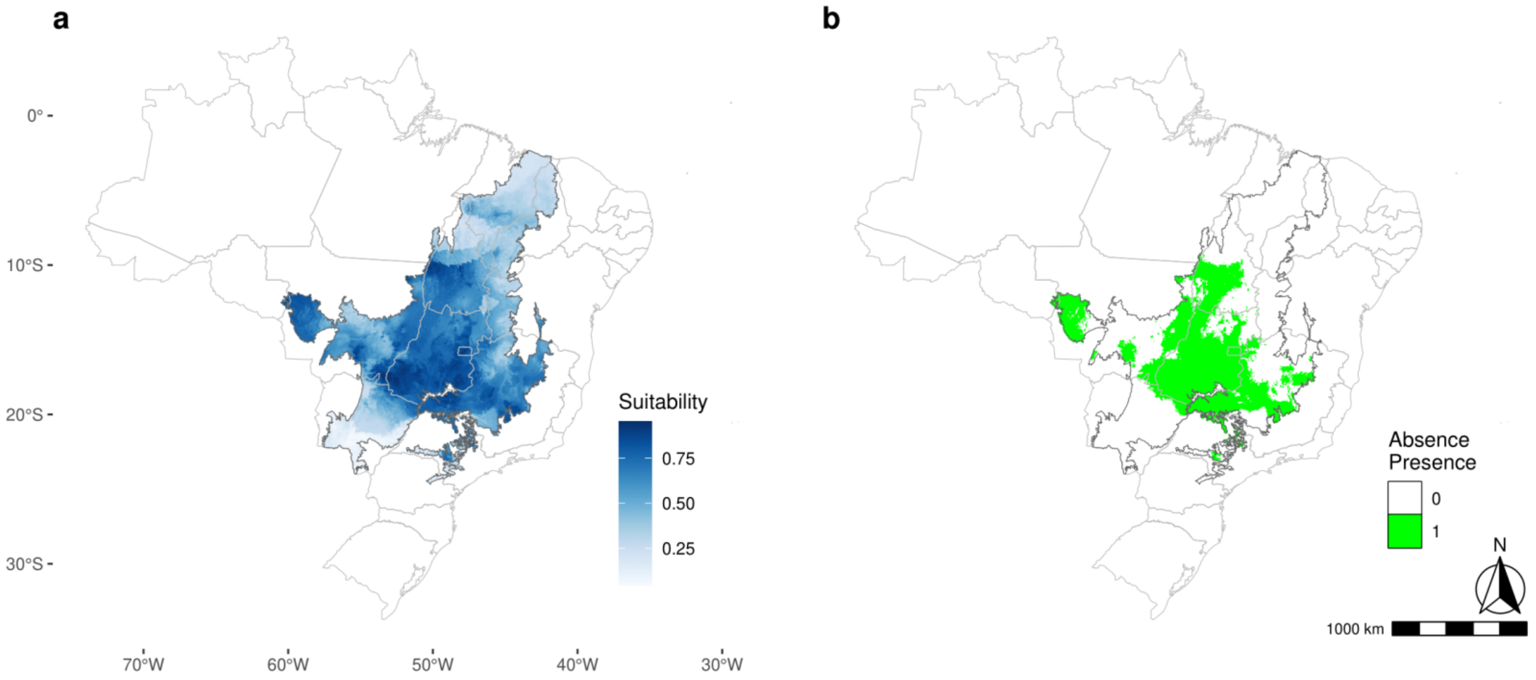

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S29

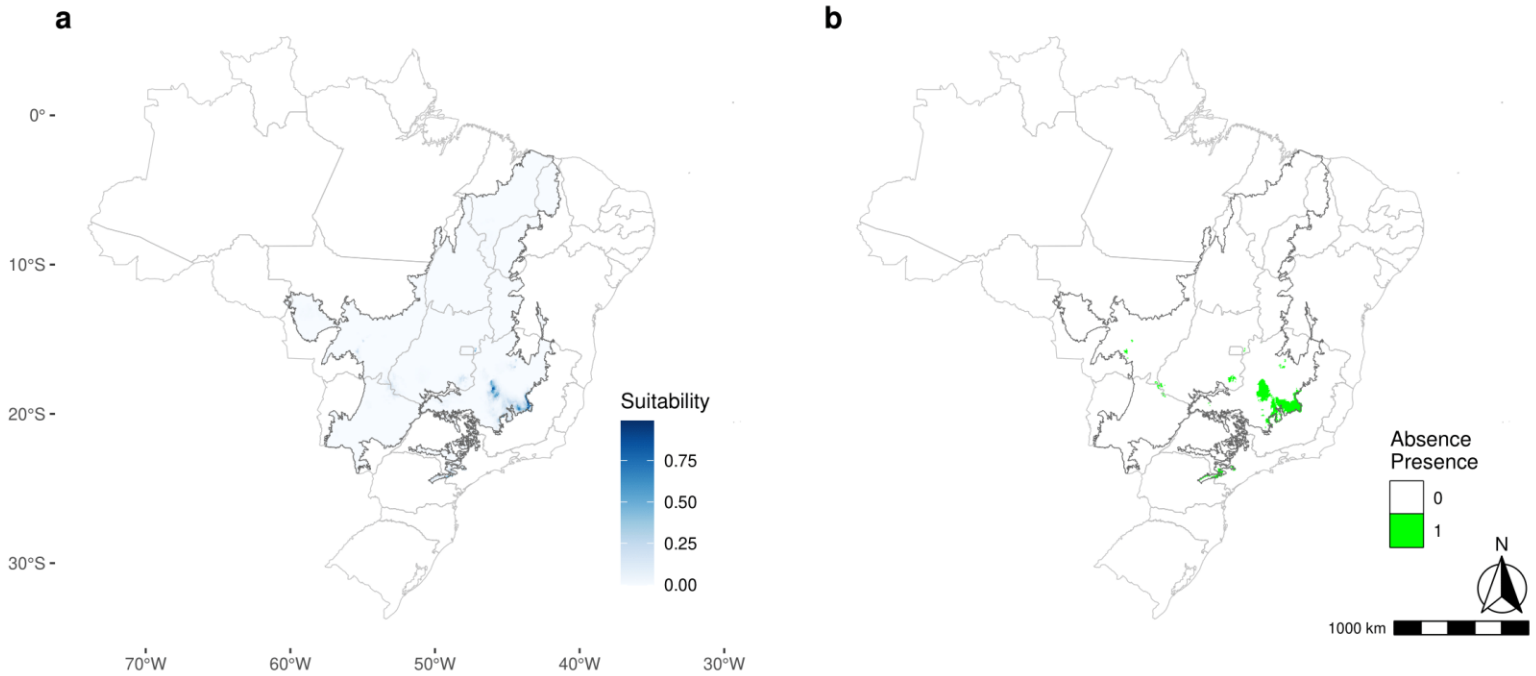

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S30

