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Addressing the urgent climate and biodiversity crisis through strategic ecosystem restoration in Brazil

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A B S T R A C T

Ecosystem restoration is crucial worldwide to address environmental challenges. Many countries, including Brazil, have committed to restoring degraded landscapes at national and international levels. Brazil aims to restore twelve million hectares of degraded areas by 2030, which requires strategic decision-making to allocate resources effectively and balance biodiversity gains with societal benefits. Our modeling approach uses extensive biodiversity field data to identify priority areas for restoration across Brazil's diverse phytogeographic domains. By focusing on expanding native species habitats and enhancing connectivity, we aim to maximize ecological returns. Precisely, we pinpoint areas within each Brazilian phytogeographic domain with the greatest potential for habitat enhancement, including the Amazon's arc of deforestation, central Cerrado, the limits of Caatinga, Pampa, and Pantanal, and the coastal areas of the Atlantic Forest. Restoring 30 % of these areas—approximately 76 million hectares—could significantly benefit 11,028 species by increasing available habitat by up to 10 % and improving landscape functional connectivity by 60 %. Moreover, this restoration effort would capture up to 9.8 million tons of atmospheric carbon, contributing to global climate goals. As Brazil strives to meet national and international targets, we also advocate for economic incentives to support restoration practices within each phytogeographic domain. Integrating prioritization modeling into decision-making ensures optimal biodiversity and carbon stock outcomes to guide more effective restoration efforts. This comprehensive strategy helps advance restoration goals and underscores the vital role of science-based planning in safeguarding our planet's natural heritage.

1. Introduction

Ecological restoration can reverse land use degradation and biodiversity loss while enhancing ecosystem services and human well-being (Gann et al., 2019). Such importance of restoration is highlighted by the United Nations, which has declared 2021–2030 as the UN Decade on Ecosystem Restoration (Sewell et al., 2020), as well as by international commitments such as the Paris Agreement to curb the amount of domestic greenhouse gas emissions (Seddon et al., 2019; UNFCCC, 2015), the Kunming-Montreal Global Biodiversity Framework (CDB, 2022), and the Sustainable Development Goals (SDG) (United Nations, 2015).

Brazil hosts various ecosystems with different structural and functional characteristics, such as grasslands, wetlands, savannas, and tropical forests, and that experience high rates of land use change and degradation (Pacheco and Meyer, 2022; Souza Jr. et al., 2020). The country has significant potential for restoration (i.e., degraded regions that could be restored), particularly in the Brazilian Atlantic Forest (Bastin et al., 2019; Brancalion et al., 2019; Strassburg et al., 2019; Manes et al., 2022; Zwiener et al., 2017), Cerrado (Medeiros et al., 2022), and Caatinga (Araujo et al., 2024) regions. The Brazilian National Plan for the Recovery of Native Vegetation (PLANAVEG) sets a goal to restore 12 million hectares of native ecosystems by 2030 (MMA, 2017) as a reflection of the country's international commitment to the Paris Agreement (Federative Republic of Brazil, 2023). In addition, the country is also adopting the Kunming-Montreal Global Biodiversity Framework (GBF) (MMA, 2023), which proposed restoring 30 % of the degraded areas that could be restored (hereafter: restorable regions) by 2030 (CDB, 2022; Dinerstein et al., 2019; Leadley et al., 2022). Adopting the GBF brings challenges for all countries, as it needs urgent and integrated actions (Leadley et al., 2022).

Ecological restoration, considering the recovery of original ecosystems and using native species, sets positive impacts on biodiversity conservation, reducing extinction risks, maintaining habitats for native species, increasing ecosystem connectivity, and recovering ecosystem structure and functioning (Benayas et al., 2009; Toma et al., 2024; Wiens and Hobbs, 2015). Proximity to natural areas can enhance restoration success (Crouzeilles et al., 2020) and significantly increase ecosystem connectivity. Connecting restored areas with remnant ecosystem fragments is pivotal in restoration planning as connectivity facilitates gene flow, species movement, migration, and recolonization dynamics (Antongiovanni et al., 2022; Crouzeilles et al., 2020; Jacquemyn et al., 2003); however, despite its great potential to benefit biodiversity, ecosystem connectivity is not widely considered in restoration planning studies (though some examples can be found in Antongiovanni et al., 2022; Crouzeilles et al., 2015; Miranda et al., 2021).

Ecological restoration also contributes to the recovery of ecosystem services, such as carbon stock and sequestration (Benayas et al., 2009; Gann et al., 2019). In forested ecosystems, restoration promotes carbon capture and storage mainly by aboveground biomass, while in grasslands and open ecosystems, these processes are primarily promoted by soil or belowground biomass (Lewis et al., 2019; Yang et al., 2019). Therefore, restoring natural ecosystems is crucial to mitigating climate change (Bustamante et al., 2019; Lewis et al., 2019; Zwiener et al., 2017).

Restoration projects are challenging in megadiverse landscapes, such as the Brazilian territory, due to the contrast between and within ecosystems and substantial gaps in empirical studies (Guerra et al., 2020a). Differing biophysical and socio-economic factors, such as stakeholder engagement (e.g., including traditional knowledge and sustainability actions in restoration planning, considering social and environmental contexts, and the active participation of local stakeholders in all restoration processes), along with project definition, implementation, and monitoring (e.g., considering ecological and social goals, reference ecosystems, habitats heterogeneity, and current land uses, planning restoration according with local contexts, costs, current policies and governance) will influence the success of restoration in complex ways that need to be accounted for (Chazdon et al., 2016, 2017; Gann et al., 2019; Menz et al., 2013; Toma et al., 2024). Considering these factors by decision-makers increases the chances of obtaining favorable outcomes regarding ecosystem and ecosystem services recovery, governance, and human wellness (Gann et al., 2019). This is why the systematic conservation planning (SCP; Margules and Pressey, 2000) approach offers practical solutions to prioritize restoration areas by optimizing multiple benefits (e.g., biodiversity and ecosystem services) while considering trade-offs (e.g., restoration costs), contributing to achieving successful restoration outcomes.

