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RESEARCH ARTICLE

Planning for the Restoration of Functional Connectivity in Brazil

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ABSTRACT

Aim: Land use and land cover (LULC) change is the main driver of biodiversity loss, causing habitat loss and fragmentation that hinders species movement and negatively impacts populations. While habitat fragments are structurally disconnected, functional connectivity can still occur depending on the species' dispersal abilities. Incorporating landscape connectivity into restoration planning helps identify strategic areas significantly enhancing connectivity. Here, we present an unprecedented, nationwide continuous spatial layer representing each restorable pixel's contribution to functional connectivity, using Brazil as a case study.
Location: Brazil.
Methods: We performed a dynamic pixel-based analysis across each Brazilian biome to assess the potential increases in the Integral Index of Connectivity (IIC) resulting from restoring each restorable pixel in the landscape. For that, we defined hypothetical species with medium, high and very high dispersal abilities and calculated the IIC for the different natural LULC in each biome. Then, we ran a dynamic pixel-based restoration analysis to assess the contribution of each restorable pixel to functional connectivity.
Results: Our resulting dataset represents the relative contribution of connectivity for each restorable pixel in the landscape, considering all dispersal abilities and LULC in each biome. Since we are assessing the contributions of individual pixels to overall biome landscape connectivity, most values are expectedly low. However, pixels with the highest contributions to connectivity show a stand-alone contribution biome-wide and thus were interpreted as priorities for restoration. Notably, we show nested regions as priorities for restoration, with a trend of higher priority rankings (e.g., the top 5% most important regions) being surrounded by subsequent rankings of priorities.
Main Conclusions: Our study is the first to evaluate the impact of restoration planning efforts on functional connectivity across all Brazilian biomes. We identified priority areas for restoration within each Brazilian biome, providing valuable information to guide decision-making and policy implementation. The innovative pixel-based analysis used in the study can be replicated in other regions, aiming to make restoration planning more efficient.

1 | Introduction

Land use and land cover (LULC) change is the most earth-shattering driver of biodiversity loss, extensively transforming ecosystems and fragmenting once-continuous landscapes (Newbold et al. 2016; IPBES 2018). LULC change has several impacts on biodiversity, which are spatially structured (Banks-Leite et al. 2022). For instance, populations at the edge of their habitat range could be less resilient as they experience more stress due to climatic factors and interspecific interactions (Banks-Leite et al. 2022; Orme et al. 2019). Habitat loss, fragmentation and degradation are causing the extinction of thousands of species, which consequently impacts ecosystem functions and services (Banks-Leite et al. 2020). Large distances between habitat fragments hinder species' movements and may be considerable obstacles for dispersal (Hejkal, Buttschardt, and Klaus 2017). Such a structurally disconnected landscape may lead to population isolation and decline, lack of gene flow and biotic homogenisation (Haddad et al. 2015; Taylor et al. 1993). Furthermore, fragmented landscapes increase impacts on populations by hindering species' movements towards more suitable habitats in response to climate change, which could lead to local extinctions (Diniz et al. 2022; Heller and Zavaleta 2009).

Although habitat fragments might be structurally disconnected, functional connectivity can occur for some species, depending on their dispersal ability (Tischendorf and Fahrig 2000). 'Functional connectivity' represents how species can move through the landscape (Hilty et al. 2020), so species with high dispersal abilities could perceive a fragmented landscape as functionally connected (Vogt et al. 2009). Improving functional connectivity is then crucial to ensure population viability, as it allows the flux of individuals among habitat fragments, enabling (re)colonisation dynamics and migration processes, thus contributing to enhanced genetic diversity and population persistence (Driscoll et al. 2013; Jacquemyn, Butaye, and Hermy 2003; Préau et al. 2021; Riva et al. 2024). Consequently, it leads to an improvement in ecosystem resilience through ecosystem processes and services (Lewis et al. 2023; Mitchell, Bennett, and Gonzalez 2013; Préau et al. 2022). In this context, even when fragments are not physically connected, ecosystem restoration may reduce habitat fragmentation by enhancing functional connectivity through ecological corridors and stepping stones, provided that a species' dispersal ability is great enough to reach them (Hilty et al. 2020), thus promoting biodiversity conservation (Crouzeilles et al. 2015; Rivas et al. 2024). Furthermore, effective measures to manage fragmentation will improve habitat loss and degradation simultaneously (Banks-Leite et al. 2020). Modelling functional connectivity has several advantages, including that it is more realistic, more informative and is possible to incorporate climate change and population dynamics (Liczner et al. 2024).

Since limited resources and conflicting LULC interests often preclude the restoration of all relevant areas, it is essential to identify strategic areas to be restored with higher contributions to functional connectivity (Soares et al. 2023). Evaluating connectivity gains before restoration implementation could improve other aspects, such as ecosystem services and potential adaptation to climate change (Préau et al. 2022). Associating connectivity model results with conservation and restoration strategies would maintain and improve the current and future connectivity, as well as support decision-making to better achieve restoration or conservation goals (Liczner et al. 2024). Several studies have already modelled the potential contributions of landscape restoration to improve connectivity in one or multiple scenarios (e.g., Antongiovanni et al. 2022; Crouzeilles et al. 2015; Tambosi et al. 2013). Such studies often compare connectivity before and after the restoration of a predetermined group of degraded areas into restored planning units (pixels) (e.g., Crouzeilles et al. 2015; Molin et al. 2018; Niemeyer et al. 2020; Oliveira-Junior et al. 2020; Tambosi et al. 2013). Although such an approach provides a robust analysis of the cost–benefit of different restoration scenarios and strategies (Metzger et al. 2017), there are some limitations due to the use of static, predetermined restoration scenarios. First, this approach considers only a specific static landscape configuration to identify a set of planning units to restore, assessing the collective contribution of the predetermined group of planning units. This hinders the identification of areas with higher contributions for restoration in the landscape that may not be considered in the designed scenarios. Most studies are limited to local scales since the scenarios often include drivers and states related to locally guided goals and local environmental legislation (e.g., Cable et al. 2021; Hernández et al. 2015; Niemeyer et al. 2020). Additionally, studies are commonly species-specific, which have limitations of the application and replicability of the results (e.g., Cable et al. 2021).

