



Combining connectivity and species distribution modeling to define conservation and restoration priorities for multiple species: A case study in the eastern Amazon



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ABSTRACT

Increasing the connectivity of protected areas is an urgent need to ensure the conservation of forest species and help them to shift their ranges due to anthropogenic drivers. However, efforts to do so considering the joint effects of habitat fragmentation and climate change are still scant. Here, we aimed to outline a framework that incorporates spatial, temporal and multi-taxa criteria to pinpoint locations that connect protected areas in the eastern Amazon. We analyzed three mosaics of protected areas, and data on 603 species (bees, birds, bats) and developed two models using species movement flow (MF; through circuit theory) and habitat suitability (HS; through species distribution models). Considering only the MF, northward areas are the main candidates for corridors, most of which presenting forest cover (68% of the 928,379 ha). This result changes when we analyze the HS, since the corridors are mostly positioned in a different direction (westward) and less than half have forest cover (45% of the 925,058 ha). Candidate areas for both approaches totaled 135,171 ha, with 86% still covered by forest. Our results rely on methodological and taxonomic redundancy (to depict a range of movement and/or habitat requirements) for an efficient strategy to prioritize areas for connectivity. Dynamic restoration simulations showed that the location and order of restoration are important to ensure increased availability of habitat. Our approach can help address two important biodiversity threats (habitat loss and climate change) and maximize the selection of the best corridors to protect species in a rapidly changing world.

1. Introduction

Deforestation is a historical threat to tropical forest ecosystems around the world (Taubert et al., 2018). Tropical landscapes are becoming highly fragmented due to the increasing rates of forest habitat loss, with detrimental effects on biological flux. As a consequence, biodiversity losses and ecosystem services reductions have been reported (Barlow et al., 2016), raising questions on how effectively isolated areas are safeguarding biodiversity (Schulze et al., 2017; Schleicher et al., 2019). In this way, planning spatial networks of protected areas has been proposed as a potential method to conceive a more effective system of reserves focused on maximizing habitat connectivity

(e.g., Saura et al., 2017).

Recently, it has been argued that human-induced climate change is imposing an additional threat on biodiversity due to unprecedently rapid shifts in temperature and precipitation regimes (Scheffers et al., 2016). The effects of these accelerated climatic shifts on ecosystems can have a dramatic impact on the accomplishment of conservation goals and, in turn, result in the waste of important and scarce conservation investments (Millar et al., 2007). In addition to defining the regions that contribute most to connectivity, the prioritization of strategies for connecting protected areas should consider the climatic suitability of the sites considered for selection (Loarie et al., 2009; Burrows et al., 2014). Additionally, conservation strategies should be able to embrace

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preventive measures to avoid unsuccessful investments and anticipate undesirable shifts in the landscape's suitability to maintain its biodiversity and ecosystem services (Huang et al., 2020). Nevertheless, little attention has been given to the synergistic effects of habitat fragmentation and climate change (but see Giannini et al., 2015, Sales et al., 2019, Campos et al., 2020).

Ecological corridors have been widely used as a management activity to increase habitat connectivity on fragmented landscapes (Hilty et al., 2006). These linking structures have positive effects on biodiversity and species dispersal (Haddad et al., 2014). At large spatial scales, corridors can be defined as the best potential routes for animal dispersal and movement and do not necessarily correspond to continuous habitat strips, as commonly viewed at smaller spatial scales (Hilty et al., 2006). In fragmented landscapes, these zones of high biological flux should be seen as sets of habitat patches surrounded by a permeable intervening matrix, including potential sites to be conserved or restored, depending on whether they are forested or deforested, respectively.

Despite the ecological importance of corridors for biodiversity, the identification and implementation of corridors are not trivial tasks because movement behavior data are scarce and unknown for most species, hindering an estimation of multispecies habitat connectivity based on empirical information (Abrahms et al., 2017). Moreover, the monetary cost of implementing corridors is usually high, and funding is often limited, thus demanding prioritization efforts through the development of proper frameworks with optimal criteria (Jalkanen et al., 2020). Basically, financial limitations imply that we must obtain the best and most accurate approaches for the management problem at stake without necessarily having the best datasets to achieve this goal. Therefore, our decisions should be driven, as much as possible, by the best available knowledge to provide the greatest possible guarantee that the objective of protecting species will be achieved with the prioritization scheme we choose to follow (LaPoint et al., 2013).

Reconnecting isolated fragments by forest restoration can be an effective way to create areas large enough to slow the rate of species extinctions (Laurance et al., 2011). However, tackling this shortcoming in Amazon tropical forests is not a trivial task since this biome still presents multiple knowledge gaps related to fragmentation (Teixido et al., 2020). The National Forest of Carajás, a protected area located in the eastern Amazon, is an exception. This area has been surveyed since the mid-1990s, and a substantial biodiversity database is available (Costa et al., 2018, Miranda et al., 2019, Borges et al., 2020a, Giannini et al., 2020). Carajás is now a structurally isolated fragment of forest (Souza-Filho et al., 2016), covered by an important part of the remaining pristine forest in the southeastern areas. This situation poses an important opportunity to develop a framework using available data to identify ecological corridors aiming to reconnect isolated protected areas.

Our goal was to outline a framework that incorporated spatial, temporal and multi-taxa criteria to identify a set of ecological corridors that could connect protected areas in the eastern Amazon and help species find suitable habitats while considering fragmentation and climate change. We built two models (species movement flow (MF) and habitat suitability (HS) to analyze the connectivity of three mosaics of protected areas and the climate suitability of 603 species of fauna (bees, birds and bats). The proposed framework will enable us to design ecological corridors and prioritize areas that could help species track their ecological requirements under land use and climate change. Deforestation in the Brazilian Amazon is not homogeneous, being concentrated mainly in the eastern and southern limits (i.e., deforestation-arc), and started in the 1970s with infrastructure projects, such as the trans-amazon road, and programs that incentivized land occupation (Aldrich et al., 2020; Fearnside, 2005). Our study area is located in the south-eastern Amazon and is composed of a mosaic of virtually disconnected protected areas (called Carajás Mosaic – see below) surrounded by a deforested matrix. The peak of deforestation surrounded Carajás occurred between 1984 and 2004, with an annual rate of approximately 75,000 ha of conversion of forested areas to

pasture (Souza-Filho et al., 2016). Although the protected areas of Carajás are well preserved, recent data on deforestation monitoring conducted by the Brazilian Space Research Institute (INPE) and by the IMAZON (a non-profit organization dedicated to conserving the Amazon forest) showed an increase in forest loss rates in the municipalities surrounding the protected areas in the last two years.