Several studies have identified priority areas for restoration for the Amazon (Strassburg et al., 2022), Atlantic Forest (Guerra et al., 2020a; Strassburg et al., 2019; Zwiener et al., 2017), Caatinga (Antongiovanni et al., 2022; Iguatemy et al., 2022), Cerrado (Schüler and Bustamante, 2022), Pampa (Iguatemy et al., 2022), and Pantanal (Iguatemy et al., 2022). These studies considered different species, objectives and criteria (e.g. biodiversity, climate change mitigation, costs, or connectivity), and used different methods to identify priority areas. However, none of these studies have identified priority areas for restoration optimizing biodiversity conservation at a national scale in Brazil. Here, we determined priority areas for restoration across the six Brazilian phytogeographic domains using the SCP multicriteria approach to maximize biodiversity gains through the proportional enhancement of habitats for species and functional landscape connectivity. For that, we used a Linnear Programming approach, which allows the identification of quantifiable solutions with better quality when compared to other SCP methodologies (Beyer et al., 2016; Pouzols et al., 2014). Specifically, we aimed to i) maximize habitat gains for native species, ii) maximize ecosystem connectivity for biodiversity, and iii) estimate the amount of carbon captured as a co-benefit of global relevance provided for the prioritized areas if restored. Our prioritization is a pioneering approach at this scale, as we included forested and non-forested land covers and used massive species' data obtained and validated by the nationwide Brazilian Biodiversity Research Program – PPBio (*Programa de Pesquisa em Biodiversidade*) for modeling. PPBio is a Brazilian broad-scale research program that inventories and monitors different taxonomic groups and ecosystems (Ministry of Science and Technology, 2005; Rosa et al., 2021). Using data validated by specialists in each biological group is a crucial strategy to improve the robustness and applicability of our results.

2. Methods

We applied a SCP multicriteria optimization algorithm (Strassburg et al., 2019, 2020) to identify priority areas to be restored in the Brazilian territory and to quantify the variation of potential restoration benefits to the biodiversity across different scenarios based on linear programming. Linear optimization solutions offer several advantages over commonly used heuristic algorithms in conservation, including enhanced computational speed, better solution quality, and guaranteed quantification of solution quality (Beyer et al., 2016; Pouzols et al., 2014).

Fig. 1. Land use in the six Brazilian phytogeographic domains (MapBiomas project collection 7 for 2021; MapBiomas, 2021, Souza Jr. et al., 2020). Green areas show natural vegetation cover, and yellow indicates restorable regions (such as agriculture and silviculture lands). Anthropic areas include urban, constructed, and mining areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.1. Study region

Our study region encompasses six phytogeographic domains: Amazon, Atlantic Forest, Caatinga, Cerrado, Pampa, and Pantanal (IBGE, 2019; MMA, 2020) (Fig. 1). Since these phytogeographic domains are composed of different ecosystems and land uses, they are submitted to different land conversion pressures. By 2021, Brazil had 252 million hectares of degraded land and areas characterized by agriculture, pasturelands, and silviculture lands within each of these biomes (hereafter referred to as restorable areas) (Fig. 1), of which 34 % were in the Cerrado, 28 % in the Atlantic Forest, 24 % in the Amazon, 11 % in the Caatinga, 3 % in the Pampa and 1 % in the Pantanal. Our study aims to identify priority areas to maximize biodiversity benefits by focusing on pasturelands, agriculture, and silviculture as restorable lands. These areas are assessed for their potential contributions to biodiversity conservation, considering that other anthropic areas, such as urban and mining regions, are not convertible. Much of these restorable land uses in Brazil consist of degraded or abandoned lands suitable for restoration.

According to the PLANAVEG, each phytogeographic domain has different area-based restoration goals: >4.5 million ha for the Amazon, 4.5 million ha for the Atlantic Forest, 2.1 million ha for the Cerrado, 500,000 ha for the Caatinga, 300,000 ha for the Pampa, and 50,000 ha for the Pantanal (MMA, 2017). As the GBF goal for 2030 is to restore 30 % of restorable areas, we have considered restoring 30 % of each phytogeographic domain. This represents the recovery of 75.6 million hectares of native ecosystems. Identifying 30 % of priority areas provides a foundation for further restoration planning, which can include considerations of costs, land productivity, and other criteria that may reduce the percentage of the restorable regions in practice.

2.2. Species dataset

We used data from 8692 plant species (angiosperms only), which correspond to 24 % of the 36,112 Brazilian angiosperms (Flora e Funga do Brasil, 2024), and 2699 animal species, of which 2108 are vertebrates (933 birds, 353 amphibians, 320 fish, 263 reptiles, and 239 mammals), and 591 are invertebrates (including 441 insects, 79 arachnids, 63 molluscs, five decapods, and three polychaetes) occurring in the Brazilian territory. Vertebrates represent 22 % of Brazilian vertebrates, and invertebrates represent 1 % of the Brazilian invertebrates (Boeger et al., 2024).

Although we ran spatial prioritization analyses for terrestrial habitats, we included aquatic species (both freshwater and marine), as they could benefit from the riparian forests and restoration of coastal ecosystems. We obtained the species occurrence data and their threatened status to build the species distribution models (SDMs) from the data provided by the PPBio Project researchers. Data from the PPBio research represented 19 % of all data, and PPBio data were essential for endemic plant and animal species, representing 75 % and 97 % of all data, respectively (see Table S1.1.). We also gathered data from the GBIF (Global Biodiversity Information Facility) database (gbif.org), the *Instituto Chico Mendes para a Conservação da Biodiversidade* - ICMBio (Chico Mendes Institute for Biodiversity Conservation), and the *Centro Nacional para a Conservação da Flora* - CNCFlora (National Center for Flora Conservation).

Once we had the occurrence database, we excluded all duplicated records and data from all species with less than ten occurrence records and selected only one record point per pixel (~25 km^2). Then, we applied geographic filters to correct coordinates errors and excluded records with latitude and longitude equal to zero or outside the Brazilian territory. We performed the geographic filter using the *spfilt* v1 package (https://github.com/diogosbr/spfilt) available for the R environment (R Core Team, 2023).

Before the cleaning process, our database had 742 threatened species (465 plants and 277 animals), 7749 species occurring in a unique phytogeographic domain (hereafter: endemic species; 6783 plants and 966 animals), and 10,806 species with widespread distribution (6343 plants and 4463 animals). The final database comprised 2908 endemic species (2410 plants and 498 animals), 797 threatened species (528 plants and 269 animals), and 530 both endemic and threatened species (436 plants and 94 animals). The remaining species were considered widely distributed. Table 1 shows the data values after the cleaning process.