Contrastingly, large-scale dynamic assessments might provide more informative data to support restoration prioritisation efforts (Banks-Leite et al. 2020, 2022; Liczner et al. 2024). These analyses consider the identification of which individual planning units within the entire landscape could provide the greatest contribution to overall landscape connectivity if restored (Antongiovanni et al. 2022; Tambosi et al. 2013). Dynamic analysis could have practical applications to foster biodiversity agendas, especially in areas of invaluable biodiversity that experience high levels of habitat loss, serving as an excellent input for systematic conservation and restoration planning for biodiversity (Antongiovanni et al. 2022; Tambosi et al. 2013; Riva et al. 2024). However, due to the very high computational power needed, such dynamic analyses are seldom used in scientific literature for such biodiversity conservation goals (Niemeyer et al. 2020).

Here, we provide an unprecedented nationwide continuous spatial layer that represents each restorable pixel's contribution to functional connectivity. We used Brazil as the case study, considering its outstanding biodiversity, extensive habitat loss and fragmentation and ambitious restoration goals (e.g., restoring 12 million hectares by 2030; MMA 2017a). We performed a dynamic pixel-based analysis for each Brazilian biome to assess the potential increases in the connectivity index due to the restoration of each restorable pixel in the landscape. The outcomes of our study should be useful to support decision-making on the prioritisation of areas in restoration planning, including (i) the prioritisation of areas based on their potential improvement for the landscape's connectivity, (ii) national environmental law enforcement related to systematic restoration planning and (iii) international agendas coupling biodiversity conservation and climate goals for Brazil.

2 | Methods

2.1 | Study Area

Brazil is a megadiverse country composed of six natural domains that encompass different ecosystems, LULC, anthropic pressures and degradation levels (MMA 2020; Figure 1). We used the classification of Brazilian domains proposed by Oliveira-Filho (2017): Amazon, Atlantic Forest, Cerrado, Caatinga, Pampa and Pantanal—nationally and hereafter referred to as 'biomes'. We used the official biomes' limits from the Brazilian Institute of Geography and Statistics (IBGE; IBGE 2004). The Amazon and the Atlantic Forest are mainly composed of forested ecosystems (e.g., tropical and subtropical moist forests, hereafter referred to as forested biomes), while the Cerrado, Caatinga, Pampa and Pantanal are mainly non-forested (e.g., savannas, grasslands and wetlands, hereafter referred to as non-forested biomes).

In general, the foremost pressures on Brazilian biomes are agricultural expansion (including crops and cattle ranching), infrastructure and urban development (Solórzano, Brasil, and Oliveira 2021; Souza Jr. et al. 2020). In recent years, Brazil has made a series of restoration commitments to address such challenges. For example, in the Nationally Declared Contributions (NDCs) of the Paris Agreement, Brazil has pledged to restore 12 million hectares of native ecosystems by 2030 to aid in the climate mitigation goals (MMA 2017a), which could substantially halt the biodiversity crisis if strategically placed. This is also the target of the National Plan of Native Vegetation Recovery (PLANAVEG; MMA 2017a), which presents different goals for each biome: more than 4.5 million ha for the Amazon and the Atlantic Forest (76% of the Brazilian restoration goal), 2.1 million ha for the Cerrado (17%), 500,000 ha for the Caatinga (4%), 300,000 ha for the Pampa (2%) and 50,000 ha for the Pantanal (1%) (MMA 2017a). PLANAVEG is currently being reformed to ensure the fulfilment of Brazilian climate and sustainability goals and to organise the restoration process (Conservation International 2023). This reorganisation presents an opportunity to revise the priority areas for restoration to meet the national objectives.

