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Planning forest restoration within private land holdings with conservation co-benefits at the landscape scale

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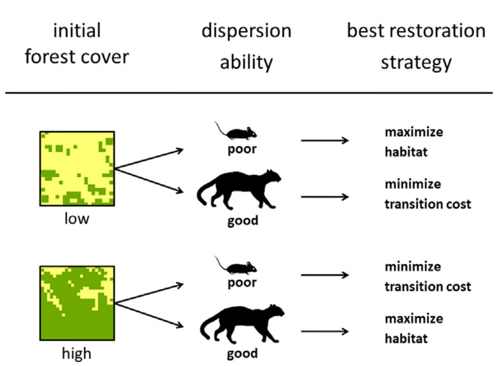
HIGHLIGHTS

- Planning restoration in private lands is paramount to achieve cost-effectiveness.
- Planed restoration achieves 12x more biodiversity benefits than random restoration.
- Biodiversity benefits can be achieved even under severe spatial constraints.
- Prioritizing the increase in habitat availability hastens biodiversity benefits.
- Planed law compliance of Brazilian private lands increases landscape permeability.

GRAPHICAL ABSTRACT

Different combinations of initial forest cover and dispersal ability require different restoration strategies to increase cost-effectiveness. Cost-effectiveness is calculated based on gain in habitat availability per cost. For species with good dispersal in high forest cover landscapes, focusing on minimizing transition cost is sufficient to achieve higher cost-effectiveness. This strategy aims at minimizing restoration cost incorporating the probability for natural regeneration. The most worrisome combination - species with poor dispersal in low forest cover - require a strategy focused on increasing habitat availabilty. Using this strategy achieves higher habitat availability earlier than alternative strategies and for low additional cost, even under sever spatial constraints. Performing spatial planning in restoration achieved up to 12 times higher habitat availability and saved up to 4.5 million USD compared to random restoration, most commonly done in real world scenarios due to a lack of spatial planning at the landscape scale.



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ABSTRACT

Forest loss is mainly due to the conversion of forest to agriculture, mostly in private lands. Forest restoration is a global priority, yet restoration targets are ambitious and budget-limited. Therefore, assessing the outcome of alternative decisions on land-use within private lands is paramount to perform cost-effective restoration. We present a novel framework that incorporates spatial planning for forest restoration

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within private lands with conservation co-benefits at the landscape scale. As a case study, we used three real landscapes of 10.000 ha with differing amounts of forest cover in the Atlantic Forest region of Brazil, and three hypothetical animal species with different dispersal abilities. We estimated the total amount of forest that landholders must restore to comply with the Native Vegetation Protection Law, which requires landholders to reforest 20% of their land within a 20-year time frame. We compared the cost-effectiveness of five restoration strategies based on the improvement in habitat availability and restoration costs. The most cost-effective strategy depends on a landscape's initial amount of forest cover and the species of concern. We revealed that spatial planning for restoration in private lands increased habitat availability up to 12 times more than random restoration, which was always the least cost-effective strategy. Cost-effective large-scale restoration in Brazil depends on public policies that assist landholders to comply with the law and on prioritizing areas for restoration within private lands. We show that by adding habitat availability as target in spatial prioritization, benefits for biodiversity can be hastened at low additional cost, even in real world scenarios with severe spatial constraints. Despite constraints, spatially planned restoration for law compliance in Brazil increased landscape permeability by creating corridors and stepping stones. Our framework should be used to plan restoration in Brazilian private lands and can be customized for other regions worldwide.

1. Introduction

Human induced deforestation, forest fragmentation and degradation are serious and ubiquitous threats to biodiversity and ecosystem services (Lewis et al., 2015). Today only ca. 31% of the World's forest area remains (FAO, 2018) and conservation alone will no longer suffice. As a consequence, the United Nations General Assembly has declared 2021 – 2031 the UN Decade on Ecosystem Restoration (FAO, 2019). Forest landscape restoration (*sensu* IUCN, 2018. Available at https://www.iucn.org/theme/forests/our-work/forest-landscape-restoration; called "forest restoration" hereafter) has become a global priority, spurred by numerous initiatives around the world. The New York Declaration on Forests and the Bonn Challenge (Climate Focus, 2015), for example, are international commitments seeking to restore up to 350 million hectares of deforested and degraded ecosystems by 2030. These ambitious targets face many political, socio-economic, environmental and legal challenges (Metzger et al., 2017).