2.3. Biodiversity benefits

2.3.1. Potential habitat gains

First, we built species distribution models (SDMs) for the Brazilian biodiversity to determine the overall suitable area for each species (see Appendix S1). For this, we used 29 environmental variables (obtained from CHELSA, CGIAR-CSI, USGS, and INPE; see further details in Table S1.2.) with a spatial resolution of 4.3 km, including 23 climatic and six topographic variables and carried out a principal component analysis (PCA) and used the scores of six principal components (De Marco and Nóbrega, 2018; Dupin et al., 2011).

Then, we built SDMs using five methods, selected models with True Skill Statistics (TSS) > 0.4 and created an ensemble to obtain the final model. Further, we generated binary models using the TSS as a threshold that maximizes sensitivity plus specificity (Shabani et al., 2018) (See a detailed explanation in Appendix S1). All SDMs were projected for South America. Once we had the potential distribution of each species, we adjusted all maps' extensions according to the phytogeographic domain where each species occurs. If a species occurs in two or more phytogeographic domains, the map was cut for all the domains with the presence of the species.

Based on the SDMs, we estimated the potential benefits to biodiversity conservation that can be provided by restoration due to the increased availability of adequate habitat for species. Within the suitable areas for each species, we estimated how much the restoration of each given pixel can contribute to overall habitat availability within species' suitable areas (Strassburg et al., 2020). Specifically, we quantified the habitat gains using a function based on the inverted species-area relationship for each species, considering the ratio between its current and potential habitat extent given restoration within its suitable distribution area (see more details in Strassburg et al., 2019, 2020; Thomas et al., 2004). The sum of the potential proportional habitat gains by restoring a pixel was the benefit value used as a proxy of biodiversity conservation in the prioritization (see Strassburg et al., 2019, 2020 for more details).

2.3.2. Potential functional connectivity gain

We also quantified biodiversity conservation benefits through restoration's contribution to overall landscape functional connectivity. This was based on the graph theory in which adjacent fragments are considered functionally connected depending on the species' dispersal abilities, i.e., connectivity only exists if the species can surpass that distance between fragments (Pascual-Hortal and Saura, 2006). In our approach, we used the Integral Index of Connectivity (IIC, Pascual-Hortal and Saura, 2006) to represent the potential contribution of restoration of a given pixel to overall landscape functional connectivity for biodiversity (see Manes et al., 2024). We separately simulated the restoration of each restorable pixel in the landscape in each phytogeographic domain to avoid overestimating connectivity among different regions. After simulating the restoration of each restorable pixel in the landscape for each phytogeographic domain, priority was given to those areas that would have a greater contribution to the overall index of functional connectivity if restored.

Given the nationwide scale of the analyses, only species with great dispersal abilities could be considered. To assess functional connectivity in the shortest distance possible from a habitable pixel to the closest nearby one, species need to be able to disperse at least for ~6.5 km — i.e., leave a habitable pixel (i.e., a pixel with a given natural land cover),

Table 1
Threatened, endemic, and widespread species are included in the prioritization and discriminated by the phytogeographic domain. 'Threatened' consists of all non-endemic species categorized as endangered in the IUCN Red List (2023). 'Endemic' includes all endemic non-threatened species. 'Threatened & endemic' consists of all endemic and threatened species. 'Widespread' includes all non-endemic and non-threatened native species.

	Amazon	Caatinga	Cerrado	Atlantic Forest	Pampa	Pantanal	Total
FAUNA							
Threatened	65	24	14	76	70	20	269
Endemic	96	5	21	375	0	1	498
Threatened & endemic	12	4	8	68	2	0	94
Widespread	540	1289	50	149	19	314	2361
Total	713	1322	93	668	91	335	3222
FLORA							
Threatened	44	73	60	98	15	238	528
Endemic	746	361	90	712	491	10	2410
Threatened & endemic	5	30	65	104	144	88	436
Widespread	138	2292	362	2046	43	1088	5969
Total	933	2756	577	2960	693	1424	9343

transpose an un-habitable pixel of 4.3 km and reach the center of the closest adjacent habitable pixel. Thus, analyses were run for species with medium, high, and very high dispersal abilities, gaining 2, 5, and 10 pixels, respectively (i.e., ~6.5, 20, and 40 km, respectively) (see Manes et al., 2024).

Using multiple dispersal abilities increases model robustness to account for many species with in-between dispersals (e.g., Crouzeilles et al., 2015). Separate connectivity analyses were run for each dispersal ability and land cover type. Ensemble maps were created considering all land cover types and all dispersal abilities to produce the overall contribution for biodiversity in each phytogeographic domain. Final ensemble maps are ranked 0–1, showing the proportional increment in the connectivity index stemming from the restoration of each given pixel to overall phytogeographic domain functional connectivity. Thus, higher-ranked pixels are considered priorities for restoration since they provide higher contributions to overall phytogeographic domains' connectivity for biodiversity.

2.3.3. Prioritization model

We built different prioritization scenarios to optimize phytogeographic domain-specific biodiversity conservation and functional connectivity resulting from restoration. We consider all land converted from natural ecosystems to agriculture, pasturelands, and silviculture as restorable lands. Conversely, we considered natural areas as those with native ecosystem cover (forests, savannas, wetlands, and natural grasslands). All analyses were processed at a macroecological scale, with a spatial resolution of 4.3 km, obtained and aggregated from MapBiomas (2021).

We used the method described in Strassburg et al. (2019, 2020) to identify priority restoration areas. This involved running an optimization algorithm based on an objective function that determines the necessary restoration area of native ecosystems in each Brazilian phytogeographic domain to maximize habitat gains for native species and enhance functional connectivity. We applied the following objective function:

$$max \sum_i^{n_p} x_i(w_s s_i + w_b b_i)$$

$$\text{subject to } \sum_i^{n_p} x_i A_i < T$$

$$x_i \leq u_i \, \forall_i \in n_p$$

In this case, x_i is the decision variable representing the proportion of an ecosystem type to be restored within each pixel (or planning unit) *i*. The components represent the returns (benefits) of restoration to biodiversity conservation, with the components of habitat gains (*b*) summed across all species and functional connectivity (*s*). n_p is the total number of planning units. The first constraint limits the total area of habitat to be restored (*A*) (km^2), in which *A* varies depending on the target used for each run. The second constraint ensures that the proportion of the planning unit restored ranges from zero to a maximum value (*u*), which accounts for the proportion of the planning unit that is already covered by that ecosystem type or represents a land use that cannot be restored (such as urban areas).