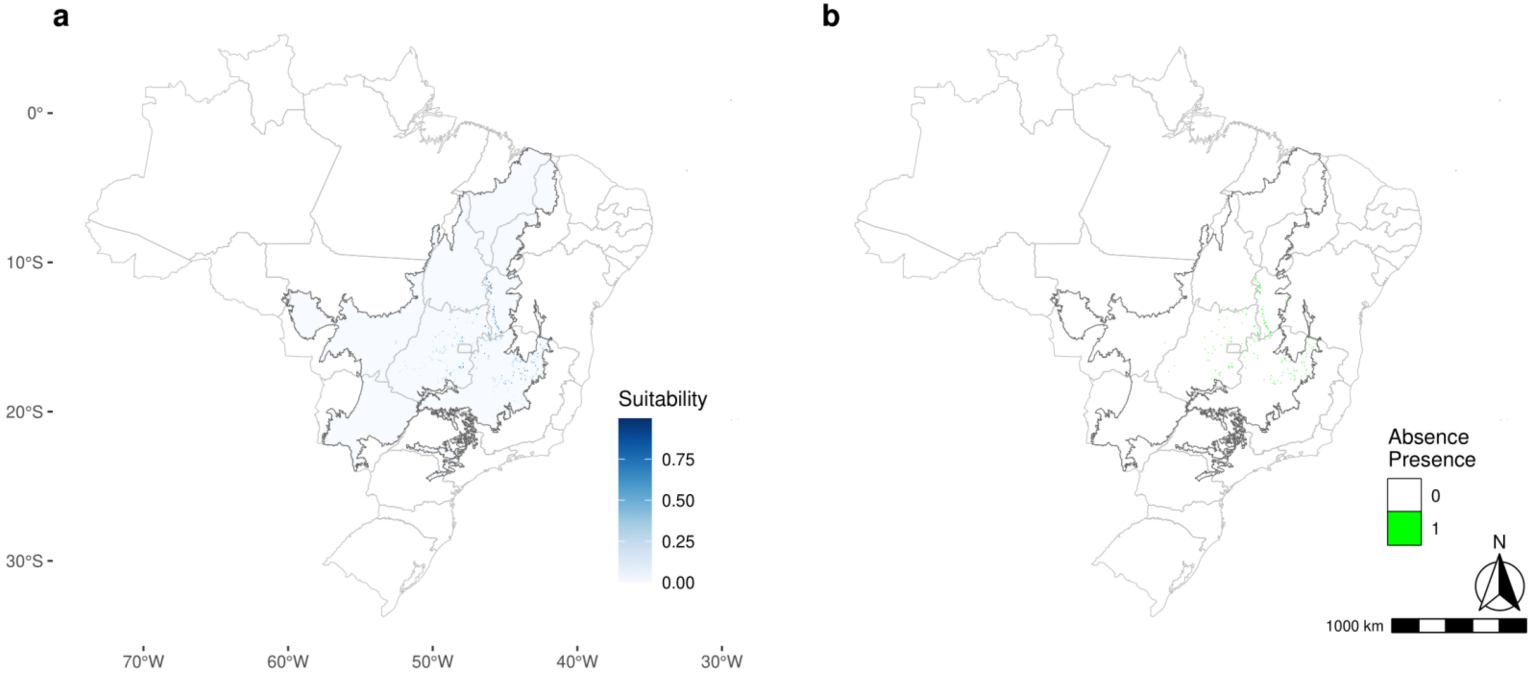

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S31

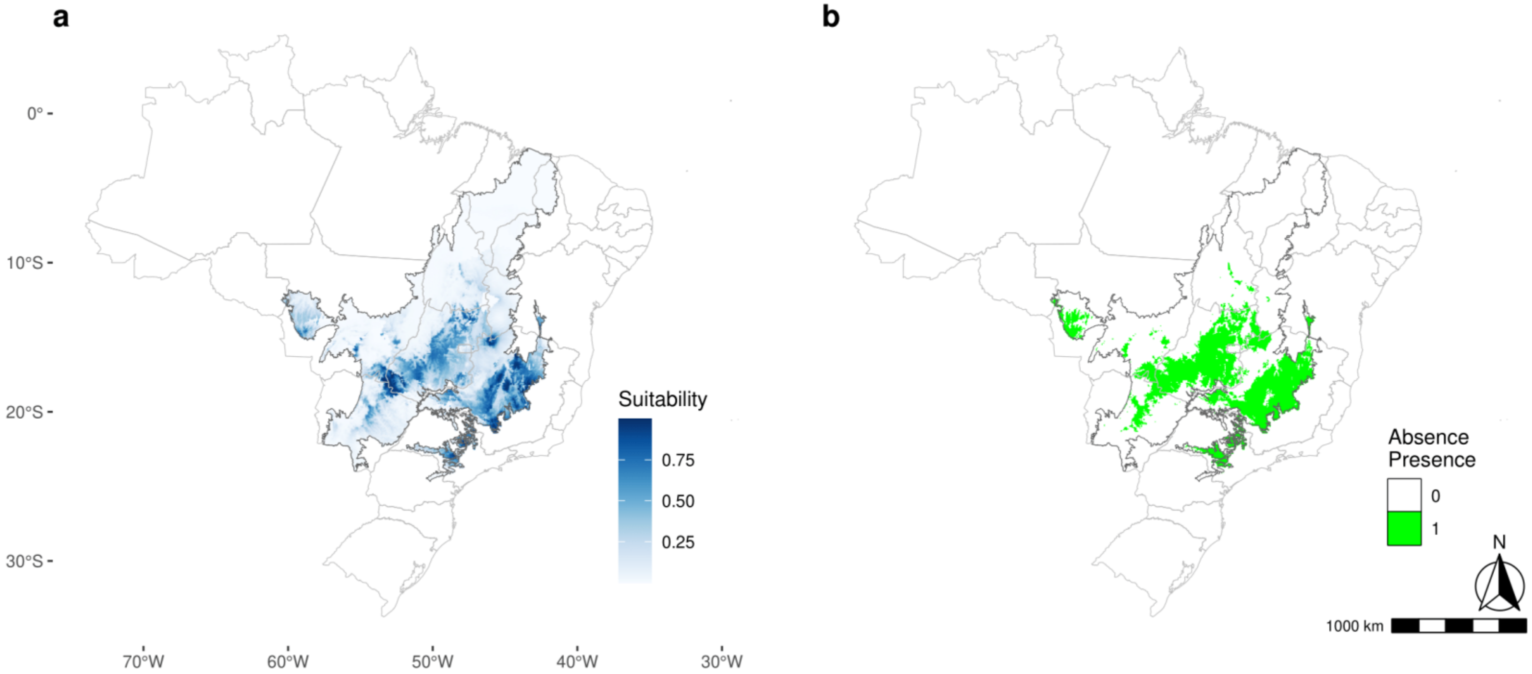

a
b
0° -
10°S -
20°S -
30°S -
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S32