Deforestation is strongly associated to the conversion of forest to agriculture (Gibbs et al., 2010; Soterroni et al., 2018). Given that ca. 11% of the World's remaining forests and most agricultural land are privately owned (FAO, 2018), land-use decisions within private land holdings play a key role in conservation of forests, ecosystem services and biodiversity (Brancalion et al., 2012; Liu et al., 2016; Strassburg et al., 2019). Because forest restoration is extremely expensive and budget-limited (Brancalion et al., 2012; Banks-Leite et al., 2014; Chazdon & Guariguata, 2016), it is difficult for most landholders to undertake it (Strassburg et al., 2019). Well planned restoration within private land holdings is important to remove barriers and gain landholder's acceptance (Polyakov & Pannell, 2016). It may as well avoid negative outcomes, such as competition for land or displacing deforestation to other regions (Latawiec et al., 2015).

Landholders may be encouraged to set aside productive lands for restoration if it is a more economically interesting activity. That may include, for example, the sustainable exploitation of (non)-timber products, rather than conventional crops (Brancalion et al., 2012; Melo et al., 2013), or financial support through certification and incentive schemes (by public or private initiatives) in exchange for environmental conservation efforts (Brancalion et al., 2012; Polyakov & Pannell, 2016). Finally, landholders may be obliged to comply with environmental laws (Melo et al., 2013; Latawiec et al., 2015; Rother et al., 2018), setting aside land for restoration in order to avoid fines and other penalties (such as denied access to loans and imprisonment, Soterroni et al., 2018). The decision to restore will often depend on the cost of setting aside land for restoration instead of using it for other practices (Budiharta et al., 2016; Mills et al., 2014; Brancalion et al., 2012). The costs for restoration implementation are also relevant, ranging from lower-cost methods, such as assisted or spontaneous natural regeneration, to higher-cost methods, such as active restoration based on tree planting (Helmer et al., 2008; Holl and Aide 2008; Crouzeilles et al., 2017). The best restoration method will depend on a landscape's characteristics and history. For example, the probability for natural regeneration is reduced in areas where previous land use was intense, distance to forested patches is high, and soil is severely exposed, because under those circumstances seed bank, propagules, and soil nutrients tend to become less available (Chazdon, 2003; Lamb et al., 2005; Crouzeilles et al., 2017). Thus, the selection of priority areas for forest restoration should account for alternative targets and decision-making on land-use, and the complex relationships between socio-economic and ecological/biophysical factors in order to achieve more cost-effective solutions (Rappaport et al., 2015; Chazdon & Guariguata, 2016; Metzger et al., 2017).

Additionally, in order to be effective, decision-making on forest restoration should also account for the potential return of biodiversity to restored areas, especially organisms involved in seed dispersal and nutrient cycling. The return of biodiversity will depend upon habitat availability (Crouzeilles et al., 2015), a concept that accounts for a landscape's capacity to support populations of a given species, including habitat quality, quantity, configuration and a species' ability to disperse between habitat patches (Hodgson et al., 2009; Saura & Rubio, 2010; Crouzeilles et al., 2014).

Brazil is a suitable case study for exploring how to incorporate alternative strategies for forest restoration into spatial prioritization at the land holdings scale. Around 53% of the remaining native vegetation in Brazil is in private rural properties (Soares-Filho et al., 2014). According to the Brazilian Native Vegetation Protection Law (Law N° 12.651/2012), rural landholders must protect a certain amount of the native vegetation on their properties (e.g. 20% of the property size in the Atlantic Forest) and should restore their environmental debts (i.e. the total amount of forest that landholders must restore to achieve compliance with this law), if they exist, within a time frame of 20 years. The legislation currently requires that all landholders declare the amount and position of native vegetation within their land (Zakia & Pinto, 2013). This Rural Environmental Registry has the potential to become a central instrument for prioritization of areas for restoration of native vegetation in Brazilian private lands. Unfortunately, restoration in private lands is carried out haphazardly, i.e. the choice of sites for restoration is uncoordinated, which increases the costs and reduces effectiveness (Strassburg et al., 2019). The importance of landscape spatial planning to achieve cost-effectiveness has been previously reported (e.g. Budiharta et al., 2016; Metzger et al., 2017). However, to our knowledge, no spatial planning analysis focused on the cost-effectiveness of alternative restoration strategies within private lands. Here, we develop a general framework to incorporate spatial planning for forest restoration within private land holdings with conservation co-benefits at the landscape scale. We illustrate this in the highly fragmented Atlantic Forest hotspot, in the state of Rio de Janeiro, Brazil.