The user-defined parameters *w* weighs the relative contribution of the habitat gain and functional connectivity components, respectively. We included this parameter since the equivalence of weights will vary according to the restoration planning and outcomes. The objective function can be solved over various relative weights to understand how these components trade-off. The model was solved iteratively in 20 increments of the target area *A* to approximate the nonlinear function describing biodiversity values; the target was not prioritized at once only. Exact solutions to this linear programming problem were found using R Symphony version 0.1–28 (Hornik et al., 2019).

2.3.4. Scenarios

We developed four scenarios that represent i) single-criterion solutions (maximization of habitat gain or connectivity, respectively), ii) multicriteria solutions (maximization of habitat gain and connectivity simultaneously, testing different weights to find the most balanced scenario), and iii) a control scenario, where restoration is uniformly placed across all restorable areas in each phytogeographic domain, as a benchmark for no spatial prioritization. Single-criterion solutions deliver the maximum gain of one benefit and show the result for the other non-optimized benefit, while multicriteria solutions optimize both benefits in a balanced way. As we looked for a scenario that maximizes gains of habitat and connectivity, we created nine multicriteria scenarios allocating different weights for the habitat gain benefit. Then, we compared them to choose the most balanced scenario (i.e., the scenario with the highest values for both benefits in each phytogeographic domain) (Fig. S2.1.). As the connectivity benefit had more impact in the multicriteria prioritizations, we assigned weights (1, 2, 5, 10, 20, 50, 100, 250, 500) to the habitat gain benefit to find the most balanced scenario. We performed twelve scenarios: two single-criterion scenarios, nine multicriteria, and one control scenario.

Once we had a prioritization for each scenario, we compared the benefit gains for habitat and connectivity by depicting each scenario in a scatterplot (Fig. S2.1, S2.2). We identified the scenario that maximized gains for both benefits by selecting the scenario with the maximum values in both axes in the scatterplot (Fig. S2.2.). Here, we presented the results for the chosen multicriteria scenario for each phytogeographic domain and compared them with the single-criterion scenarios. For the comparison analyses, we considered the target of restoring 30 % of the restorable area of each phytogeographic domain, as proposed in the GBF target 2.

2.3.5. Assessing carbon stock as a restoration co-benefit

Carbon stock is an associated co-benefit of native ecosystem restoration. We obtained the carbon gains assuming that restorable areas (i.e., agriculture, pasturelands, and silviculture lands) were restored according to each phytogeographic domain's priority areas of the multicriteria scenario.

We used a raster with Brazil's potential aboveground and belowground carbon stock for mature phytogeographic domains. Potential carbon stock in the aboveground biomass map was obtained with a Random Forest model based on the current aboveground carbon stock (Englund et al., 2017) and in environmental, land use, and climatic variables. Aboveground carbon stock was calculated for all restorable areas, considering the original land covers according to the MapBiomas vegetation areas. Further, belowground carbon stock was obtained using equations to estimate belowground biomass from aboveground carbon per phytogeographic domain. We also used different equations for forested and non-forested land covers (Mokany et al., 2006) and specific conversion values for annual and perennial agriculture (Mazzilli et al., 2014; MCTI, 2020), grazing and silviculture (MCTI, 2020).

Finally, the potential carbon gains by restoration of native vegetation were obtained by subtracting the carbon values of current carbon stocks from potential carbon stocks (See Strassburg et al., 2019, 2020 for further details). We calculated the potential carbon stock per phytogeographic domain by multiplying the priority areas raster with the potential carbon stock raster in the R environment.

3. Results

We identified priority areas for restoring native ecosystems with the highest potential to recover habitat for native species and enhance ecosystem connectivity in both single- and multicriteria scenarios (Fig. 2–4). The maps showing priorities for all the restorable areas per phytogeographic domain are in Appendix S3.

Single-criteria scenarios showed that priority areas differ for each benefit (Figs. 2–3). For instance, high-priority areas for maximizing habitat gain are mainly located in the limits of each phytogeographic domain (Fig. 2). In contrast, priority areas for maximizing connectivity are scattered within phytogeographic domains, except in the Amazon, where priority areas are in the southeastern limit (Fig. 3). Although phytogeographic domains share essential areas for each benefit, the general pattern is that habitat gains maximization prioritizes different areas compared to connectivity maximization (Figs. 2–3).

The multicriteria scenarios showed that the top priority areas for restoration are in the arc of deforestation in the Amazon, central Cerrado, the limits of Caatinga, Pampa, and Pantanal, and the coastal areas of the Atlantic Forest (Fig. 4). The selected scenarios for each phytogeographic domain are reflecting essential areas for both benefits. Therefore, they differ from single-criterion maps. We found trade-offs between both benefits.

For instance, in the Atlantic Forest, the priority areas for restoration in the multicriteria scenario are in the north of the coastal region and the