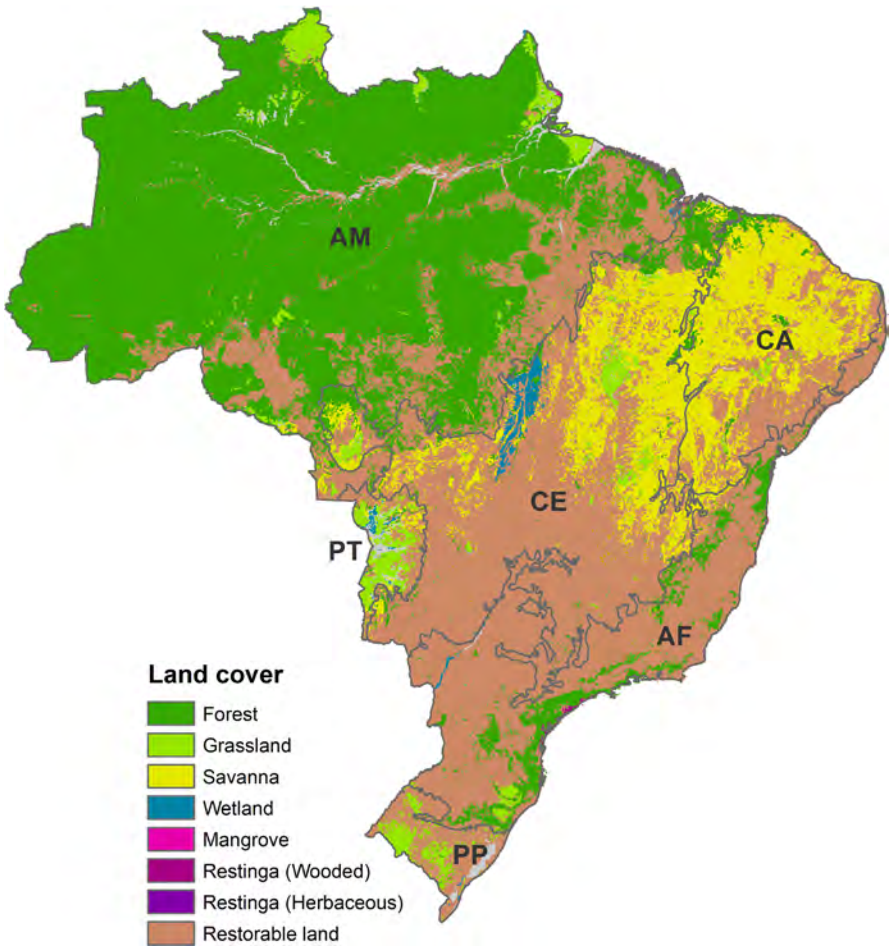

FIGURE 1 | LULC map for all Brazilian biomes. The map shows only planning units (pixels) with > 50% of each natural vegetation LULC, consisting of forests, savannas, grasslands, wetlands, mangroves and wooded or herbaceous sandbank vegetation (*restinga*). The restorable lands consist of planning units with any amount of land currently under use for pasture, agriculture or silviculture. Areas shown in grey were excluded from the analysis since they are neither natural vegetation LULC nor restorable lands (e.g., water). AF, Atlantic Forest; AM, Amazon; CA, Caatinga; CE, Cerrado; PP, Pampa; PT, Pantanal.

2.2 | LULC Maps

We obtained country-wide LULC maps from the MapBiomas project collection 7 for 2022 (MapBiomas 2021; Souza Jr. et al. 2020). All analyses were carried out separately for each biome to avoid bias in connectivity calculations among different biomes and considered connectivity within each biome.

Restoration's contributions to increasing connectivity were also analysed separately for each natural vegetation LULC class (namely, forest formation, savanna formation, wetland, grassland, mangrove, wooded and herbaceous sandbank vegetation; Table S1). It means, we only allowed the connectivity to occur between the same types of LULC. For the remaining LULC classes, we created two separate datasets for restorable and non-restorable lands. Restorable lands are composed of all pasturelands, agricultural areas and silvicultural areas (including pasture, temporary crops, soybean, sugarcane, rice, cotton, other temporary crops, perennial crops, coffee, citrus, other perennial crops, forest plantation and mosaics of uses; Table S1, Figure S1). Non-restorable lands are composed of unchangeable LULC (e.g., urban areas and water), which were excluded from the analysis.

We resampled each natural LULC and restorable lands dataset to obtain planning units (pixels) of ~4.4 km resolution for the analysis. We used the 'average' method to produce layers showing the proportion of each LULC class in each given planning unit. We used this resolution due to the large spatial scale of our country-wide analysis and the large computational power required to run pixel-by-pixel analysis. Nevertheless, this resolution is within the necessary scale for country-wide analysis and is compatible with other relevant global databases commonly used in macroecological studies, such as Worldclim (Fick and Hijmans 2017) and CHELSA (Karger et al. 2020) databases. We used the geographic information system of Albers equal-area conic projection with Datum EPSG:4283, which preserves area rather than absolute positional accuracy, thus maintaining pixels with the same exact size to avoid bias in the analysis throughout the country. All spatial analyses were performed in the R environment using the 'terra' package (Hijmans et al. 2024).

2.3 | Functional Connectivity Index

We used the Integral Index of Connectivity (IIC, Pascual-Hortal and Saura 2006) to assess the contribution of each restorable planning unit to overall landscape functional connectivity. The IIC is based on 'graph theory', which assesses the connection (named 'links') between habitat fragments (named 'nodes' and characterised by their area), that is, the pairwise relationship between two fragments connected by a link (Pascual-Hortal and Saura 2006). Two fragments are deemed connected if the Euclidean distance between them is shorter than a species' dispersal ability so that more interconnected fragments grant a greater degree of landscape connectivity. The IIC applies to any landscape and is considered one of the most appropriate indexes to perform this type of analysis due to its ability to assess functional connectivity through changes in the landscape (e.g., restoration of native vegetation) (Pascual-Hortal and Saura 2006). We ran connectivity analyses using the *Makurhini* package in the R environment (Godínez-Gómez and Ayram 2020; R Core Team 2024).

Due to the large spatial scale of the analysis, we modelled connectivity for species capable of moving through large distances, following other macro-ecological analyses (e.g., for hypothetical species: Saura et al. 2011, Gurrutxaga, Rubio, and Saura 2011, Molin et al. 2018, and Niemeyer et al. 2020; for plants: Hernández et al. 2015; for large mammals: Crouzeilles et al. 2021, Niculae et al. 2016, and Cable et al. 2021; and for birds: Saura and Pascual-Hortal 2007, and Tambosi et al. 2013). We defined medium, high and very high dispersal abilities as hypothetical species able to reach 2, 5 and 10 planning units (pixels), representing approximately a distance of 6.5, 20 and 42 km, respectively. These dispersal abilities were chosen based on published information regarding Brazilian large animals. For example, the puma (*Puma concolor*), a large-bodied felid, has a very high dispersal capacity, in which individuals can disperse, on average, 51 km/day (Maehr et al. 2002; Thompson and Jenks 2010). Other species with high dispersal capacities in Brazil include the jaguar (*Panthera onca*), which can travel between 7.9 and 28.8 km/day (McBride and Thompson 2018), the tapir (*Tapirus terrestris*), which is capable of straight-line movements over 20 km (Fragoso, Silvius, and Correa 2003; Paolucci et al. 2019) and the harpy eagle (*Harpia harpyja*), with a dispersal capacity of 31 km/day on average (Naveda-Rodríguez et al. 2022; Urios, Muñiz-López, and Vidal-Mateo 2017).