2. Materials and methods

2.1. Proposed framework

Our framework is based on seven main steps (Fig. S1): 1) map the study area's ecological, biophysical and geopolitical attributes; 2) quantify current habitat availability for species with different dispersal abilities; 3) quantify environmental debts within each property; 4) quantify potential for natural regeneration and restoration costs in each planning unit (1 ha pixel); 5) quantify the contribution of each potentially restored planning unit to habitat availability; 6) prioritize planning units for restoration under different strategies; and 7) simulate restoration in selected planning units for each strategy, then quantify the sum of costs for restoring the landscape and post-restoration habitat availability.

Forest restoration may consider different benefits and costs as targets. Here we considered biodiversity benefits, the opportunity cost and transition cost (which included opportunity cost, the costs for restoration implementation and probability for natural regeneration). Generally, landholders' target is to minimize income loss by restoring in areas with lower opportunity cost, i.e. the cost of restoring an area instead of using it for another activity. However, the final costs involved in the whole transition from agriculture to forest (i.e. transition cost) include not only the opportunity cost, but also the costs for restoration implementation (e.g. tree planting, fencing, management, etc.). This transition cost may be minimized by, for example, allowing natural regeneration, i.e. the spontaneous or assisted recovery of native vegetation, in specific sites (Molin et al., 2018). Biodiversity conservation may also be an important target for some landholders (e.g. due to conservation awareness, Alves-Pinto et al., 2016), as well as for the scientific and conservation communities. This target can be achieved, for example, by increasing the amount of forest cover and connectivity in the landscape (Crouzeilles et al., 2015). In the real world, however, most landholders restore in a haphazard manner within their lands, with no spatial planning or objective target (Strassburg et al., 2019). Therefore, our multi-criteria framework includes five key different restoration strategies, in an attempt to assess how different targets, treated simultaneously or in isolation, affect the cost-effectiveness of restoration actions (Fig. S1): 1) Minimizing opportunity cost; targeting restoration in planning units with lower agricultural revenues; 2) Minimizing transition costs; targeting planning units with lower transition cost, calculated based on opportunity cost, costs for restoration implementation, and on the planning units' probability for natural regeneration (which is negatively correlated with the costs for restoration implementation; see Step 4 below); 3) Maximizing habitat availability; targeting planning units with higher individual contribution to habitat availability for each species; 4) Maximizing habitat-availability-to–transition-cost ratio; targeting planning units with both higher individual contribution to habitat availability for each species and lower transition costs (calculated as the ratio between these two variables); and 5) Random restoration; haphazardly selecting planning units for restoration, representing the non-systematic restoration that happens in the real world. Not every strategy follows all seven steps of the framework.

We illustrate how this framework can be applied to solve complex real-world problems with the specific case of the Native Vegetation Protection Law in Brazil. This framework, however, can be applied in, or customized to, other regions of the world, alternative targets and/or additional restoration outcomes and costs.

2.2. Case study

The Brazilian Atlantic Forest is one of the biodiversity hotspots in the world (Myers et al., 2000; Laurance, 2009; Jenkins et al., 2015), and only about 28% of its original extent remains (Rezende et al., 2018). The few large (>100 ha) forest fragments remaining are mostly within Strictly Protected Areas (IUCN categories I-IV), but >80% of the remaining forest is within private land holdings where fragments are < 50 ha in size (Ribeiro et al., 2009).