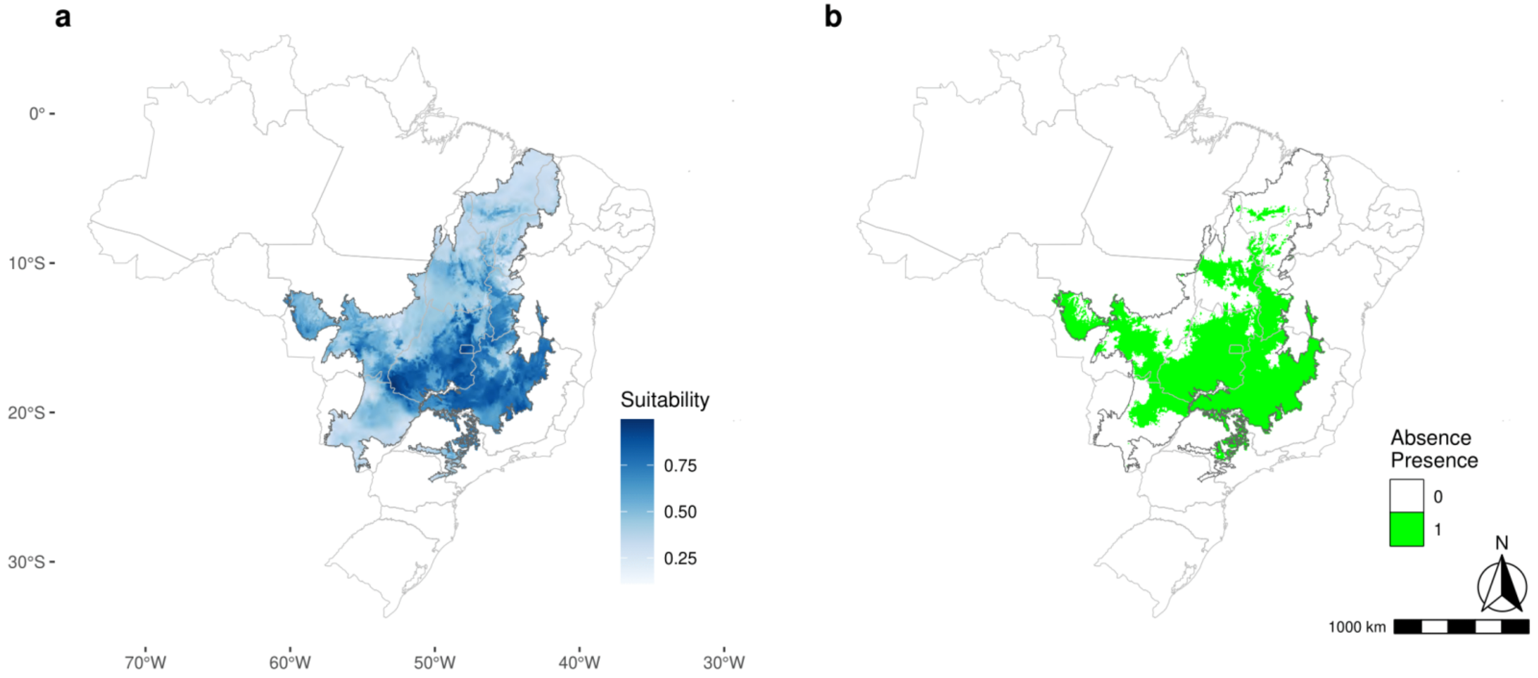

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S33

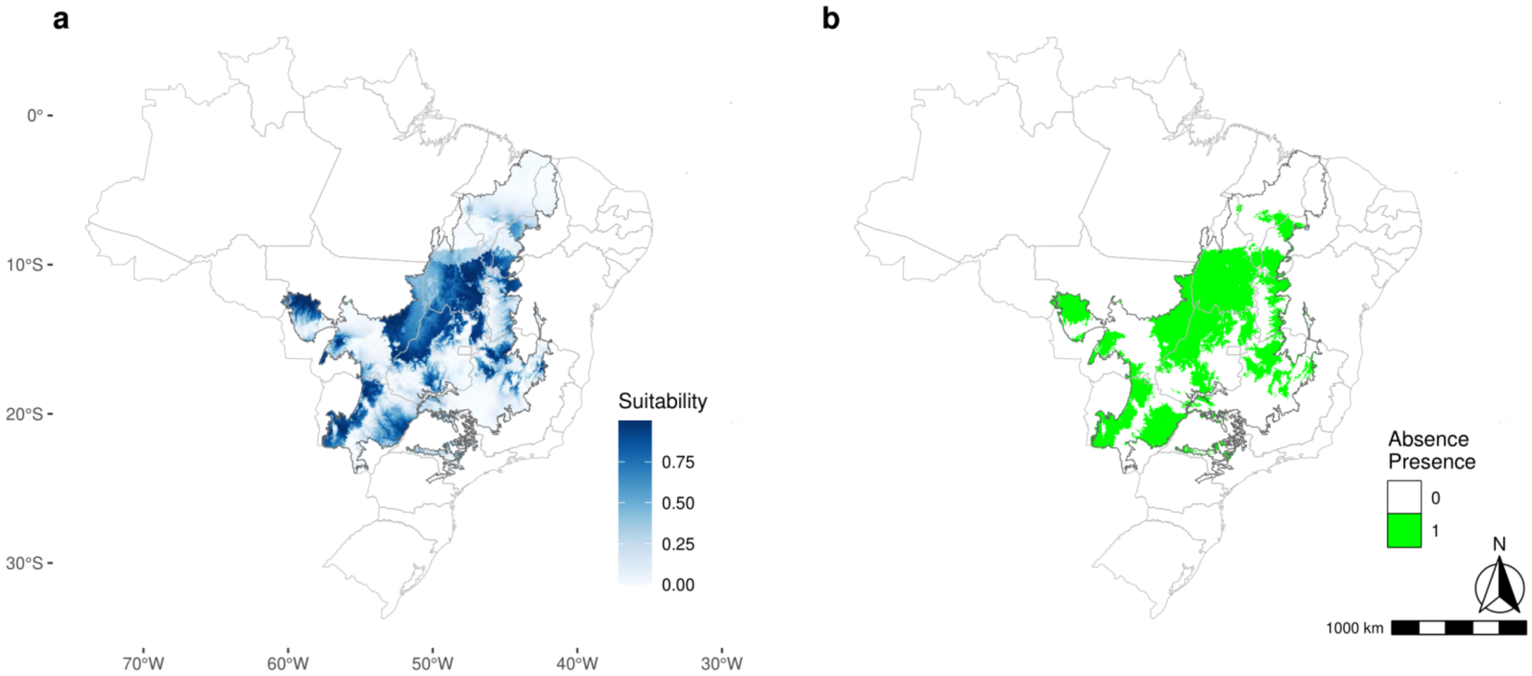

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S34

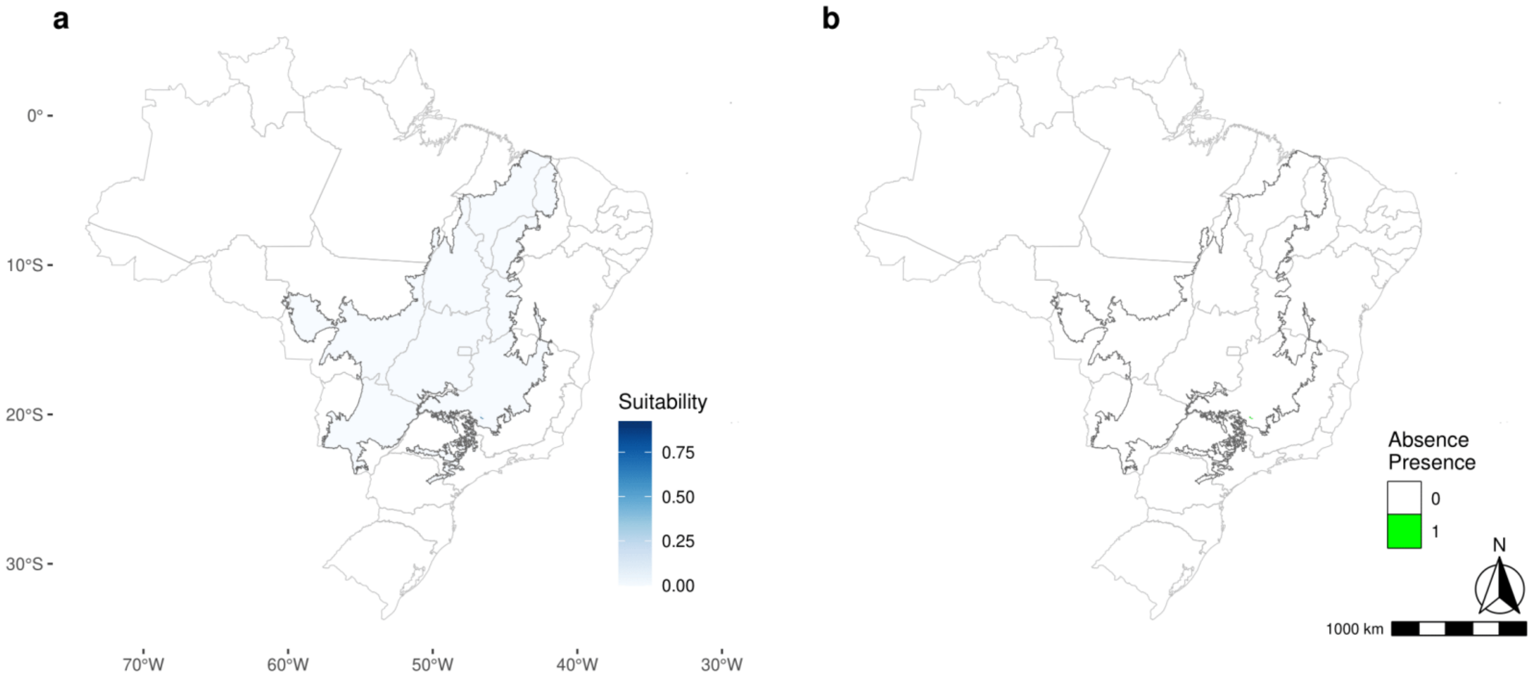