Although many natural LULC are present in each biome, some classes presented too few planning units to establish connectivity and were not incorporated. Thus, we calculated the connectivity index for forests, savannas, wetlands and grasslands in all biomes (except for wetlands in Caatinga and savannas in Pampa, due to its low representation in these biomes). Additionally, a handful of planning units for coastal ecosystems were also considered (mangroves for the Amazon, Caatinga and Atlantic Forest, and wooded and herbaceous sandbank vegetation for Pampa and the Atlantic Forest). Since our pixel-based analysis requires the presence-absence information for each LULC, we transformed the continuous LULC proportion data into presence-absence for each LULC (Figure S2). We considered all planning units with $> 50\%$ of a natural LULC as 'presence', thus assuming that each planning unit is entirely composed of each given LULC. To be conservative, we only assumed connectivity among fragments if species could reach the centroid of a planning unit (Figure S2). This choice of parameters assumes that a species must reach the core of planning units that mostly represent each LULC. On the other hand, such restrictions reduce the number of planning units for less representative LULC classes (Figures S2 and S3). Contrastingly, the restorable land consists of all planning units with any proportion of land currently classified as pasture, agriculture or silviculture.

We ran a dynamic pixel-based restoration analysis in each Brazilian biome to assess the contribution of each restorable pixel to functional connectivity, for each LULC class. Thus, we ran the model assuming the restoration of each available restorable planning unit into each LULC class and assessed its contribution to the overall landscape connectivity under each dispersal ability. For example, we ran the model by simulating the individual restoration of each one of the 102,692 restorable planning units to each LULC class present in the Amazon and under each dispersal ability (i.e., approximately 1,500,000 times for the Amazon alone). The resulting maps show the individual contribution of each given planning unit to overall landscape connectivity, for each LULC class and dispersal ability. We calculated the contribution based on the difference in the overall landscape connectivity index between a scenario where a given planning unit is restored and the current LULC scenario. Thus, although the pixel restoration can only serve as a connection between its surrounding fragments up to the defined dispersal abilities, the improvement in the biome-scale connectivity index after the pixel's restoration represents its role to overall biome landscape connectivity.

A given restorable pixel may be able to enhance the connectivity of more than one LULC class if restored. Since we ran the analysis separately for each LULC class, these pixels would have a higher contribution to improving overall landscape connectivity if restored, as they play an important role in connecting multiple LULCs. Once we had a map for each LULC class, we produced an ensemble map aggregating all LULC classes. This ensemble shows the overall contribution of restorable planning units to increase landscape connectivity for each dispersal ability in each biome. In the end, those planning units that are geographically important for more than one LULC class are more strategic and prioritised. Note that since we are working with large planning units, we aim to identify large regions with greater importance, but further analyses are needed to guide the spatial distribution of restoration of each LULC within these planning units. Noteworthily, greater importance for the index stems from those planning units that can connect more fragments. Thus, the overall connectivity index for each biome is mainly based on the biome's most representative LULC (e.g., forest formations for the Amazon). We normalised all ensemble connectivity index maps from 0 to 1, where 0 represents no contributions and 1 represents the greater contributions to the biome-scale landscape connectivity using a min–max normalisation approach, ensuring that all values are comparable in terms of their contributions to landscape connectivity at the biome scale. Then, we ranked the planning units to allow comparisons among biomes.

We performed these processes for each of the three dispersal abilities separately, producing an ensemble map for each one. Then, we produced a final ensemble database aggregating all dispersal abilities for each biome and produced a gradient of planning units according to their contributions to landscape connectivity and priority for restoration. After normalisation, we aggregated the normalised values for each planning unit by summing the two rasters. This produced a composite index representing their overall contributions to landscape connectivity. As a result, we were able to create a gradient of planning units based on their importance for restoration efforts. We finally ranked these planning units and selected 5%–30% of them with higher contributions to the functional connectivity in each biome.

3 | Results

Our analysis revealed areas that, if restored, would most improve landscape connectivity in each Brazilian biome. Since this analysis has considered the contribution of each individual planning unit to the overall landscape connectivity in entire biomes, most values are generally low, representing modest contributions to biome-scale landscape connectivity (Figure 2). Units with higher index values (i.e., warmer colours, Figure 2) could be interpreted as priorities for restoration due to their high capacity to contribute to the whole phytogeographic biome's connectivity.

Overall, the improvements in connectivity for species with medium dispersal ability are lower than for those with high and very high dispersal abilities (Figure 2) since these are only able to reach up to two planning units. Although modest, this contribution is especially important in the Caatinga, Pampa and Pantanal, which displayed higher values of connectivity index for medium dispersal species compared to the other biomes (Figure 3). As dispersal ability increases, there is an increased range of connectivity improvement displaying evident regions of great importance connecting fragments (Figure 2). This is particularly evident in the Pantanal, where more than 25% of restorable areas (~800 planning units) displayed values > 0.6, and 5% (~150 planning units) were in the top priority areas, with index values > 0.8 (Figure 3). Thus, restoration of any of these priority areas would contribute to substantially increasing Pantanal's connectivity.

There is a corridor-shaped region with a substantial contribution to connectivity in the Cerrado biome, near the Amazon ecotone, with > 5300 planning units with high contributions for connectivity (Figure 2). This region is particularly important because its restoration can contribute to multiple LULCs in the Cerrado, including savannas, forests, wetlands and grasslands (Figure S1). Approximately 8% of restorable land in the Cerrado displayed high potential to improve overall connectivity for species with very high dispersal, with ~4700 and ~650 planning units with index values of 0.6–0.8 and > 0.8, respectively (Figure 3). Contrastingly, our analysis worrisomely reveals that even for species with very high dispersal abilities, restoring individual planning units has little contribution to overall connectivity in the Atlantic Forest due to its extensive deforestation patterns, where only 1.5% and 0.25% of the biome's restorable areas showed index values of 0.6–0.8 and > 0.8, respectively, suggesting the need for larger restoration efforts in this biome. Similarly, the Amazon also showed few areas with high priorities for restoration, mostly concentrated in the deforestation arc, near the southeastern limit of the biome (Figure 2).