2. Methods

2.1. Study area

The study area has 11,910,834 ha and includes three sets of virtually disconnected protected areas of Amazon forest, which are referred here as the Carajás Mosaic (CM; six protected areas including the National Forest of Carajás), the Terra do Meio Mosaic (TMM; 42 protected areas) and the Parakanã Indigenous Land (PIL; one protected area) (Fig. 1). Together, these protected areas constitute the last remnant of large blocks of pristine Amazon forest. They are located within the area under the greatest deforestation pressure for the last 40 years, known as the arc of deforestation (Fearnside, 2005). The matrix is composed of a mosaic of land covers but is dominated by pasture, agriculture and abandoned areas (Souza-Filho et al., 2016). Our approach involves applying models to select areas of the matrix that reinforce the current connection between the three protected areas, potentially ensuring that this connection will remain even in the face of expanding deforestation in the surroundings. Our approach also relies on potential future habitat suitability considering the climate change. In terms of biodiversity, the protected areas harbor rich Amazon fauna and flora. The National Forest of Carajás (the largest protected area inside the CM) has at least 943 species of terrestrial vertebrates (Martins et al., 2012), and detailed information is available for three groups: bees (Borges et al., 2020a; Giannini et al., 2020), birds (Miranda et al., 2019) and bats (Costa et al., 2018). These groups provide important ecological functions, such as pollination and seed dispersal and have been selected for this reason to integrate the framework proposed here. However, robust biodiversity data for the other protected areas are still lacking.

2.2. Land cover mapping

The complete workflow of the methods used in this study can be found in Fig. 2. The land cover map for 2017 was obtained from the MapBiomass Project collection 4.0 (2018), with a cell resolution of 30 m. We resampled the original classification using the closest neighbor technique, reducing the resolution to 60 m due to computational limitations. In addition, given the study's goals and the underrepresentation of some land cover classes in the region, the original map was reclassified into a final map with four classes: forested areas, non-forested areas, infrastructure and rivers (Fig. 1). The "forest" class included all forested formations. The "non-forested areas" class included the original classes of pasture, mosaic of agriculture and pasture, annual and perennial cultures, naturally formed open-area vegetation and another non-vegetated area. The "infrastructure" class included the original mining and urban infrastructure classes. The river class remained unchanged. Additionally, a raster of the main roads was obtained from the Departamento Nacional de Infraestrutura de Transportes (DNI; <http://www.dnit.gov.br/mapas-multimodais/shapefiles>) and complemented with the identification of other major paved roads that were mapped by visual inspection of Google Earth. This final layer was included as a fifth class of land cover. We used the ArcGIS 10.5 (Esri Inc.) in all the procedures for editing, reclassifying, resampling and format conversion of the maps mentioned above.

2.3. Movement flow modeling

We used circuit theory to make inferences about the flux between protected areas in the study region (McRae et al., 2008). In this modeling