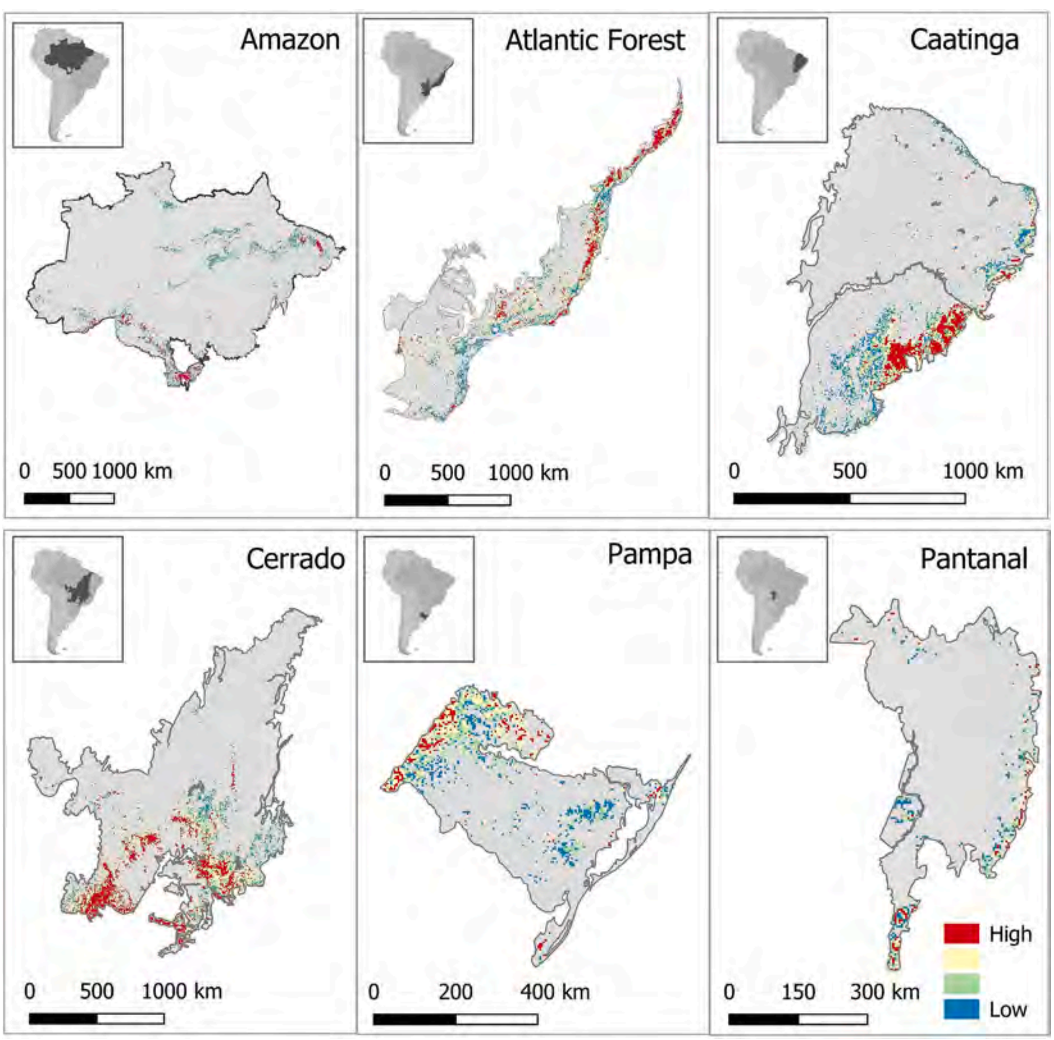

Fig. 2. Top 30 % of priority areas for restoration in the single-criterion scenario of maximizing the habitat gain for native species benefit per phytogeographic domain.

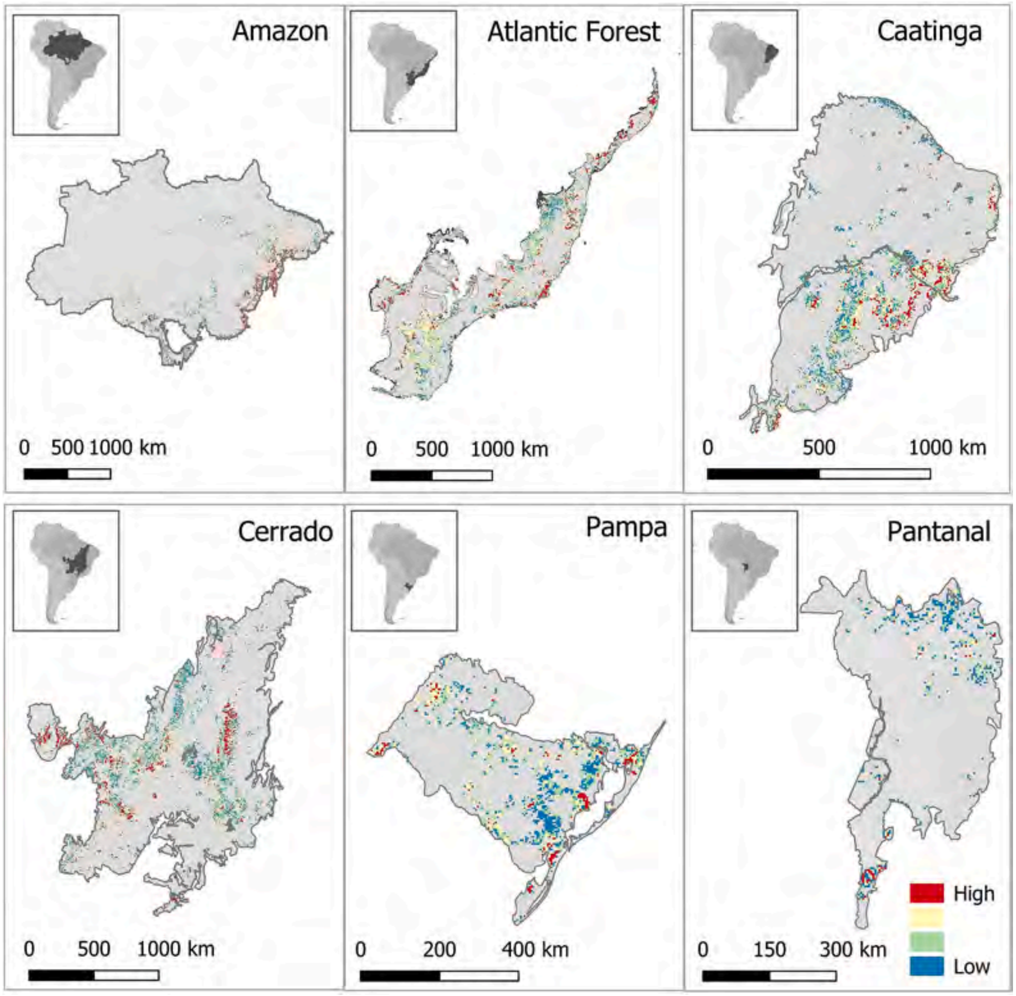

Fig. 3. Top 30 % of priority areas for restoration in the single-criterion scenario of maximizing the ecosystem connectivity benefit per phytogeographic domain.

center, and the high-priority areas are in the north coastal zone, where habitat gain is more critical (Figs. 2–4). Therefore, prioritized areas will have a higher habitat gain than connectivity. Similarly, in the Caatinga, prioritized areas are in the southeastern limit, where habitat gain maximization is extremely important (Figs. 2–4). Instead, the Cerrado priority areas are in the center, where connectivity is more important (Figs. 2–4). The Amazon, Pampa, and Pantanal prioritizations showed more spatial balance among benefits. In the Amazon, priority areas are concentrated in the southern limit, where habitat and connectivity gains will be maximized if restored (Figs. 2–4). Likewise, Pampa and Pantanal scenarios for habitat gain showed that priority areas are in the northern and southern regions, respectively (Fig. 2). At the same time, connectivity is more critical in the south and north (Fig. 3). The multicriteria scenario is prioritizing northern and southern regions equally in both phytogeographic domains (Fig. 4).