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S35

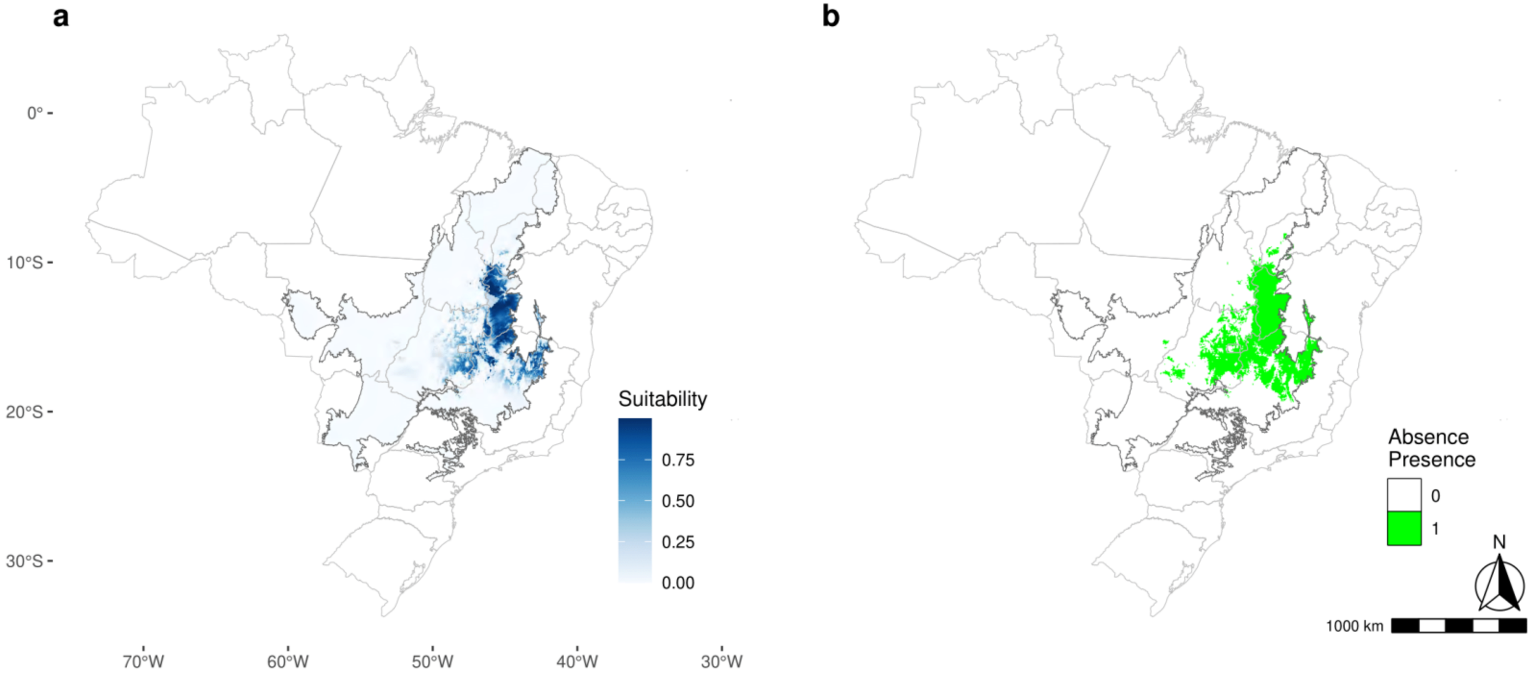

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S36

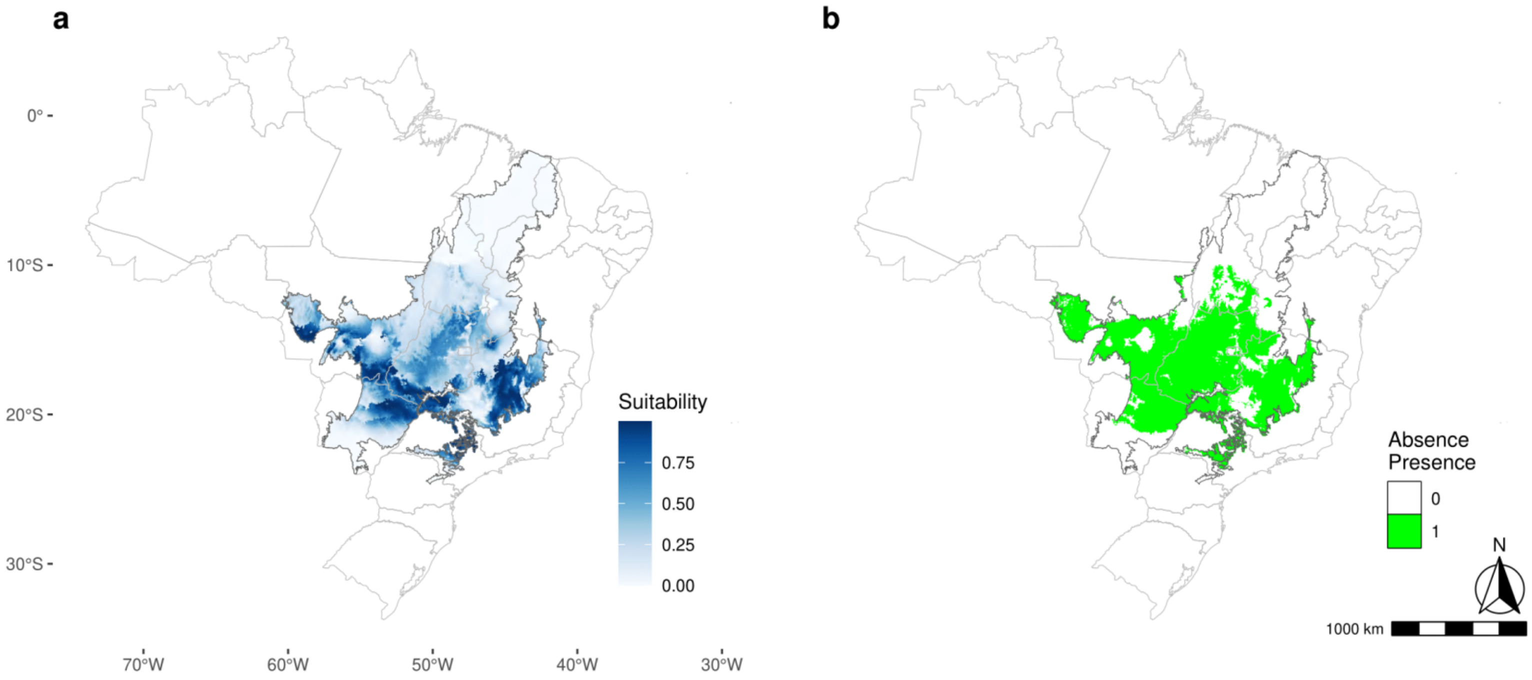

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S37