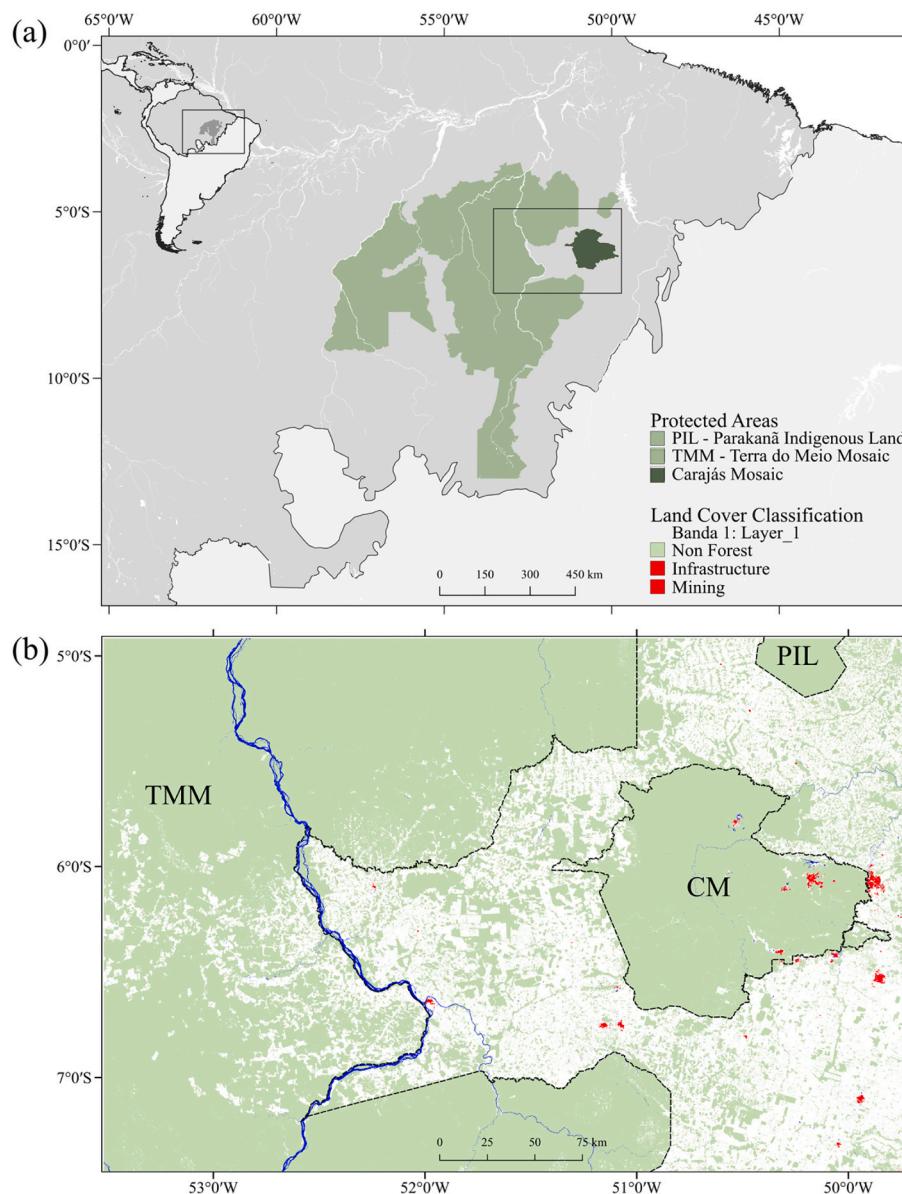


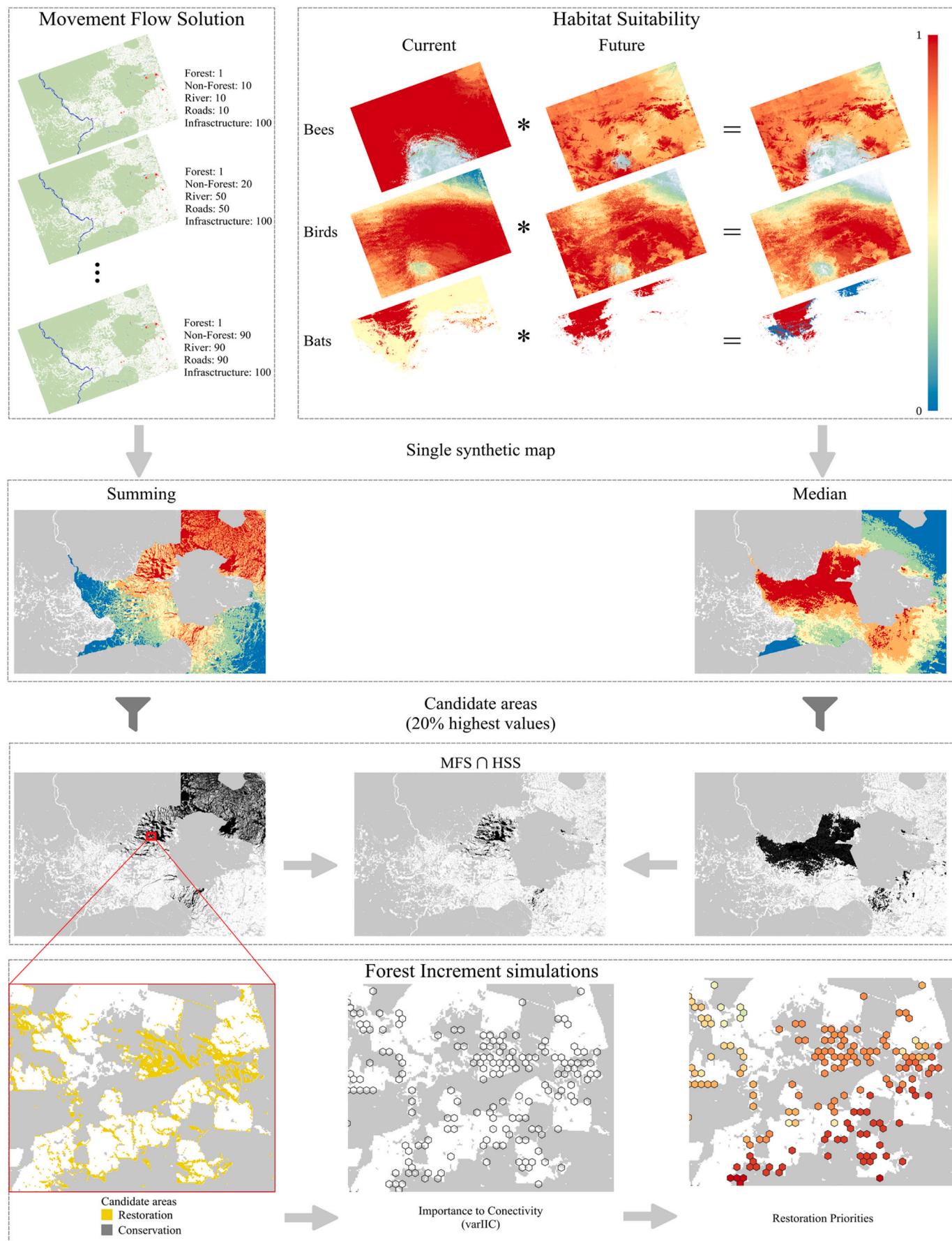
Fig. 1. A) Protected areas in the southeastern Amazon: dark green is the focal area, Carajás Mosaic (CM), and the lighter greens are other protected areas targeted to achieve connectivity, including the Parakaná Indigenous Land (PIL) and Terra do Meio Mosaic (TMM). The inner map shows the Amazon biome in South America with a zoom to the area shown on map A. B) Study area with Land Cover Classification from Mapbiomas project collection 4.0 and the categories depicted in the legend (main roads not shown). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

approach, the landscape is analogously conceived as an electric circuit, in which some cells or cell clusters (e.g., habitat patches) are taken as focal nodes (i.e., points or regions from and to which movement flow is to be modeled; McRae and Shah, 2011). The remaining landscape is represented as cell resistors presenting a certain resistance to flux (of electrons in electric systems or of individuals in ecological systems). In this representation, it is possible to use circuit theory (e.g., Ohm's law Ω) to determine the amount of current that passes through each cell. Current can be viewed as a measure of the flux of individuals in these cells (the lower the cell resistance is, the greater the electrical current is, and thus, the higher probability that an individual moves through this cell is; see McRae et al., 2008 for details). In short, by analyzing resistance surfaces, circuit models enable us to infer the best routes for animal movement; thus, this approach represents a good method that can be used to identify priority sites for ecological corridor implementation (Wade et al., 2015).

We used an alternative approach to parameterize the resistance surfaces. Instead of consulting specialists' opinions or using empirical data available from one or few species as representatives of all biodiversity (which are the most common approaches observed in the literature; Zeller et al., 2012), we tested a theoretical space of resistance

values that could be attributed to the different land classes. This theoretical space of resistance values is a set of resistance surfaces given by possible combinations of resistance values for each land class. We consider that, although simplified and theoretical, this alternative approach allows us to analyze different hypothetical resistance profiles that represent the variation in landscape permeability of ecologically distinct species. We note that MF models based on representative profiles of real species have been suggested when the empirical data needed to parameterize the models are lacking (e.g., generic focal species profiles; Watts et al., 2010).

We assumed that resistances vary between 1 and 100 Ω , a range of values commonly used in parameterizing resistance surfaces according to Bowman et al. (2020). Our study area has five land classes, which could lead us to analyze an excessive number of combinations of resistance values. We reduced this number by assuming that the forest and infrastructure classes have the lowest and highest resistance values, respectively ($R_{Forest} = 1 \Omega$ and $R_{Infrastructure} = 100 \Omega$ in all combinations). In addition, the river and road classes are likely to have a small effect on the flow of individuals because they are underrepresented in the study area. Thus, we also assumed that three resistance values (i.e., a high, a medium and a low value) are sufficient to evaluate

**Fig. 2.** Methodology workflow.

the effects of these land classes on movement (R_{rivers} or $R_{\text{roads}} = 10, 50$ or 90Ω , respectively). On the other hand, we expected that the non-forested area class, being heavily represented in the study area, would have a greater effect on forest connectivity in the landscape. Thus, we considered a set of nine values to analyze this class with a finer resolution ($R_{\text{nonforest}} = 10, 20, 30, \dots, 90 \Omega$). Altogether, we modeled 81 different land resistance profiles (i.e., all possible combinations of the resistance values; $3 (R_{\text{rivers}}) \times 3 (R_{\text{roads}}) \times 9 (R_{\text{nonforest}}) = 81$ profiles).