Restoring 30 % of the restorable areas in the multicriteria scenarios would improve habitat gain and connectivity by 40 % and 60 %, respectively (Fig. S4.1.). Habitat gain increases more than connectivity gain, especially in the Atlantic Forest, Caatinga, and Cerrado. In contrast, Amazon, Pampa, and Pantanal have almost equal gains for both benefits (Fig. S4.1.). Habitat availability would increase by up to 10 % for 11,028 species (from which 6 % are threatened, 4 % are endemic and threatened species, and 23 % are endemic), up to 20 % for 19 species (from which 10 % are threatened, 5 % are endemic and threatened species, and 5 % are endemic), and up to 30 % for one species (which is a species with widespread distribution) (Fig. S4.2.).

Furthermore, on average, our spatial prioritization increased 60 % of ecosystem connectivity compared to the control scenario. The Cerrado would have the greatest benefits, as its connectivity would increase by >80 %; In the Amazon, Atlantic Forest, and Caatinga connectivity would increase by >70 %, and in the Pampa and Pantanal, up to 50 % (Fig. S4.2.).

The selected scenarios also demonstrate contributions extending beyond biodiversity conservation. For example, restoring 30 % of restorable areas could stock up to 9.8 million tons of carbon upon ecosystems reaching maturity. (Fig. 5, Table S4.1). Furthermore, comparing the potential carbon gain from restoring all restorable areas versus restoring just 30 % of these areas reveals that the Amazon would achieve over 50 % of its maximum potential carbon stock. The Caatinga would follow with nearly 36 %, while other phytogeographic domains would reach between 25 % and 35 % of their maximum potential carbon stock (Table S4.1, Fig. S4.3).

4. Discussion

A combined action of conservation and ecological restoration is pivotal in Brazil to safeguard the biodiversity of global change impacts, recover ecosystem services, and achieve internationally agreed goals, such as nationally determined contributions (NDCs; Bustamante et al., 2019; Manes et al., 2022; Seddon et al., 2019) and the GBF Targets 1, 2, 3, and 4 (CBD, 2022). This work presents a first approach to planning the restoration of all Brazilian phytogeographic domains, optimizing biodiversity gains by increasing habitat availability and connectivity.

Our results provide a comprehensive notion of restoration priorities

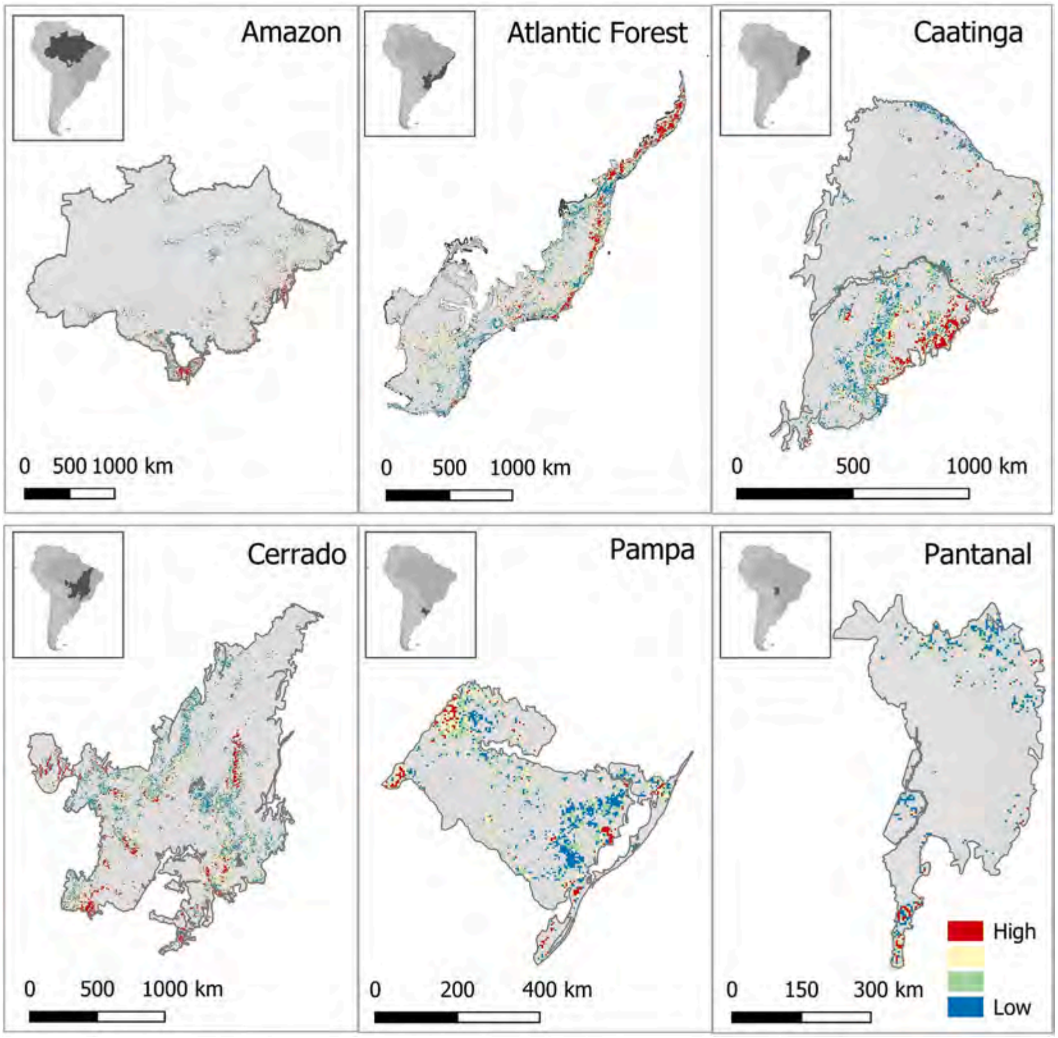

Fig. 4. Top 30 % priority areas for restoration are maximizing habitat and connectivity gains per biome. These maps show the multicriteria scenario that optimizes gains of both benefits in each phytogeographic domain.