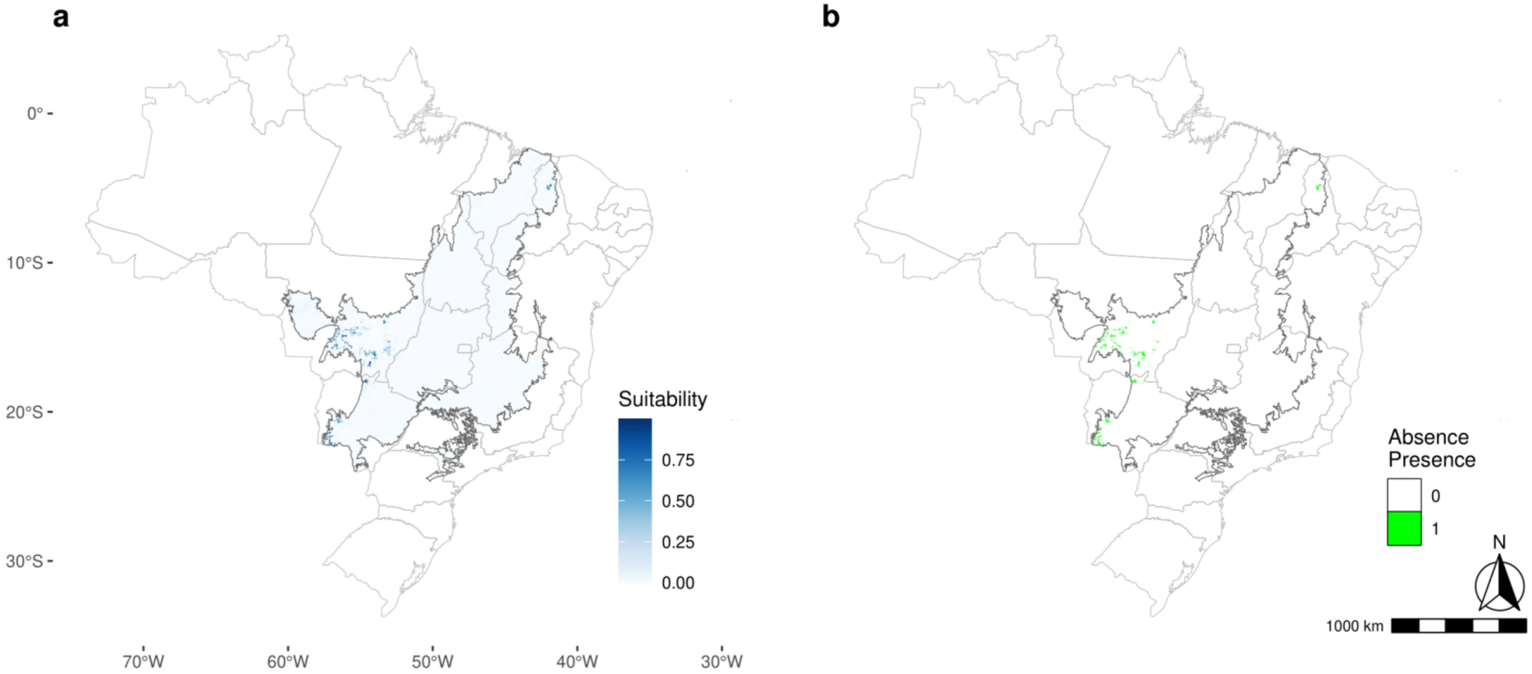

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S38

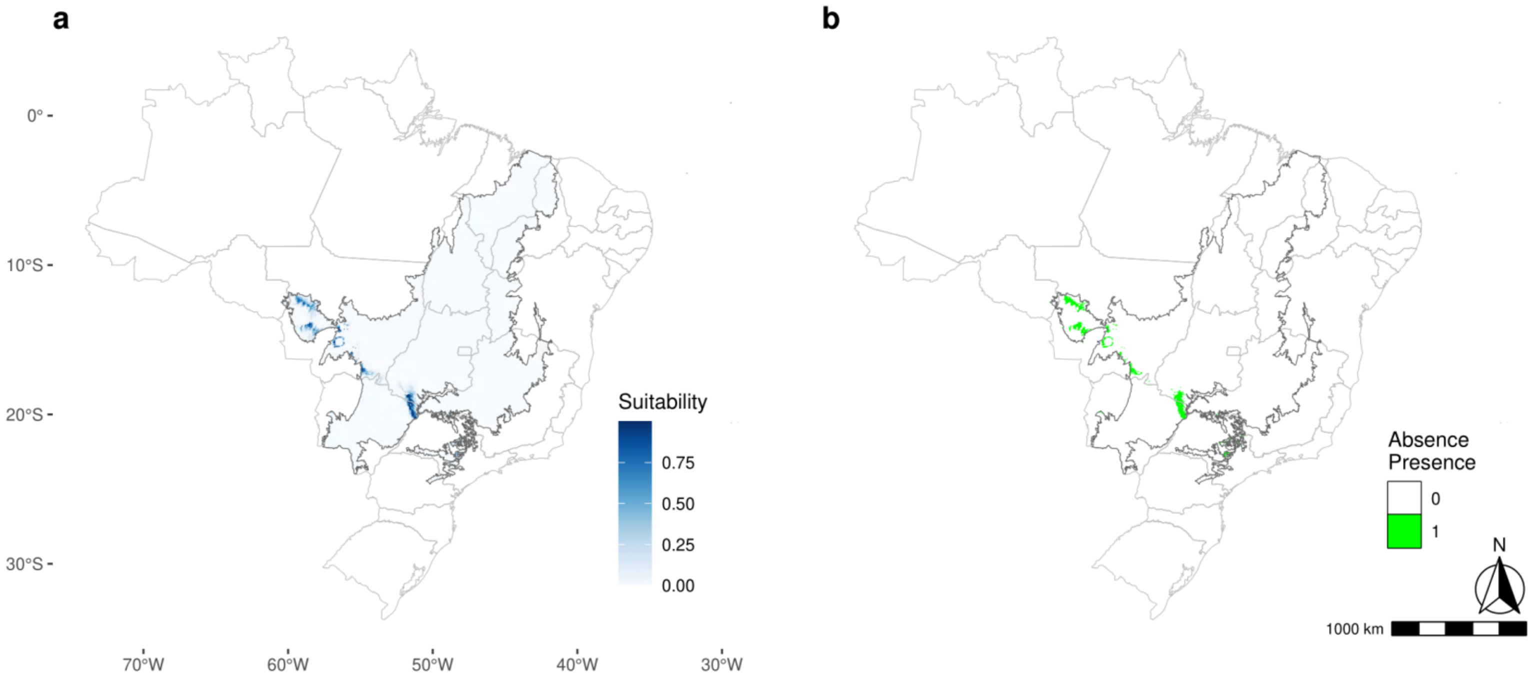

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
0.00
Absence
Presence
0
1
N
1000 km