We ran the models in the Circuitscape software (version 4) set to (i) the 8-cell neighborhood rule and (ii) the pairwise modeling mode (McRae et al., 2013). In the pairwise mode, circuit analyses are run separately for each pair of focal nodes in such a way that one node is considered to be connected to a current source and the other node is the current sink, thus grounded. The three sets of protected areas (CM, TMM and PIL) were identified as focal nodes, since ecological corridors should be defined between them. Circuitscape was independently run for each resistance profile, returning a cumulative current map, and may be taken as the final accumulated current per cell when individual pairwise results are combined. To account for a multispecies perspective while estimating a single synthetic value for each cell in the study area, we summed the cumulative current values of the less correlated profiles (i.e., Spearman $\rho > 0.99$) to provide a consensual map.

2.4. Habitat suitability modeling

We used species distribution modeling (SDM) to anticipate the impacts of climate change (Elith and Leathwick, 2009). For this step, we used published data from SDMs built in a standardized way (with the same parameters) for forest-dependent species of bats ($N = 71$; Costa et al., 2018), birds ($N = 382$; Miranda et al., 2019) and bees ($N = 150$; Giannini et al., 2020) (Table S1). In addition to data availability, these groups occupy all strata of the forest, have different dispersive capabilities (although there are no precise data for each species individually, and for this reason, they were not explicitly used in the MF models) and represent different functional roles (pollination, seed dispersal and biological control), making them prone to depict a large range of movement and/or habitat requirements (Meurant et al., 2018).

Occurrence data and climatic variables were gathered from different repositories (see the three main references above quoted for details). The models were initially built considering the entire spectrum of optimal environmental conditions of the species throughout their known occurrence range. Three sets of pseudoabsence/background data and 10 runs for cross-validation from the random division of the databases (presence + pseudoabsence) in training (80%) and testing (20%) were applied in two algorithms (generalized linear models and maximum entropy). Models were projected for the study area at a resolution of 1 km² (lowest resolution available for climate variables). The projections were performed for the present time as well as for the year 2050 considering the Representative Concentration Pathway (RCP) equal to 4.5 (RCP4.5) under two general circulation models (IPCC, 2013).

The maps were combined per species per scenario (databases + algorithms + GCMs + runs) using the committee averaging method (Thuiller et al., 2009). This ensemble method first transforms the probabilities into binary data according to a threshold (in this case, maximizing the evaluation metric, true skill statistics) and then averages the predictions of the species being present (i.e., it represents a measure of agreement between the combinations, and their values range from 0 to 1; Thuiller et al., 2009). Two consensual maps were produced for each species, with continuous values for the presence of the species in a given time. Each pair was then multiplied (current * future), producing a map in which the highest values represent locations with (1) high suitability in the present, (2) high suitability in the future or (3) some combination thereof (hereafter, habitat suitability [HS]). In the same way as the MF model, we generated a synthetic value considering all taxa together and summarized a final map using the median cell values.

Finally, to maintain the same resolution as the other layers (60 m) and allow the integration of both types of information, we resampled the final HS map using the bilinear technique. For these steps, we used the raster (Hijmans et al., 2020) and biomod2 (Thuiller et al., 2020) packages of the R programming environment (R Core Team, 2019).

2.5. Analysis

To assess the degree of agreement between the approaches and identify whether any taxonomic group would be favored, we compared the distribution of cell values between different approaches, considering 1) the contrast between general outputs of models (i.e., MF vs HS_{Total}) and 2) between the general outputs and those for each taxonomic group (i.e., MF vs HS_{bees}; MF vs HS_{birds}; MF vs HS_{bats}; and HS_{Total} vs HS_{bees}; HS_{Total} vs HS_{birds}; HS_{Total} vs HS_{bats}), using Spearman's correlation coefficient. We also calculated a local spatial correlation between the general results, in which a focal area (5 × 5 cells) was defined around each cell of the raster, and we calculated the correlation coefficient between the values of each raster using the *cor* function in R. This operation was repeated for all cells using the *focal* function of the raster package.

The results of the MF and the HS models point to several areas and are shown through a gradient of values. Notwithstanding, there is no theoretical or empirical basis that allows us to establish a cutoff threshold to determine from which value the result is considered relevant. Therefore, we decided to adopt the top 20% quantile criterion as the cutoff threshold in MF and HS to select candidate areas. From that first selection, we identified the concordant areas (intersection) for both approaches. Then, to calculate which proportion of these candidate areas has forest cover and which is deforested, we overlaid it with our land cover map. Thus, candidate areas with forest cover were considered to have priority for conservation, and the already deforested areas were considered to have priority for restoration.

Finally, to assess the best location and order for restoration actions, we carried out simulations of forest increment (i.e., we simulated the conversion of candidate areas for restoration into forest; Tambosi and Metzger, 2014), considering MF, HS and the intersection of both. Our aim in this step was to further guarantee the chances of the approaches being the most relevant to the connection considering the changes in habitat availability as new areas were restored. For that, we first divided the candidate areas for restoration into hexagonal cells of 10 ha so that the size of the units to be restored in each approach was the same. Then, we calculated the integral index of connectivity (IIC; Pascual-Hortal and Saura, 2006) for each set of candidate areas. The IIC considers the presence or absence of connection between the habitat patches (i.e., the candidate areas for conservation) depending on a limited distance between them. We assumed 100, 200 and 500 m as this limit distance to represent the dispersive capacity of different species. We used the IIC because this index allows us to detect changes in connections due to the creation of a patch (varIIC). In this way, we were able to estimate how much a hexagonal cell would contribute to habitat availability. The most important cells (those with the highest varIIC) were considered restored (i.e., converted to forest), and we re-evaluated the IIC. For each round of the simulation, we considered the "conversion" of 70 hexagonal cells. This number of cells is equivalent to 10 fiscal modules (1 fiscal module is equal to 70 ha and is a measure used by the Brazilian government to classify a rural property).

The simulations were compared in terms of the percentage of IIC increment ($[(\text{IIC}_i - \text{IIC}_1)/\text{IIC}_1] * 100$; where i is the i th simulation compared with the first IIC with no forest increment). We also assessed the contributions of direct and stepping-stone links (expressed as percentages of IIC). These analyses were conducted by combining an R script with the command line version of the software Conefor Sensenode 2.5.8 (Saura and Torné, 2009).