that maximize biodiversity conservation in Brazil. We showed that restoring 30 % of restorable areas in each Brazilian phytogeographic domain, comprising 76 million hectares, would produce substantial gains in habitat, functional connectivity, and carbon stock. Thus, 11,048 species would have their habitat expanded (representing 40 % of habitat gain), connectivity would be enhanced by 60 %, and up to 9.8-million-ton C would be stocked upon domains reaching maturity. Furthermore, our findings provide valuable insights to support the practical implementation of restoration efforts and the enforcement of environmental legislation, such as Brazil's Native Vegetation Protection Law (LPVN). Specifically, our results highlight key areas of importance for biodiversity, offering an initial guide for prioritization. However, achieving successful and lasting restoration outcomes requires additional measures, including diagnosis of biophysical and socioeconomic aspects, the development of incentives for restoration, and active engagement with landowners to ensure their commitment and participation. Restoration implementation must also consider specific strategies for practical application according to the local context, such as applied nucleation, Assisted Natural Regeneration (ANR), and passive restoration, among others. These strategies must be adapted to each phytogeographic domain and local conditions to guarantee a successful restoration outcome.

Our results concur with other restoration-focused spatial prioritizations (Antongiovanni et al., 2022; Iguatemy et al., 2022; Schüler and Bustamante, 2022; Strassburg et al., 2019, 2022; Zwiener et al., 2017). Although these prioritizations used different methods, all highlighted the high priority of restoring transition regions between domains (or ecotones). This spatial coincidence underscores the importance of the restoration of these areas in the Atlantic Forest (Strassburg et al., 2019), Caatinga, Pampa, and Pantanal (Iguatemy et al., 2022). Ecotones between phytogeographic domains tend to be highly biodiverse and complex, supporting migration dynamics, diverse and rare genotypes, and species (Kark and van Rensburg, 2006; Marques et al., 2020). These areas offer diverse habitats, and their conservation is crucial to maintaining their dynamics and biodiversity (Kark and van Rensburg, 2006; Marques et al., 2020). Ecotones are also under increased pressure for conversion to agricultural areas (FAO, 2006), adding a layer of conflict to the discussion. For instance, historical and projected vegetation loss in the Pantanal forms an "arc of conversion" within the ecotone with Cerrado and Amazon (Guerra et al., 2020b), like the pattern observed in the Amazon-Cerrado ecotone (Montibeller et al., 2020). Restoring these areas would improve connectivity among native ecosystem remnants and expand potential habitats for native species.

Priority areas for restoration often reflect historical and current agricultural occupation patterns in Brazil. For instance, the Atlantic Forest has been significantly transformed over the past 500 years (Solórzano et al., 2021; Souza Jr. et al., 2020), with priority restoration areas now located in the coastal zone. In contrast, the transformation of

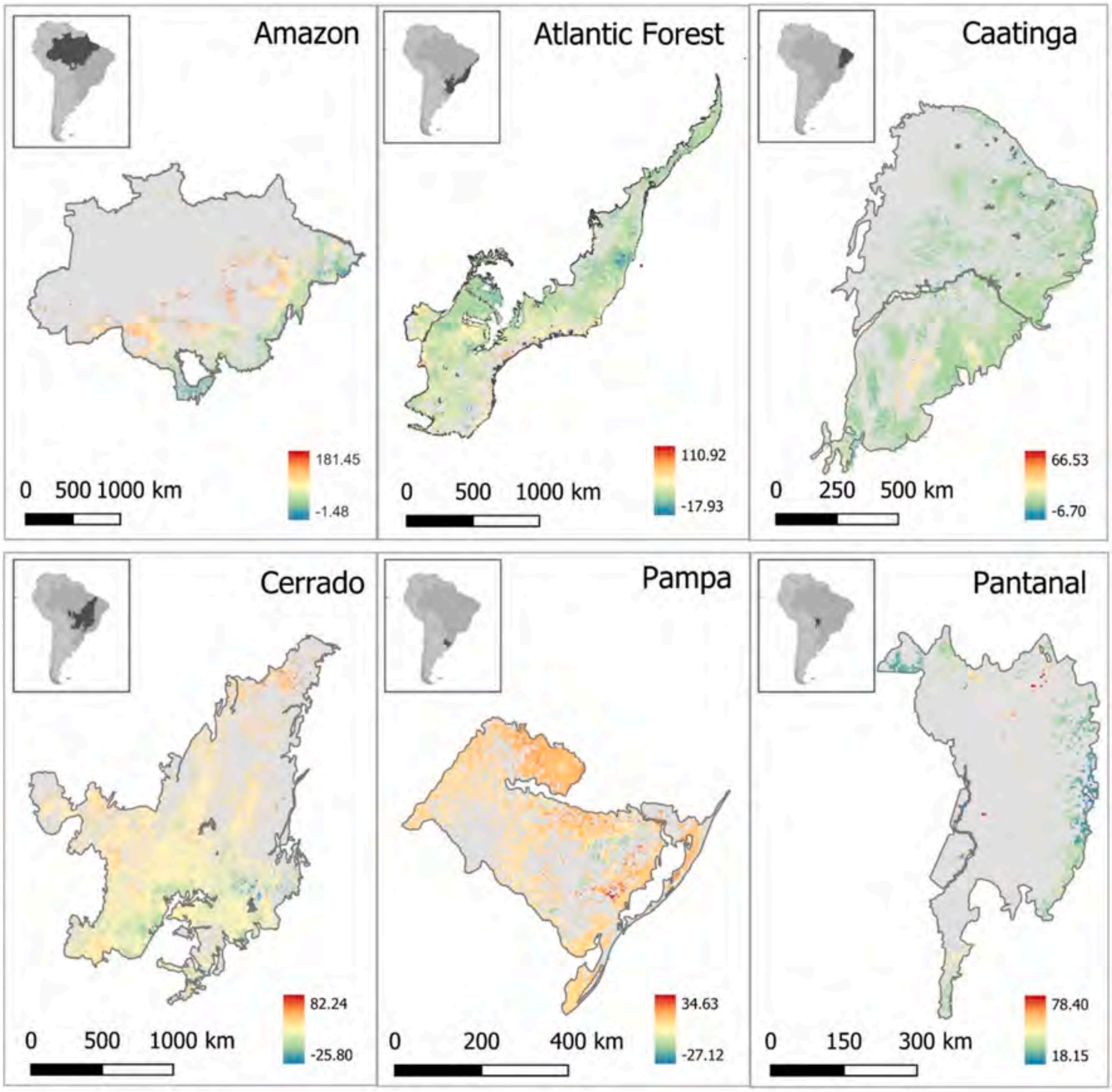

Fig. 5. Carbon gains (in tons) as a co-benefit of restoration per phytogeographic domain if the prioritized areas were restored.

the Cerrado and Amazon began in the 1970s (Guerra et al., 2020b; Montibeller et al., 2020; Souza Jr. et al., 2020).