Figure S39

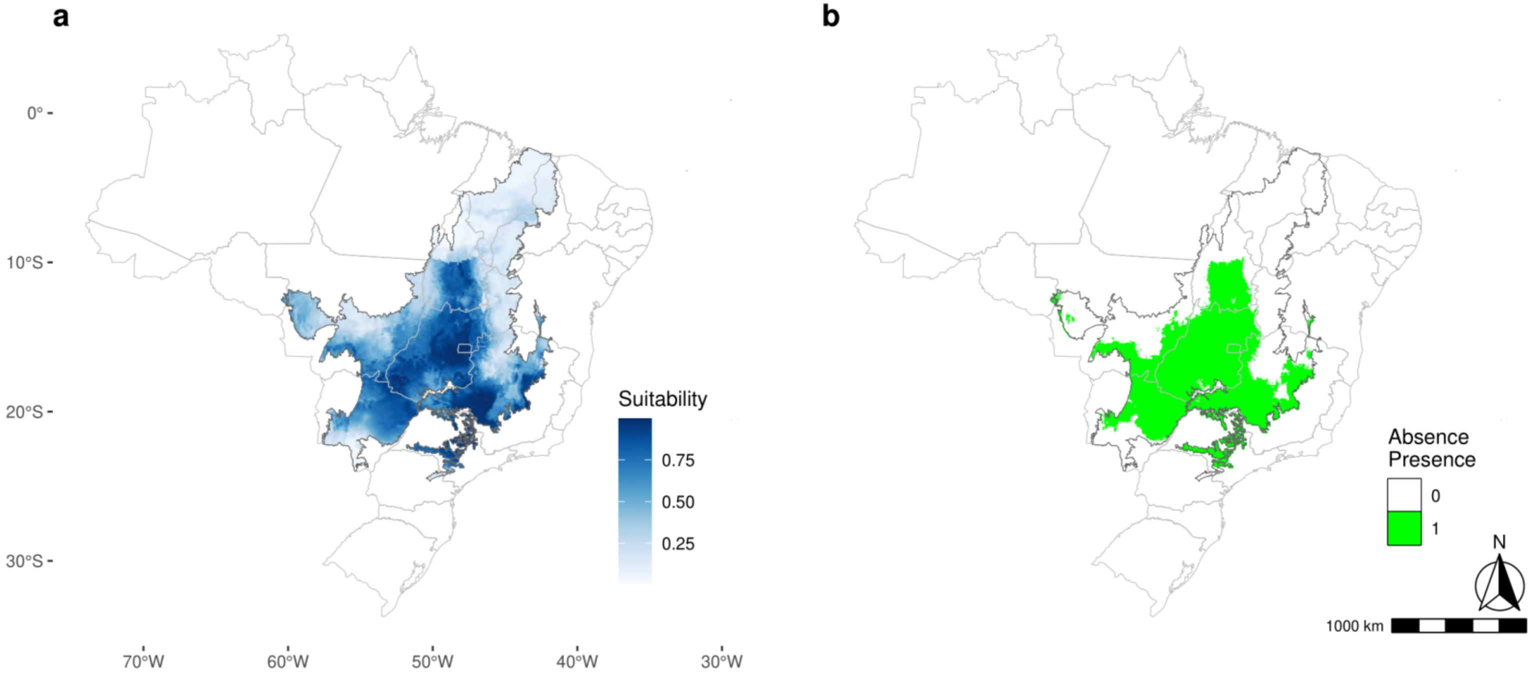

a
b
0° -
10°S -
20°S -
30°S -
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S40