Finally, the final ensemble map reveals the priority areas for restoration considering all dispersal abilities combined, highlighting the areas that are most relevant to maximise contributions for species with differing dispersal abilities (Figures 2 and 3). For example, although there is a clear corridor with values higher than 0.6 for species with very high dispersal abilities in the Cerrado, the ensemble map reduces its importance (~0.4–0.6; Figure 2), prioritising planning units that will also benefit species with smaller dispersal abilities, who are most endangered by habitat fragmentation. Thus, the ensemble map was used to identify the priority areas for restoration in each biome (Figure 4). The corridor in the Cerrado remained important for connectivity, even though its importance decreased with the ensemble approach (Figure 4). Other important areas were the Arc of deforestation in the southeastern Amazon, the ecotones

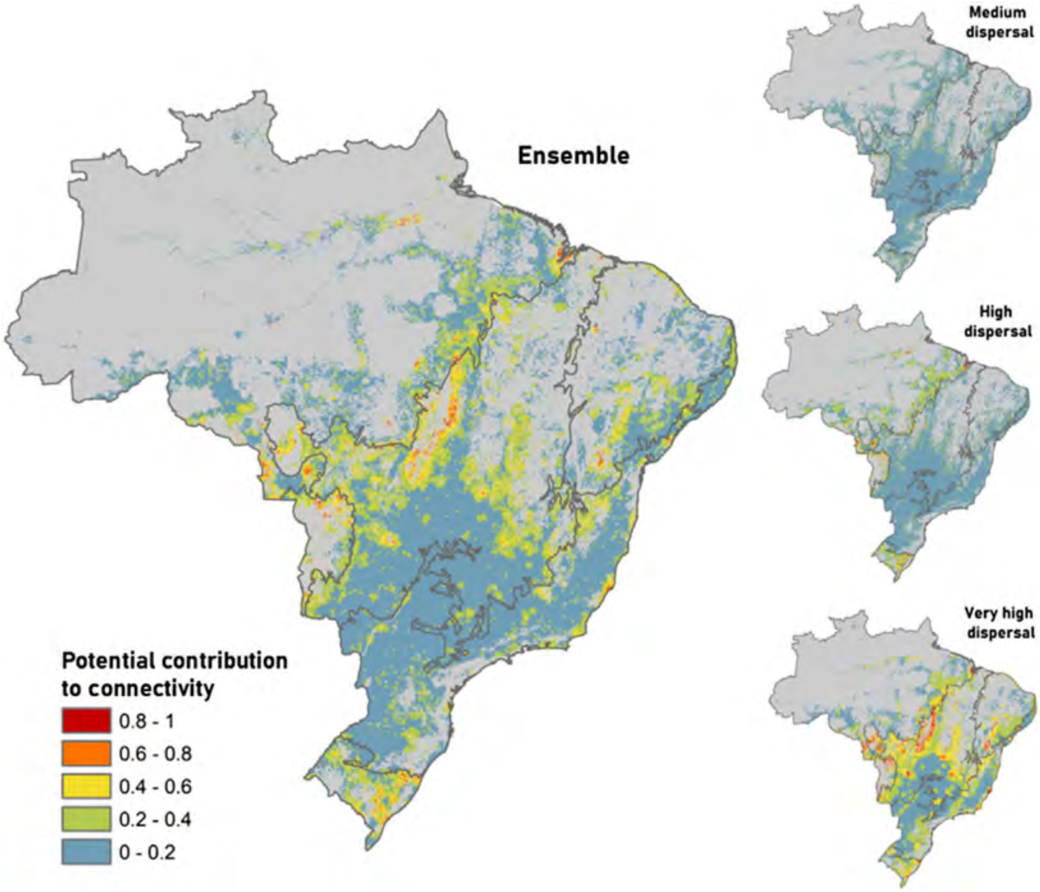

FIGURE 2 | Potential contribution to connectivity (connectivity index) ensemble considering species with all dispersal abilities together and separately (medium, high and very high dispersals). Higher values indicate greater contributions to connectivity stemming from the restoration of a given pixel. The connectivity index is shown for all restorable areas country-wide, that is, areas currently under LULC of pasture, agriculture or silviculture. Areas shown in grey were excluded from the analysis since they are non-restorable areas, that is, either currently with natural vegetation or under anthropic LULC not suitable for restoration, such as urban areas). Analyses were performed separately for each Brazilian biome, with its boundaries indicated with the dark grey lines.

between Atlantic Forest, Caatinga and Cerrado, and between Cerrado and Pantanal. Furthermore, additional priority areas were identified in the eastern region of the Atlantic Forest and Pampa (Figure 4).

4 | Discussion

We present an unprecedented and innovative nationwide macroecological effort with a pixel-based continuous database depicting the relative contribution of restoring each planning unit to enhance landscape connectivity in Brazil and revealing the most important areas to be restored in each biome. We identified two regions of particular interest: a priority corridor following the northwest region of the Cerrado, as well as the deforestation arc in the Amazon. Also, there is a trend of higher priority rankings (e.g., top 5%) being surrounded by subsequent rankings of priorities, characterising nested habitat patches with great importance for connectivity. This nested pattern facilitates the restoration implementation by reducing costs and maximising benefits. Other outputs from our database allow the identification of priority areas within each LULC class for species with different dispersal abilities, providing a comprehensive analysis suitable for applications under multiple contexts.