3. Results

The MF outputs (Fig. 3A) show a dispersion of cells with a higher cumulative current in the northern parts of the study area mainly towards the PIL but also some portions of the TMM, while the values decrease in the southwest and southeast directions. In contrast, the HS model (Fig. 3B) indicates that the northern parts have low to very low values (mainly in the northeast). The results of this model also highlight a concentration of areas with higher suitability to the west and some to the south towards the TMM. There was a weak negative correlation between the approaches, considering the values of the whole area (Spearman $\rho = -0.16$; $P < 0.001$), as well as the local spatial correlation (Fig. 3C).

The distribution of values for the MF is highly skewed to the lowest

values, while the distribution of values for the HS is more uniform, both for the general output and for each taxonomic group (Fig. 4). In addition, there are no noticeable differences between the general results of the approaches and the HS for each taxonomic group. Thus, our results showed a weak correlation with the MF model (MF vs HS_{bees}, $\rho = 0.03$; MF vs HS_{birds}, $\rho = -0.26$; MF vs HS_{bats}, $\rho = -0.02$) and a strong positive correlation with the general output of HS (HS_{Total} vs HS_{bees}, $\rho = 0.87$; HS_{Total} vs HS_{birds}, $\rho = 0.92$; HS_{Total} vs HS_{bats}, $\rho = 0.83$; all $P < 0.001$).

After selecting the cells with the highest values, we found that under the MF approach, we had 630,050 ha (67.9%) for restoration (deforested) and 298,329 ha (32.1%) for conservation (forested) (Table 1; Fig. 5A). This amount of area for conservation was distributed in 28,488 polygons, of which 15,999 had up to 1 ha and 89 had 1000 ha or more (Table 1). Using the HS approach, deforested areas (prone to

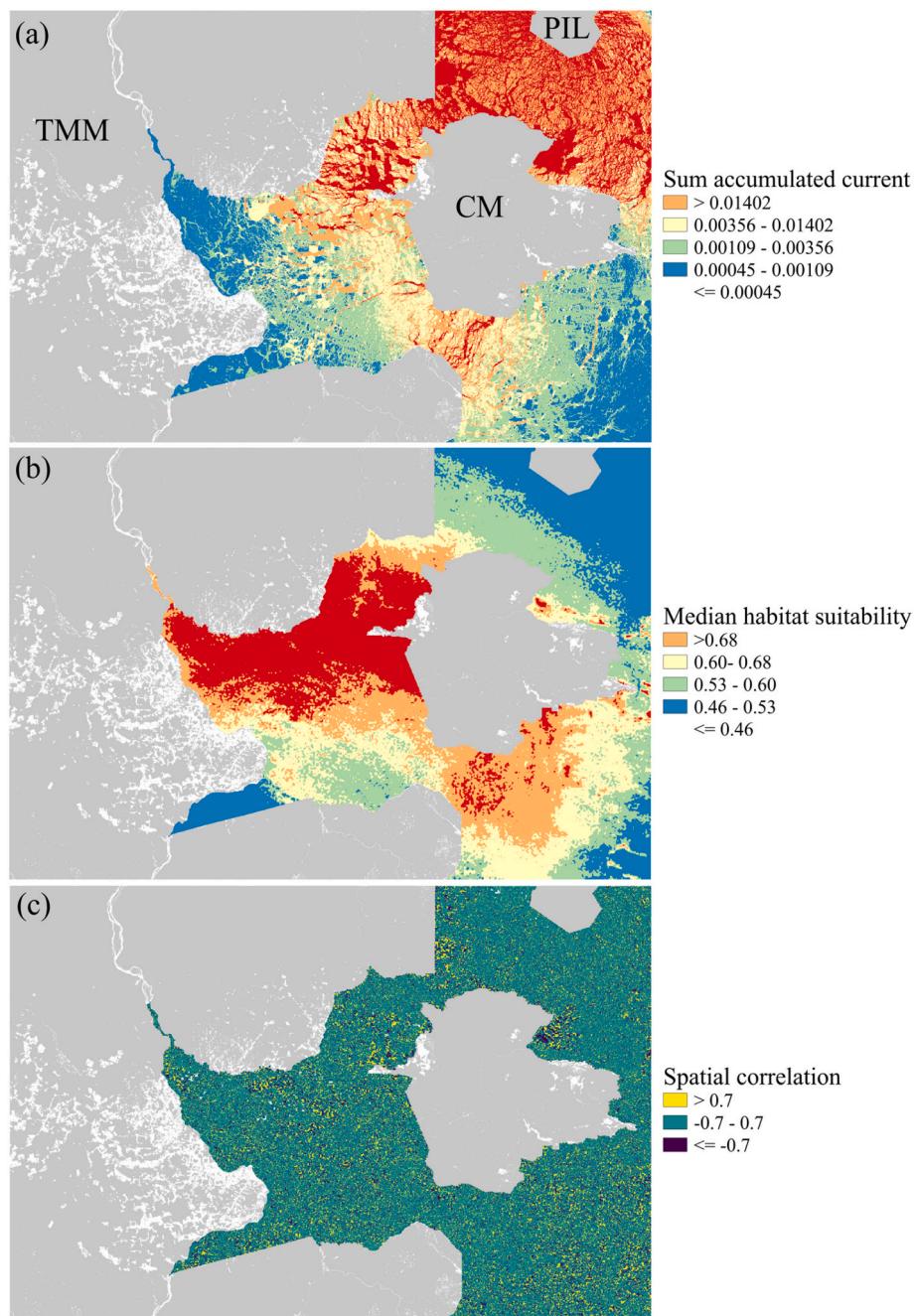


Fig. 3. Maps with results of A) movement flow model; B) habitat suitability model; and C) spatial correlation between models. Values in the legends refer to the quantiles of 20, 40, 60 and 80%.