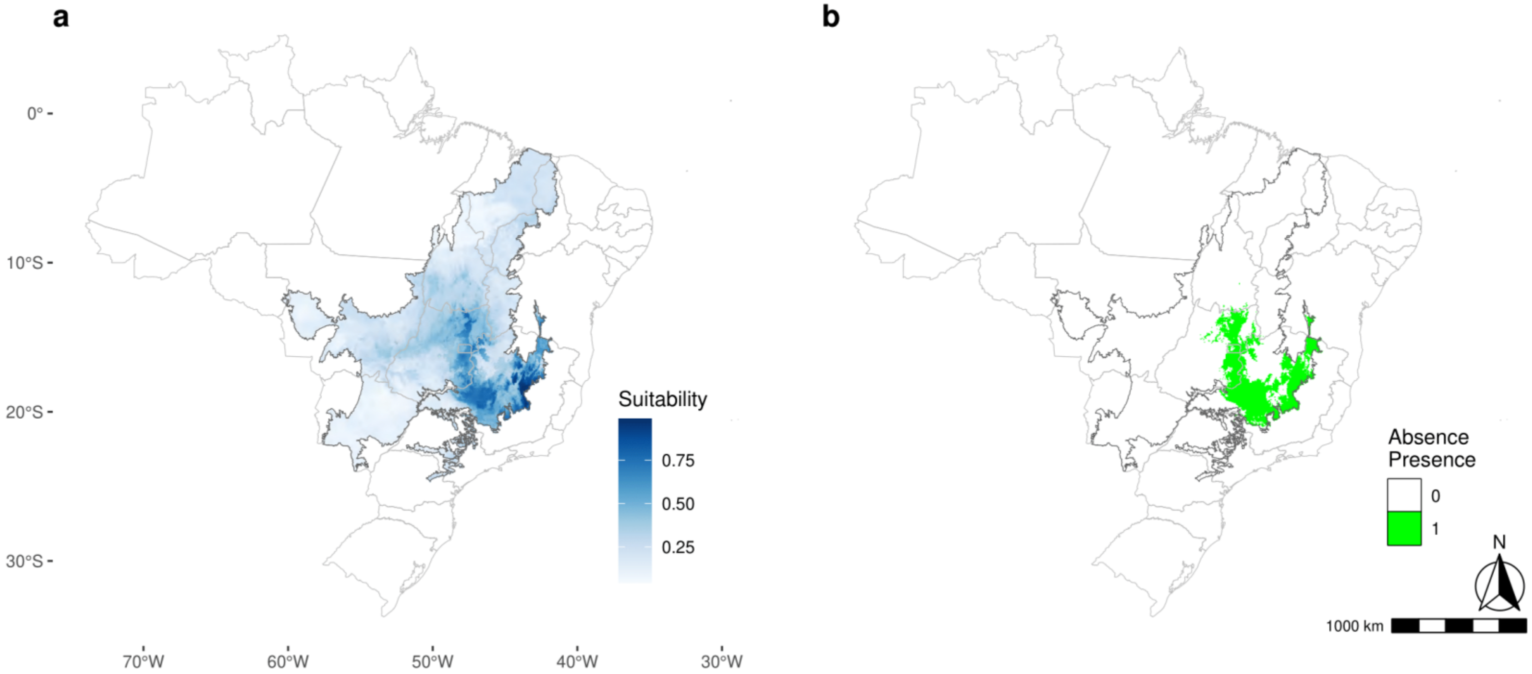

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S41

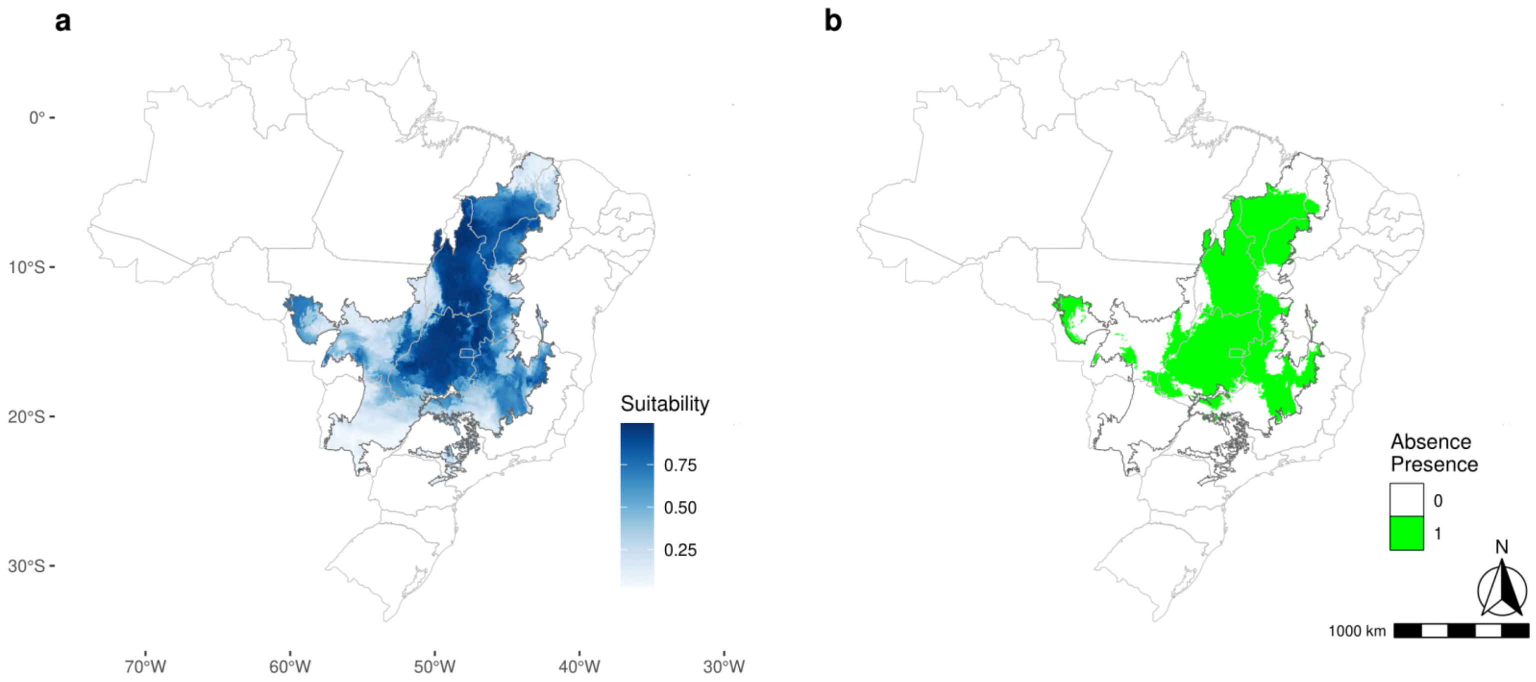
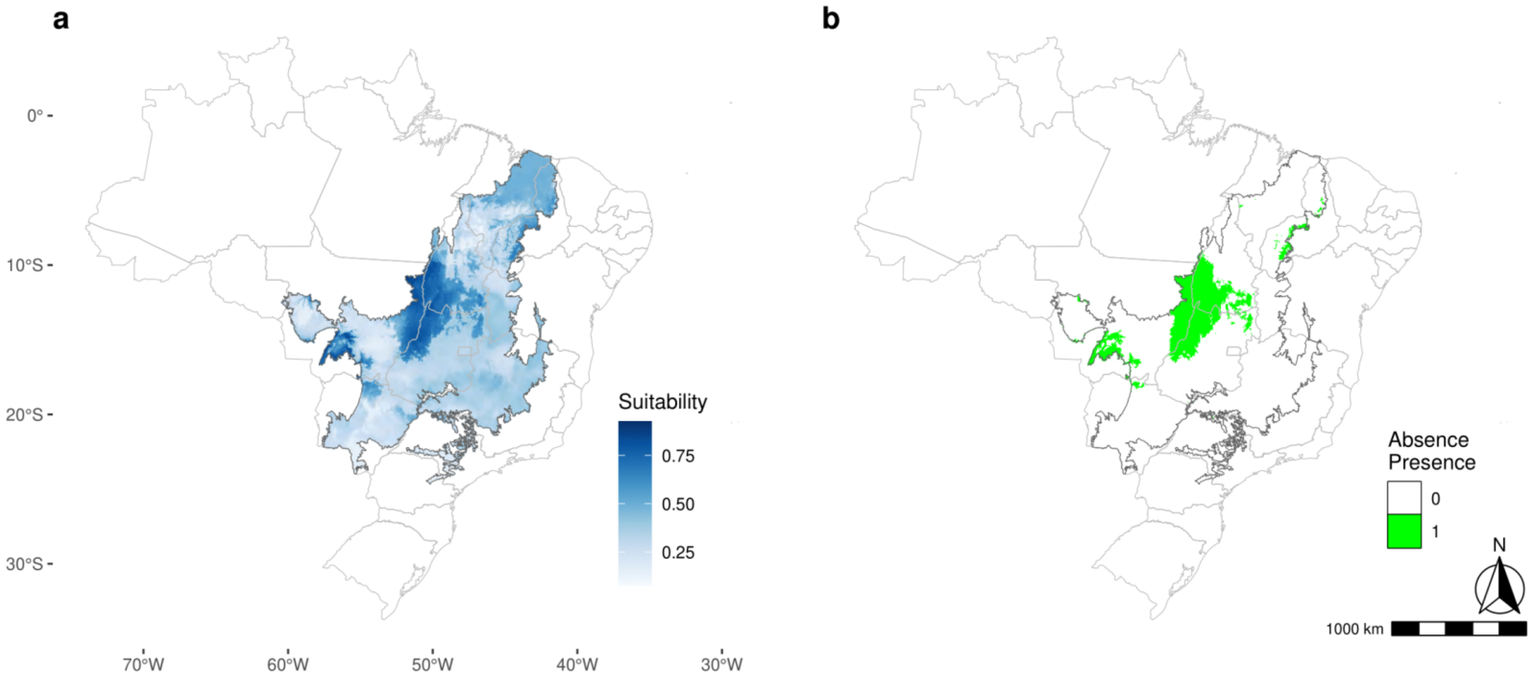

a
b
0° -
10°S -
20°S -
30°S -
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S42



a
b
0° -
10°S -
20°S -
30°S -
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S43