Since our analysis aimed to identify the stand-alone contribution of pixels to overall biome connectivity, most planning units have an expectedly low relative contribution. However, the pixels identified with greater contributions can improve biome-wide connectivity even if restored on their own and thus were interpreted as priorities for restoration. This is especially relevant for the non-forested biomes in Brazil, where a large proportion of individual stand-alone planning units would benefit all types of species assessed, especially species with lower dispersal abilities. For these species, restoration is more impactful adjacent to existing fragments, enhancing their size, and less effective in connecting distant fragments (Gilby et al. 2018; Jones and Davidson 2016). The high potential in the non-forested biomes is probably related to their smaller size and intermediate amounts of degradation. First, the contribution of restoration of a single planning unit to overall biomes' connectivity tends to be higher under smaller biome landscapes, since the area restored is proportionally higher. Second, due to their intermediate stages of degradation, fragments tend to be not too close to already be connected nor too far apart from each other so that species cannot reach them, allowing the restoration of a single planning unit to act as stepping-stones improving connectivity indexes (Tambosi et al. 2013). This is even more evident for species with very high dispersal abilities, where clear areas with

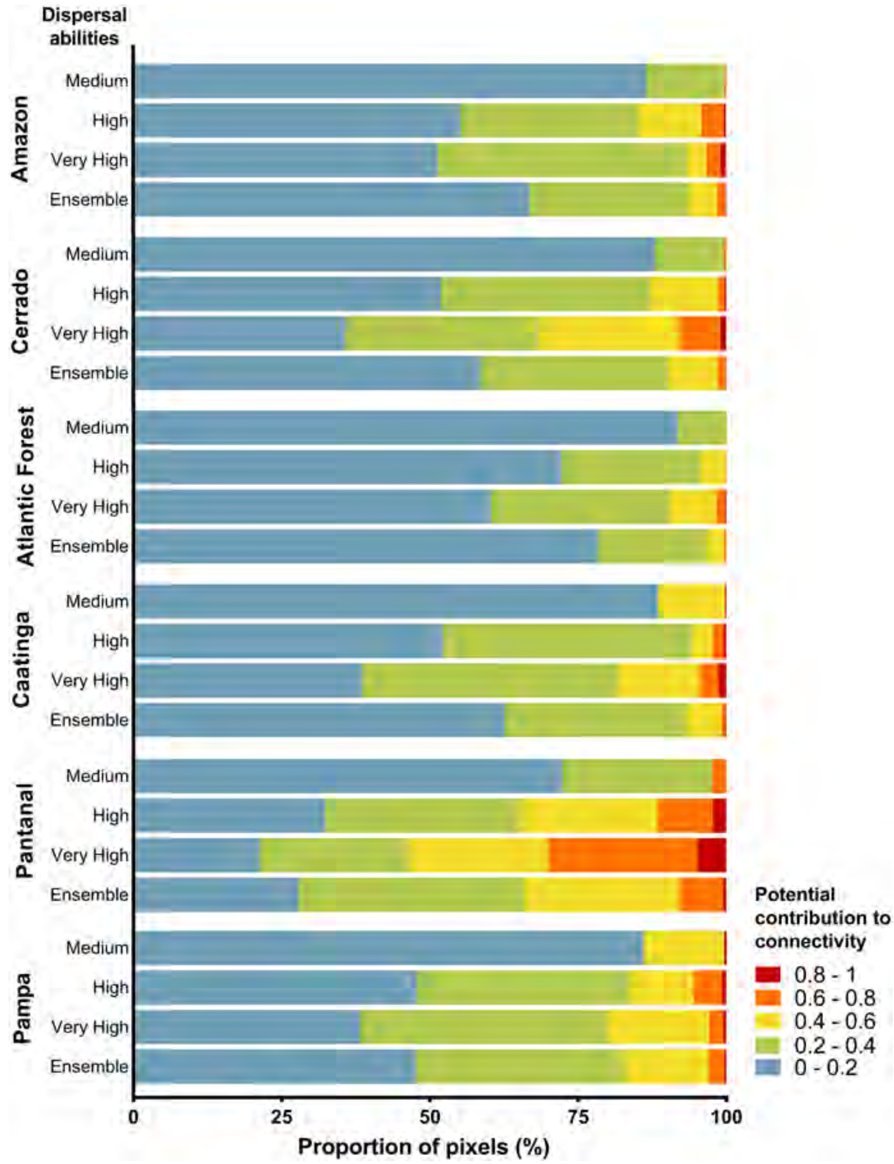

FIGURE 3 | Proportions of restorable planning units (pixels) with respective potential contributions to connectivity (connectivity index) in all biomes. The graph shows values for each dispersal ability (medium, high and very high) separately and together in a final ensemble. Higher values indicate greater contributions to connectivity stemming from the restoration of a given pixel. Restorable areas are currently under LULC for pasture, agriculture or silviculture.

great contributions for connectivity emerge (e.g., 25% of restorable units in Pantanal showing high contributions). Enhancing connectivity in non-forested biomes would benefit both savannas and grasslands (Figure S3). Given the challenges of restoring savannas, identifying key areas is crucial for guiding restoration efforts (Lewis et al. 2023). Grasslands, also threatened ecosystems, require more attention, especially as a proposed Brazilian bill (Bill 364/19) could weaken their legal protections by classifying them as rural lands (Overbeck et al. 2022, 2024).

Contrastingly, the forested biomes showed overall lower values of potential contributions to connectivity. As opposed to the non-forested biome's intermediate levels of degradation, landscapes with a high proportion of native vegetation (e.g., the Amazon) can recover themselves through autogenic processes, whereas severely fragmented landscapes (e.g., the Atlantic Forest) require much higher investments and more robust restoration efforts (Tambosi et al. 2013). Thus, restoration contributions are modest in the Amazon since it has an overall highly connected form, with priorities concentrated in the Deforestation Arc (Montibeller et al. 2020). Contrastingly, the restoration of individual planning units seems to be insufficient to improve connectivity in the Atlantic Forest since severe stages of degradation demand much higher investments to restore large areas at once. Only 1.5% of restorable land displayed a high connectivity index in the Atlantic Forest, highlighting the importance of these areas and the need for ambitious restoration efforts (Hatfield, Orme, and Banks-Leite 2018; Niemeyer et al. 2020; Tambosi et al. 2013). Thus, considering the context of the Atlantic Forest, a more locally guided approach is needed to assess the cost benefits of different scenarios with larger restoration goals (e.g., ecological corridors), as already assessed by different studies (e.g., Crouzeilles et al. 2015; Molin et al. 2018; Niemeyer et al. 2020; Tambosi et al. 2013). Such disparity in