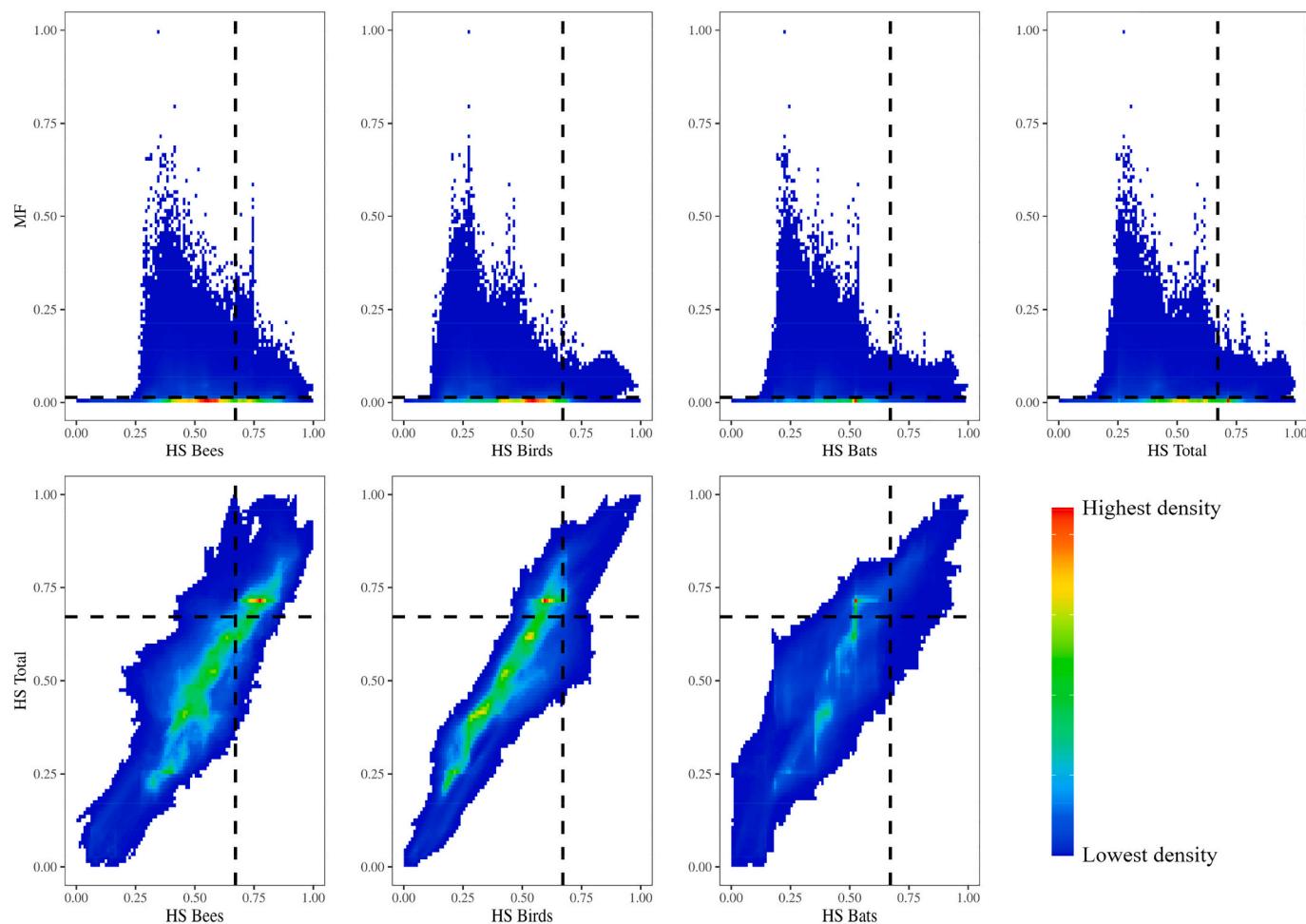


Fig. 4. Density scatter plots comparing the cell values in the movement flow (MF) with habitat suitability (HS) models. Values were rescaled from 0 to 1. Upper panels: MF (y-axis) and HS (x-axis) for bees, birds, bats and total. Lower panels: HS total (y-axis) and HS for bees, birds and bats (x-axis). Hotter colors indicate a higher density of points, and dashed lines depict the cutoff thresholds for candidate areas.

Table 1

Characterization of candidate areas for ecological corridors. Numbers before the slash in (%) are in relation to the total per approach and after the slash in relation to the study area.

Approach	Type	Area (ha)	(%)	n _{pol} ^a	n _{pol} ^a ≤ 1 ha	n _{pol} ^a ≥ 1000 ha
Study Area	Forest	8,184,848	0.69	–	–	–
	Non-Forest	3,630,987	0.30	–	–	–
	Infrastructure	18,282	0.001	–	–	–
	Water	76,717	0.006	–	–	–
	Total	11,910,834	1.00	–	–	–
Movement flow	Conservation	630,050	0.68/0.05	28,488	15,999	89
	Restoration	298,329	0.32/0.03	–	–	–
	Total	928,379	1.00/0.08	–	–	–
	Conservation	419,205	0.45/0.04	10,939	5252	56
	Restoration	505,853	0.55/0.04	–	–	–
Habitat Suitability	Total	925,058	1.00/0.08	–	–	–
	Bees	406,079	0.44/0.03	11,362	5407	49
	Restoration	512,931	0.56/0.04	–	–	–
	Birds	404,799	0.44/0.03	12,136	5690	65
	Restoration	519,499	0.56/0.04	–	–	–
Both	Bats	394,177	0.43/0.03	11,414	5414	70
	Restoration	521,899	0.57/0.04	–	–	–
	Conservation	117,002	0.86/0.01	4845	3001	22
	Restoration	18,738	0.14/0.002	–	–	–
	Total	135,741	1.00/0.01	–	–	–

^a n pol = number of polygons, i.e., fragment of continuous forest.