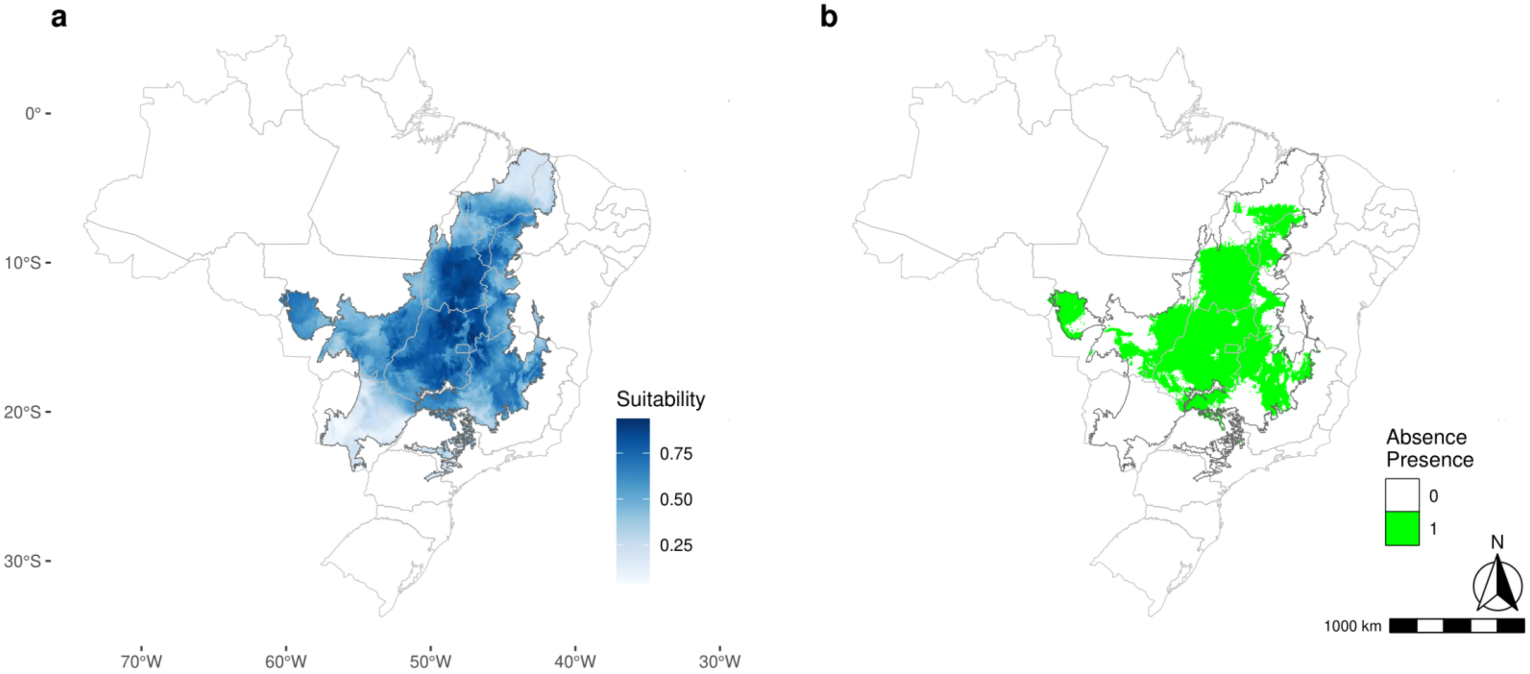

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S44

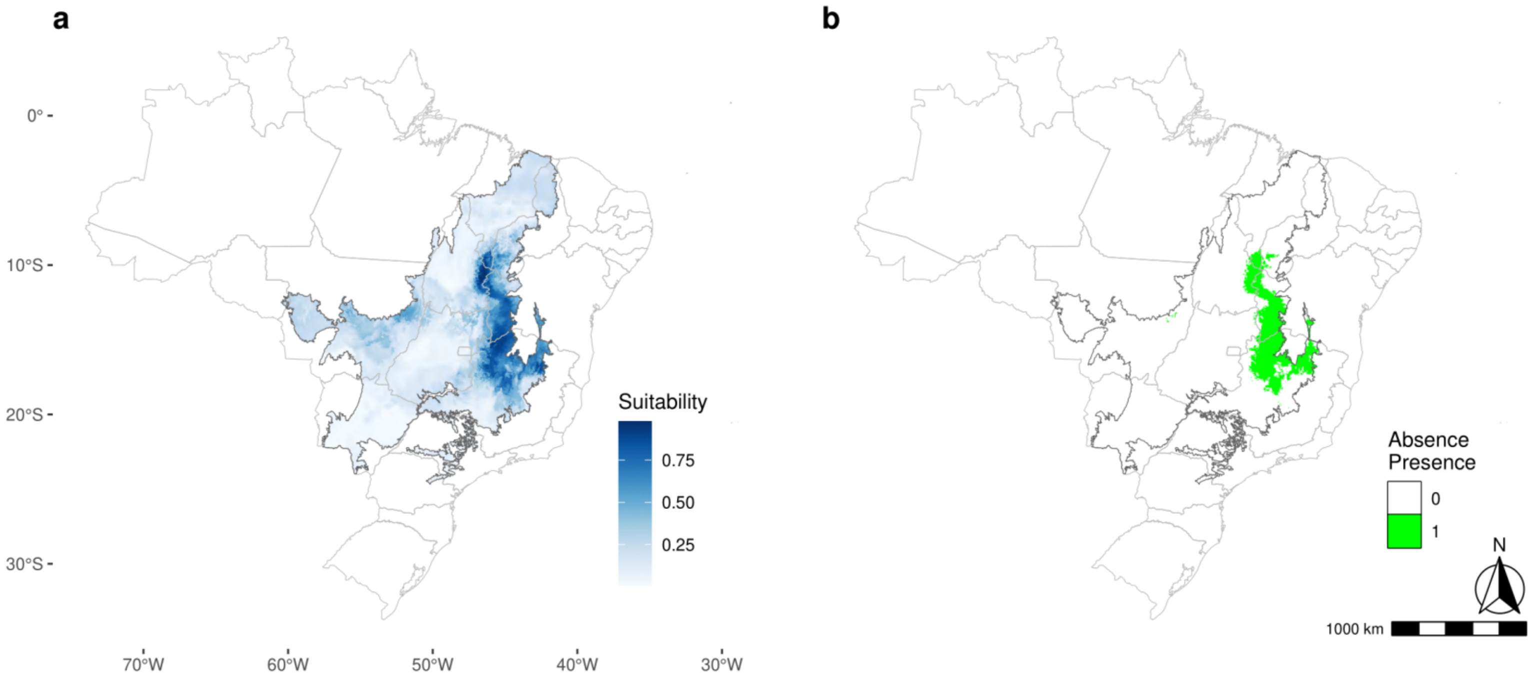

a
b
0°
10°S
20°S
30°S
70°W
60°W
50°W
40°W
30°W
Suitability
0.75
0.50
0.25
Absence
Presence
0
1
N
1000 km

Figure S45

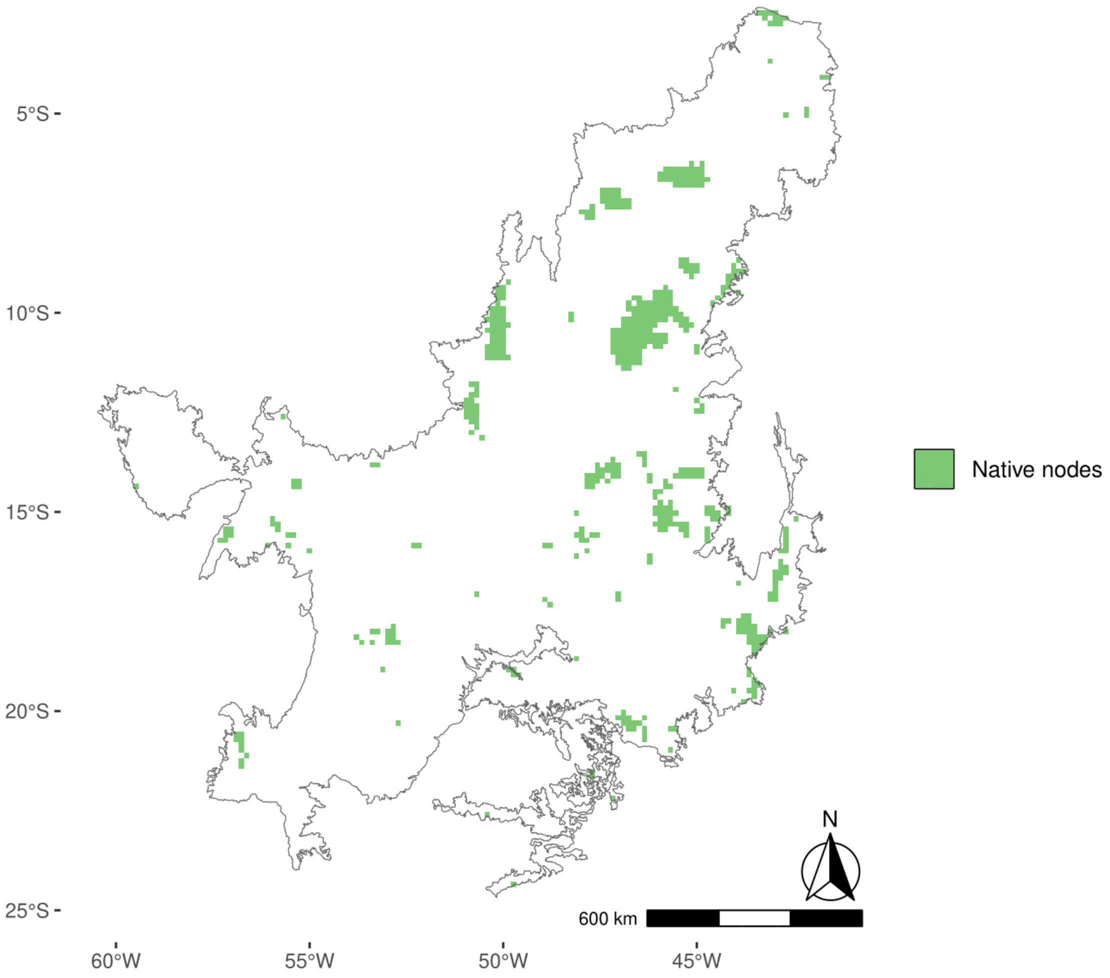


Figure S46