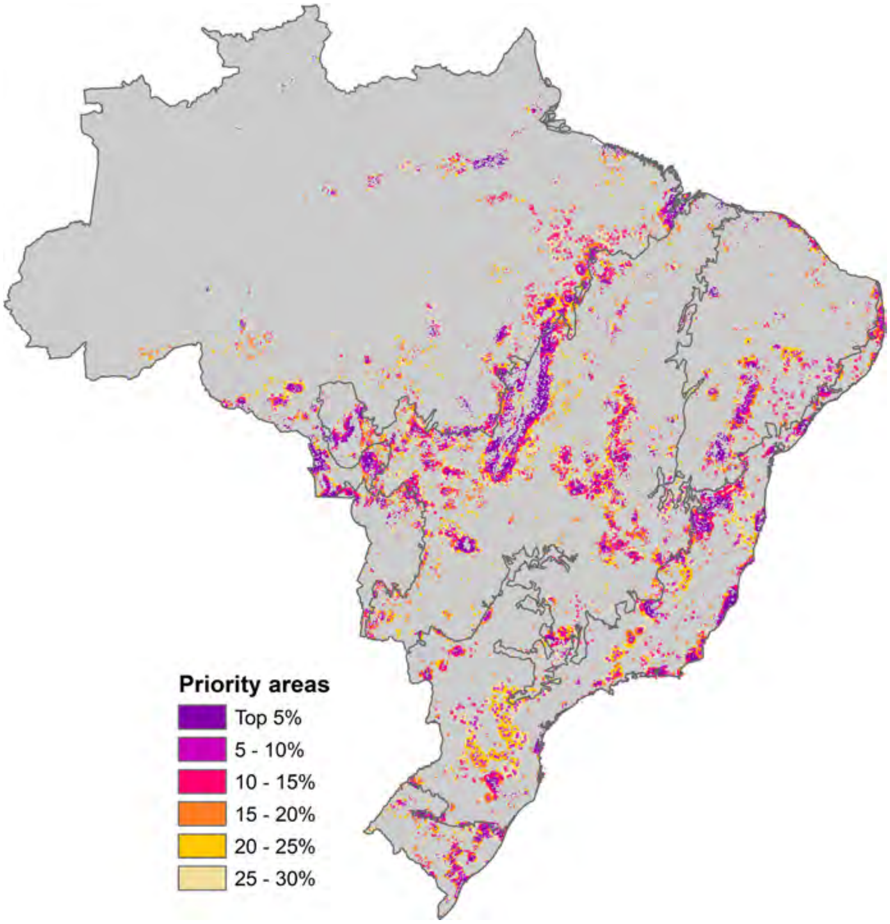

FIGURE 4 | Priority areas for restoration to improve functional connectivity for biodiversity. Priority areas were derived based on the ensemble connectivity index benefiting species with all dispersal abilities. Areas are shown as the top 5%, 10%, 15%, 20%, 25% and 30% in relation to the total restorable area in each biome, that is, areas currently under LULC of pasture, agriculture or silviculture.

restoration contributions among biomes under different stages of degradation is an important alert to the difficulty of recovering connectivity patterns post-degradation. Therefore, strong efforts must be made to recover biomes with high levels of degradation, such as the Atlantic Forest, but also halt degradation in other biomes before they reach such thresholds of connectivity loss. However, additional factors influencing natural recovery beyond active restoration should be considered, such as natural regeneration, which can enhance landscape connectivity. For example, in the Atlantic Forest, the number of forest fragments has increased primarily through natural regeneration (Vancine et al. 2024). Therefore, integrating both restoration efforts and natural regeneration processes can significantly improve connectivity in the mid-term.

Notably, although our database can identify important regions of greater connectivity contributions, further local assessments are needed to guide on-the-ground restoration implementation. Specifically, restoration efforts may require further multicriteria analysis at the local scale to identify the best spatial disposition and LULC types for implementing restoration activities, which should encompass socio-economic variables (e.g., opportunity and restoration costs of productive land) and legislation (e.g., the Brazilian Native Vegetation Protection Law—NVPL) (Adame et al. 2015; Halpern et al. 2013; Molin et al. 2018; Strassburg et al. 2019, 2020), among other aspects. This is especially relevant in the context of identifying the previous LULCs that were natural in the given region before deforestation and accounting for the habitat configuration within each planning unit (Gann et al. 2019; Toma et al. 2023). Identifying original LULC is pivotal in restoration efforts to establish properly the reference ecosystem and avoid biotic homogenisation (Gann et al. 2019; Holl, Luong, and Brancalion 2022; Toma et al. 2023). Knowledge of the proportion of restorable land in each given planning unit can also aid the selection of on-the-ground prioritisation for restoration implementation (Figure S1, Gann et al. 2019; Toma et al. 2023). Additionally, the large scale required for our country-wide analysis is inherent in further limitations. For example, due to the macro-ecological nation-wide scale of our study, we were unable to include species with low dispersal abilities (e.g., forest specialists) nor consider specificities about their habitat preference. Indeed, habitat preference data are scarce and only available for specific biological groups; thus, using it would make our analysis too restricted to a limited set of species. Nevertheless, we recognise that such local analyses are needed for more accurate and robust results at the local scale (Crouzeilles et al. 2015, Issii et al. 2020; Préau et al. 2022), and many are already available for the Brazilian biomes (e.g., Antongiovanni et al. 2022; Cavalcante et al. 2022; Crouzeilles et al. 2015; Schwaida et al. 2023; Tambosi et al. 2013). Furthermore, due to the wide scale of our study, we did not consider the internal conditions of land units, and for that, we could be underestimating functional connectivity, as we ignored the presence of possible corridors and stepping stones. Thus, further analyses considering the internal conditions of land units and corridors are needed. We could also underestimate connectivity as we did not consider the ecotones between biomes. We also assumed that species are able to disperse within a single type of natural vegetation cover, which may lead to an underestimation of connectivity results. Our results provide a large-scale analysis to identify important areas for improving connectivity, but further analyses are needed at finer scales, considering dispersion ability between different natural vegetation covers and considering ecotones' connectivity to support restoration planning and public policy implementation. Finally, we applied a 50% habitat presence threshold per pixel as a conservative approach to transform layers with proportions of vegetation to binary presence-absence information for each LULC, which excluded many pixels from our analysis and may have further underestimated our results. For example, thresholds of 35%–45% natural cover can sustain species in forests like the Amazon and Atlantic Forest (Arroyo-Rodríguez et al. 2020; Banks-Leite et al. 2014; Ochoa-Quintero et al. 2015; Rigueira, da Rocha, and Mariano-Neto 2013), while the Cerrado requires 47% (Muylaert, Stevens, and Ribeiro 2016). Using a generalised threshold without considering biological criteria may compromise restoration outcomes by creating trade-offs with costs and local communities (Banks-Leite et al. 2021; Brancalion et al. 2019; Strassburg et al. 2020). Although our methodological choices and large-scale analysis are associated with inherent limitations, these conservatively mostly underestimate the contribution of restoration to connectivity, and further local-scale analysis may highlight an even more robust pattern of ecological interactions.