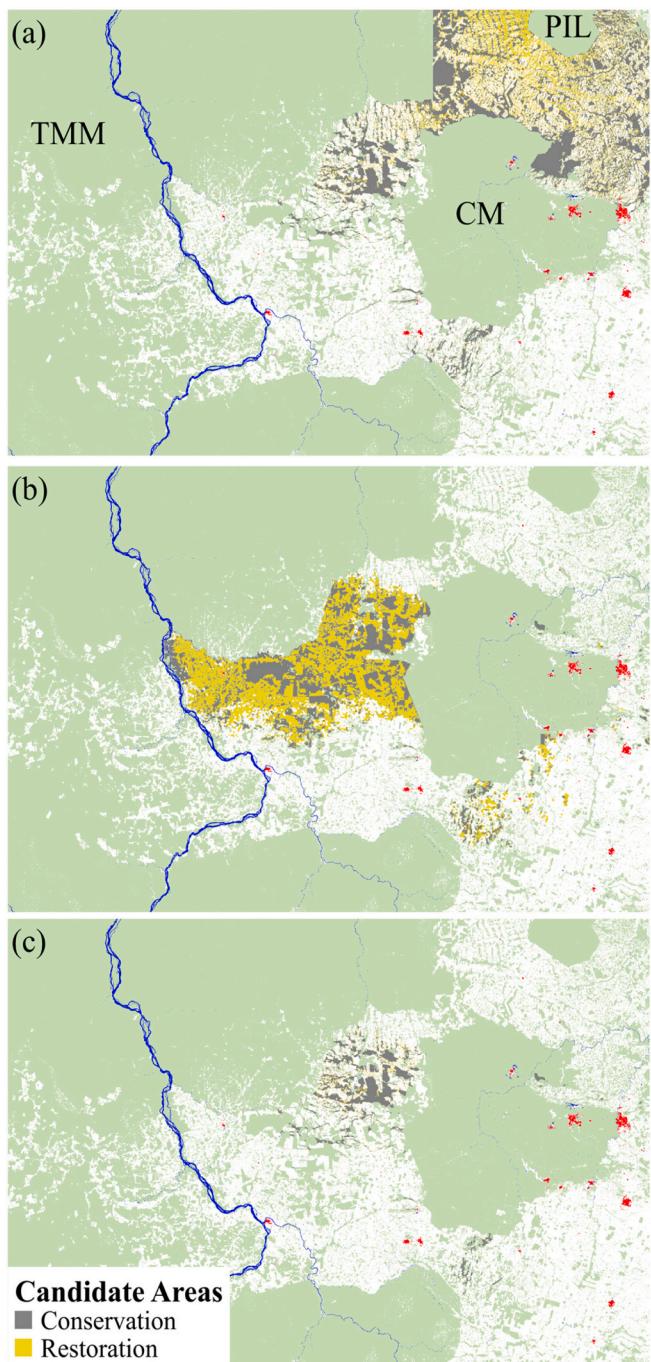


Fig. 5. Maps with land cover classes from Mapbiomas (see Fig. 1) depicting candidate areas for corridors considering A) movement flow model; B) habitat suitability model; and C) intersection area between both models.

restoration) comprised 505,853 ha (54.7%) (Table 1; Fig. 5B). Forested areas (candidates for conservation) totaled 419,205 ha (45.3%), arranged in 10,939 polygons ($5252 \leq 1 \text{ ha}$ and $56 \geq 1000 \text{ ha}$; Table 1). Among these areas, some were indicated as candidates for both approaches, of which 18,738 ha (13.8%) were identified for restoration and 117,002 ha (86.2%) were identified for conservation (Table 1; Fig. 5C). These conservation areas constituted 4845 polygons, of which approximately 3000 were less than or equal to 1 ha and only 22 had 1000 ha or more (Table 1). Looking at each taxonomic group separately (Fig. S1), birds and bees had more cells with high values (above the cutoff threshold) than did bats, and the amount of area for restoration in each taxon was greater than that for all taxa combined (Table 1, Fig. 4).

Spatially, the difference between animal groups was also notable: only birds and bats indicated suitable habitats towards the south, and only bats seemed to have suitable habitats to the east (Fig. S1).

The use of forest increment simulations to prioritize areas for restoration showed an increase in the IIC for all the analyzed landscapes (individual approaches and the intersection area), as well as for all distance thresholds (Fig. S2). Two general aspects characterize the increase in IIC for most simulations. First, this increase in habitat availability appears to be greater in the initial phases and decreases in the final phases. In addition, in most simulations, this increase occurred in the stepping-stone portion, whereas direct connections presented little increase or remained stable. Only the HS approach increased the IIC linked to direct connections, although this result was not expressive (Fig. S2D-F). Considering the individual approaches (MF and HS), the greatest gains in the IIC occurred for the distance of 200 m (Fig. S2B and E), while for the intersection area (both), the greatest gain was observed at the distance of 100 m (Fig. S2G). It is also interesting to note that the 500 m distance showed high IIC increments for the intersection area; in addition, there was a substantial gain in the IIC after the 4900 ha restoration (Fig. S2I). The distribution of areas and the order of increment of restoration can be seen in Figs. S3–S5.

4. Discussion

Our work proposes alternative solutions to connect protected areas in the eastern Amazon using multi-taxa data presenting different dispersal capabilities and potential responses to climate change. When considering only the habitat configuration through circuit theory and surface resistance to the movement of species, the main corridors to connect the CM with other protected areas were located mainly in the northern region of the study area. However, the HS analysis, considering climatically suitable areas (those that are suitable now and will probably continue to be suitable in the future), showed that the areas suitable for connectivity are located to the west. Despite the very low congruence between the two approaches, with the selection of candidate areas (by the highest values), some of them are common to both. In addition, the dynamic restoration simulations showed that the location and order of restoration are important to ensure increased availability of habitat, regardless of the approach and the distance between forest patches.

Different methods for determining the corridors provided different spatial results. The MF model using circuit theory highlighted sites between protected areas considering forest fragments with the least resistance. Thus, considering the landscape configuration of our study area, where there is a greater number of forest fragments to the north (even if in large part $\leq 1 \text{ ha}$), this approach would favor cumulative current values in this direction, since the forest class has the lowest resistance. In addition, the paths between forest fragments (through classes with greater resistance) would be the shortest to have a greater cumulative current and thus would also favor a greater proportion of candidate areas with forest cover. In contrast, the areas indicated by the HS approach are more aggregated in the west. In this case, the landscape configuration is not considered; instead, the future climatic variability, in relation to the current climate conditions of the target species, is emphasized. The westward orientation was an expected result, according to the general response patterns from which these data were obtained (Costa et al., 2018; Miranda et al., 2019; Giannini et al., 2020), as well as other studies in the Amazon (for mammals: Ribeiro et al., 2018; Sales et al., 2020; and trees: Gomes et al., 2019). Therefore, in the first method, we have an approach that highlights the spatial aspect of connectivity, favoring paths that would facilitate the flow of organisms between protected areas, while the second method highlights the temporal aspect of connectivity by identifying climatically suitable habitats over time.

The ability of a forest species to occupy forest fragments will depend not only on its physical capacity to cross an open habitat matrix but also on the size, state of degradation and connectivity of the fragment

(Boesing et al., 2018; Boscolo et al., 2017). Some species can cross many tens of kilometers of degraded matrix, whereas many others are more associated with the closed canopy habitat and avoid habitat discontinuities. For example, large-bodied birds, most Neotropical bat species and habitat generalists are more likely to cross matrices between forest fragments, while small understory birds, solitary insectivores and some forestry specialists are generally reluctant to cross open areas (Moore et al., 2008). Therefore, in all steps of our methodology, we are concerned with accommodating multiple dispersive capacities. We found no significant differences between the responses of our target groups; however, bat species presented a higher priority area to the east than did birds and bees, contrary to the general western tendency observed in our study area.

Our HS results analyze the species for which accurate data are currently available (e.g., bees, birds and bats) and are representative of a range of dispersive capabilities, habitat requirements and ecological functions. However, future works should include other taxonomic groups as surrogates to test the dependence of our results in relation to the other species. A recent study already showed that species-based approaches perform better than habitat-based ones, although the number of species matters as much as the criteria used for their selection (Meurant et al., 2018).