Priority areas in these regions are near historical and ongoing vegetation loss—in the southwestern and central Cerrado, and the southern Amazon, respectively. Particularly in the Cerrado, the results showed that restoration efforts should focus on its central region (Schüler and Bustamante, 2022) to increase connectivity between remnant ecosystem fragments. Connectivity loss in the Cerrado is a critical threat to this phytogeographic domain, as connectivity could be lost when natural remnants fall below a threshold of 40 % of the native area (Grande et al., 2020). Despite the central region of the Cerrado not being recognized as highly diverse (Faleiro et al., 2013; Hidasi-Neto et al., 2019; Resende et al., 2021; Velazco et al., 2019), maximizing connectivity by restoring this region will improve the aggregation of natural areas, ensuring population viability throughout the entire domain (Arponen et al., 2012; Antongiovanni et al., 2022; Jacquemyn et al., 2003), and mitigate the impacts of land-use changes, as central Cerrado is projected to experience high habitat loss pressure up to 2050 (Faleiro et al., 2013).

Brazil has a decisive role in conserving biodiversity, and urgent actions to restore and preserve Brazilian biodiversity are needed. Encouraging research (including field data analyses), data sharing, and structural integration of data resources could enhance the inputs to support restoration planning (Cayuela et al., 2009; Costello et al., 2013; Hortal et al., 2015). investment in large-scale research initiatives, such as the PPBio program, would improve the knowledge of Brazilian biodiversity and provides useful information for conservation planning (Bustamante et al., 2019; Fernandes et al., 2017; Overbeck et al., 2018; Rosa et al., 2021). In this work, using biodiversity field data allowed for a more accurate representation of suitable regions for native species, enabling the assessment of habitat gain benefits. Since habitat gain calculations are based on species distribution models, the inclusion of expert-validated data (representing 19 % of all our data) provides credible occurrence records that enhance the quality of SDMs (Anderson et al., 2006; Beck et al., 2014; Costello et al., 2013) and consequently improve our prioritization results. Future prioritization exercises could benefit from expanding the number of species considered, such as fungi, a highly diverse group that plays a crucial role in ecosystem functioning yet has often been neglected in terms of knowledge and conservation (Dreschler-Santos et al., in prep.; Niskanen et al., 2023).

Notwithstanding the abovementioned credibility and advantages, our study still has some methodological limitations. We did not account for operational and implementation challenges or costs, such as stakeholder engagement, integration of Indigenous and local knowledge, practical challenges (e.g., the willingness of landowners, credit access, financial resources, and incentives) , restoration potential and opportunity costs of converted areas (Ban et al., 2013; Knight et al., 2006; Strassburg et al., 2020). Future steps must consider restoration implementation and opportunity costs to maximize cost-benefits and avoid land-use conflicts. The definition of restorable areas is a limitation, as restorability is influenced by complex factors that must be considered during practical restoration implementation. Furthermore, the extent of restorable areas may be underestimated, as our analysis did not account for degraded forests affected by factors such as burning or logging. Furthermore, our analysis predates the fire events in 2024 in several Brazilian ecosystems, suggesting that the restorable areas could be greater. Additionally, we did not factor in current restoration initiatives, offsetting, or political issues like land tenure, restoration deficits, and legal requirements of the Brazilian Forest Code. The lack of high-resolution countrywide data on the social components of restoration prevented such analysis at the scale of this study. Still, these aspects must be considered for local spatial planning.

Other limitations include uncertainties in models and carbon estimates, assumptions about recolonization, and the disregard of future projections of climate change, carbon storage agricultural production, and threats to biodiversity (Joppa et al., 2016; Strassburg et al., 2019, 2020; Zwiener et al., 2017). Including abundance and coexistence data in restoration prioritizations can also improve outcomes and increase restoration success (Hallett et al., 2023). Nevertheless, macroecological studies like ours are valuable tools for guiding biome-scale efforts as a first step in identifying critical areas for local-scale studies. Further, finer resolution and local-scale prioritizations are needed to support in-situ decision-making. Furthermore, restoration planning should adopt the ecosystem reference approach, which considers original phytophysiognomies, habitats, and local contexts, and reintroduce native species to avoid biotic homogenization (Arponen et al., 2012; Holl et al., 2022; Toma et al., 2024).

5. Conclusions

Efficient restoration strategies require Brazil to increase investment in research, innovation, and conservation actions. Strengthening governance and engaging subnational governments, the private and financial sectors, and local communities—while incorporating local knowledge—are crucial. Embracing Brazil's biological and cultural heterogeneity is also essential. The spatial database developed here represents a significant advancement in enhancing the decision-making process for restoration strategies at both national and subnational levels. It can improve risk and investment analyses for public, private, and multilateral financial institutions, strengthening investment strategies in priority areas. Integrating this spatial database with other official territorial management databases and tools in Brazil and providing proper training for key stakeholders could ensure its effective use. Finally, our prioritization approach could be applied in other countries with similar heterogeneity conditions and available data than Brazil, such as other Latin America countries (e.g., Mexico and Colombia), which could help to support restoration planning and implementation.

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Author contributions

Luisa Liévano-Latorre, Diogo Rocha, Luiz Gustavo Oliveira, Renata Capellão, Stella Manes ran the SDMs and/or spatial prioritization analyses. Luisa Liévano-Latorre wrote the first draft. Rafael Loyola oversaw the writing and did the final review of the manuscript. All other authors contributed with field data and/or revised different text versions.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2025.110972.

Data availability

The authors do not have permission to share data.

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