Our analysis has several practical applications to guide decision-making and planning on where to allocate restoration in Brazil. First, we provide an essential database readily available for use in analyses for systematic planning for restoration prioritisation in Brazil, with aims to inform decision-making and allow for an efficient resource and investment allocation (Adame et al. 2015; Crouzeilles et al. 2015; Molin et al. 2018; Riva et al. 2024; Strassburg et al. 2019, 2020). Although landscape connectivity is a key criterion in systematic planning (Hanson et al. 2022), this information at nationwide scale was unavailable for Brazil, and therefore, prioritisation analyses for large-scale restoration were so far unable to incorporate connectivity (e.g., Iguatemy et al. 2022; Schüler and Bustamante 2022; Strassburg et al. 2019, 2022; Zwiener et al. 2017).

Second, our database is also a valuable tool to support the implementation of national laws and agreements related to restoration planning. Achieving the restoration targets of the PLANAVEG requires several efforts and resources (Brancalion et al. 2019). Restoration planning, including connectivity, will enhance outcomes while optimising investments. Compliance with the Brazilian Native Vegetation Protection Law (NVPL) demands the restoration of self-owned private lands or offsets with the restoration of third-party private lands in all biomes (Brancalion et al. 2016). In such cases, our layer could guide the allocation of restoration aiming at law compliance while concomitantly maximising connectivity (Niemeyer et al. 2020; Rother et al. 2018). Compliance with the NVPL is a great opportunity to restore large areas in Brazil, especially in biomes that have been most deforested, such as the Cerrado and Atlantic Forests. For example, restoration of the vegetation deficit (i.e., the amount of natural vegetation coverage inside private lands that falls below legal requirements) in the Atlantic Forest and the Cerrado would increase native vegetation cover by approximately 3.3 ha and 4.6 million ha, respectively (OCF 2024). Our results could be used as a criterion to identify areas where restoration towards law compliance would deliver higher biodiversity gains for reduced costs.

Finally, incorporating connectivity into restoration planning would facilitate coupling the biodiversity and climate agendas since one of the most severe impacts of climate change is the shift of species distributions, obligating species to move towards more suitable habitats (Hilty et al. 2020; Malecha, Vale, and Manes 2023; Riva et al. 2024). Since severely fragmented landscapes often preclude species movements, improvements in landscape connectivity are commonly appointed as a paramount climate adaptation strategy (Hilty et al. 2020). Predictions of climate change for Brazil indicate that the current disposition of protected areas will not be enough to safeguard species, and restoring in-between patches is essential (Malecha, Vale, and Manes 2023; Soares et al. 2023). Including connectivity in spatial planning is especially important, as prioritised areas are more robust to uncertain climate change, reducing the advancement speed of the extinction risk rate (Albert et al. 2017; Hodgson et al. 2012). Our results can provide support to future studies of restoration planning for adaptation, which should also consider species distributions, the identification of areas for climate refugia, microclimatic gradients, and important areas for species interactions (Hilty et al. 2020; Gross et al. 2016). Thus, using spatial planning for restoration that includes landscape connectivity as a biodiversity gain would ensure the alignment of the climate and biodiversity agendas, guaranteeing win-win restoration outcomes.

Also, the incorporation of connectivity into restoration planning would help foster international agreements such as the Kunming-Montreal Agreement (CBD 2022) and the Paris Agreement and NDCs (UNFCCC 2015; Seddon et al. 2019). In particular, the Kunming-Montreal Agreement (especially Goal A and Target 2, CBD 2022) and the National Biodiversity Strategy and Action Plans (NBSAP), which was the Brazilian strategy to nationally implement the Aichi Targets (MMA 2017b), have already highlighted the enhancement of connectivity, ecological integrity and ecosystem resilience as pivotal goals, which are still far below-desired levels worldwide (Protected Planet 2020; Hilty et al. 2020). Brazil has not achieved the Aichi Target related to connectivity and already has studies highlighting lower connectivity levels between protected areas, mainly in the Cerrado and the Atlantic Forest (Saura et al. 2017).

5 | Conclusions

Ensuring the functional connectivity of ecosystems is crucial to maintaining biodiversity, ecosystem functioning and the provision of ecosystem services. To our knowledge, this is the first study to evaluate the contribution of restoration efforts to functional connectivity across all Brazilian biomes. The innovative pixel-based analysis presented here can serve as a model to be replicated in other regions. We have provided priority restoration areas within each Brazilian biome, which could guide decision-making and increase the efficiency of restoration efforts. Specifically, the results could be used in systematic restoration planning to facilitate the scale-up of restoration efforts in Brazil, contributing to the achievement of national targets and supporting strategies to link biodiversity conservation and climate policies.

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The authors have nothing to report.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Zenodo at https://zenodo.org/records/13345088, reference number https://doi.org/10.5281/zenodo.13345088.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.