A recent review claims that an optimal landscape configuration for biodiversity conservation would have more than 40% forest cover, of which 10% would be covered by large areas of forest and the remaining 30% would be covered by smaller fragments (Arroyo-Rodríguez et al., 2020). Our study area totals 11,910,834 ha, of which 8,184,848 ha are covered by forests (i.e., 69%), and CM alone has 1,286,174 ha (i.e., 11%). Therefore, one could argue that simply conserving forest patches would be enough to guarantee biodiversity conservation in this landscape. Nevertheless, two facts are worth considering. First, according to the Brazilian Forest Code, in the Amazon biome, rural properties must preserve 80% of native vegetation, and if the law were applied in our study landscape, an increase of 1,343,820 ha would still be required to reach this value of 80%. Second, on a larger scale, there are no other areas of continuous forest as large as that in the CM to the east or southeast of the study area. In any case, regardless of the debate over the effects of fragmentation on biodiversity (i.e., habitat loss and fragmentation versus habitat amount; Fletcher et al., 2018; Fahrig et al., 2019), landscape configuration will be less important if sufficient forests are available (Arroyo-Rodríguez et al., 2020). Therefore, the conservation of standing forest and the restoration of degraded lands are essential for increasing habitat availability, and it is necessary to reduce the spaces between forest patches and safeguard the long-term stability of the environment (Watling et al., 2020).

Our study does not consider the effects of future land use change, since there is no recent study that forecasted land use change for the study area. But, a potential loss of forested areas greater than 50% for the entire Amazon forest in the ‘business-as-usual’ scenario by 2050 was already projected (Soares-Filho et al., 2006). This study showed that the biggest loss of forests would be concentrated in the south-southeast of the Amazon, resulting from the model’s assumptions that larger loss of forest are related to the proximity of already deforested areas and the proximity of roads (Soares-Filho et al., 2006). Therefore, it is important to highlight that the surrounds of Carajás Mosaic is under pressure from deforestation. For example, considering all the rural properties in the Amazon and Cerrado, only 2% of them would potentially lead to illegal deforestation activities (Rajão et al., 2020). Nevertheless, a more in-depth look at the data shows that many of the analyzed rural properties with the highest rates of illegal deforestation are located in our study area (data available at https://csr.ufmg.br/radiografia_do_car/). In addition, data from INPE and Imazon showed that some municipalities surrounding the Carajás mosaic are the ones that loss the largest forested areas in the last year (July 2019 to August 2020; Fonseca et al., 2020). Therefore, there is an urgent need for policies and management to conserve and restore the Amazon forest.

It has recently been shown that the success of restoring tropical forests, in terms of biodiversity and vegetation structure, is greater through natural regeneration than that obtained from active restoration (Crouzeilles et al., 2017). The authors argued that this result was probably because, in a dynamic and random process, regeneration is initiated through the colonization of opportunistic and locally adapted species, resulting in a greater diversity of locally adapted plant species. Therefore, forest remnants and the heterogeneity of the landscape are important for regeneration, intensifying the speed and success of this process. Our study area has 687,861 ha of secondary forests, of which 370,415 ha (54%) are under 5 years old, 205,843 ha (30%) are between 5 and 10 years old and 111,603 ha (15%) are over 10 years old (data accessed from Silva et al., 2020a). The economic cost of natural forest regeneration and active restoration (planting seedlings or seeds) is another important factor that should be considered. In the Amazon, the cost of natural regeneration is approximately 54 US\$/ha, while the cost of planting seedlings and seeds can reach 5300 and 1134 US\$/ha, respectively (Benini and Adeodato, 2017). These figures demonstrate that the costs vary widely depending on the strategy that is adopted. However, these values can be justified when we consider that other ecosystem services can also be restored, especially carbon sequestration and mitigation of climate change, the restoration of soil fertility, and the regulation of air quality (Zeng et al., 2019), in addition to water protection (O’Donnell et al., 2018) and food production (Melo et al., 2020). The region around Carajás mosaic has different types of human occupation, and several municipalities present a high dependence on biodiversity to ensure water resources (Pontes et al., 2019) and food security (Borges et al., 2020b). In addition, agroforestry systems, for example, constitute one of the restoration strategies that reconcile human presence with sustainable use of natural resources - a fundamental aspect for the success of management and conservation actions. Thus, protecting local traditional communities, which depend on biodiversity, as well as protecting biodiversity per se are priorities that must be reconciled in the search for a pluralistic perspective on biodiversity conservation (Pascual et al., 2021).

Finally, our approach could be improved if data on species dispersal and adaptability to climate change were available, since deforestation has increased rapidly in recent years (Walker et al., 2020) and can lead to more land-use change and isolation of protected areas, causing further local climate change (Staal et al., 2020; Silva et al., 2020b). It is also important to note that we used a limited description of the study area (i.e., five classes of land cover). Thus, we suggest that future studies account for a more refined classification of the analyzed landscapes (for instance, a distinction of primary and secondary forest) to adjust the land prioritization for conservation and restoration. Furthermore, some steps, more specifically the cutoff threshold used for the selection of candidate areas and the number of areas converted to forests in the increment simulations, were arbitrary choices. Therefore, it would be important to analyze other thresholds and the number of cells added to each round of the forest increment simulation. Another necessary future step is to ascertain the areas prioritized by our approach *in loco*, considering the feasibility of implementing the corridors, especially due to the potential presence of conflicts derived by human settlements based on illegal land use and/or irregular occupation (Aldrich et al., 2020; Rajão et al., 2020).

5. Conclusion

Incorporating different criteria into a multi-taxa prioritization framework enabled a more refined selection of sites when attempting to increase connectivity through ecological corridors between protected areas in the eastern Amazon. This approach is important because it considers the joint effects of the two most important current threats to species, land use change and climate change, on data scarcity scenarios. The presented framework is flexible enough to be adapted to other regions and can incorporate species adaptability and dispersal capacity if

these data are available. Our approach is especially useful for stakeholders in their decision-making processes focused on local initiatives, but it can also be applied to larger scales to facilitate the movement of species in a rapidly changing world.

CRediT authorship contribution statement

Conceptualization: TCG, LSM, MA; Data curation: LSM, WFC, LT, RCB, RMB; Formal analysis: LSM, MA, RJ, RMB, LRT; Funding acquisition: TCG; Writing - original draft: TCG, LSM, MA; Review & editing: all authors.

Declaration of competing interest

The Instituto Tecnológico Vale is a nonprofit and independent research institute, and the choice of questions, study organisms and methodological approaches were exclusively defined by the authors. The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary data

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