The Tinguá Biological Reserve (REBIO Tingua) is a Strictly Protected Area that covers 26,260 ha of Atlantic Forest in southeastern Brazil, holding several threatened, rare and endemic species, as well as protecting important watersheds that supply water to the state of Rio de Janeiro (www.bvambientebf.uerj.br/arquivos/rebio_tingua.htm), one of the most densely populated states in the country. It is one of the seven Atlantic Forest Biosphere Reserves created by UNESCO (http://www.rbma.org.br/). Thus, REBIO Tingua is critical for both biodiversity conservation and provision of ecosystem services at the regional scale, and must be considered a source of species when solving spatial restoration prioritization problems in the region. The 10-km buffer zone surrounding the reserve is defined by Brazilian environmental legislation (CONAMA 13/1990) with the objective of minimizing negative human impacts on Protected Areas and ensuring quality of life to local people. REBIO Tingua's buffer zone, however, has a long history of disturbance, degradation and fragmentation due to intense urban expansion, conversion to agriculture and conversion to pasture (MMA, 2006). We used the 10-km buffer zone around the REBIO Tingua as study region, from which we selected three landscapes with 10,000 ha (Fig. 1).

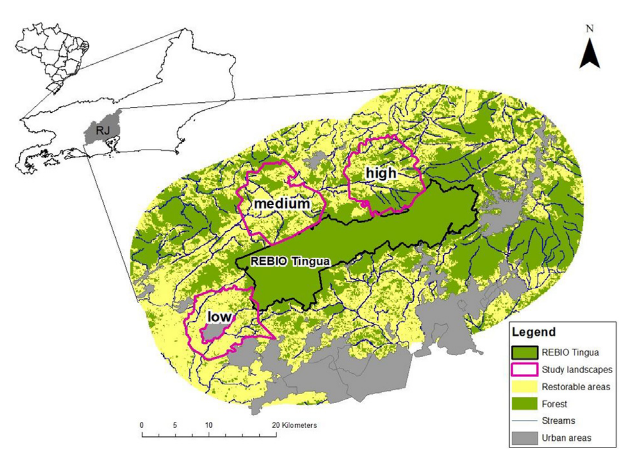

Fig. 1. Study Area located in the state of Rio de Janeiro, Brazil. Restoration simulations were performed in the 10-km buffer zone surrounding the Tingua Biological Reserve (REBIO Tingua), at three study landscapes with different initial amounts of forest cover: low (13%), medium (24%) and high (44%). Restorable areas are currently agricultural fields or pasture lands.

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2.3. Analysis

Step 1 was to map the study area's ecological/biophysical and geopolitical attributes. Within the 10 km buffer zone surrounding the REBIO Tingua, we mapped the following attributes: forest cover, land use, stream network, land slope, slope orientation, land curvature, counties division, probability for natural regeneration, and the Rural Environmental Registry information. See the Supplementary Materials for more details on attribute mapping.

We selected three 10,000 ha landscapes within the REBIO Tingua's buffer zone, with different environmental debts and initial amounts of forest cover: "low" (13% forest cover), "medium" (24%), and "high" (44%) (Fig. 1). Landscape size was based on previous studies in the Atlantic Forest that addressed the effect of landscape configuration on biodiversity (e.g. Martensen et al., 2008; Pardini et al., 2010) and because landscapes need to be large enough to allow simulations of species with good dispersal ability (e.g. 3000 m) (Crouzeilles et al., 2014). The landscapes were divided into 1 ha planning units, used as the unit for analysis.

Step 2 was to quantify current habitat availability for species with different dispersal abilities. Habitat availability considers not only total habitat amount in a landscape, but also a landscape's connectivity, measured here through hypothetical animal species' ability to move within a network of habitat patches (Saura & Pascual-Hortal, 2007). We calculated habitat availability (eqn (1)) using the Integral Index of Connectivity (*IIC*) instead of the Probability of Connectivity index (*PC*) because the *IIC* supports a larger number of planning units, performs faster analysis and is better at detecting long-term population dynamics (e.g. individual movements) as it uses binary, rather than continuous, information to determine whether two patches are connected in a path (Bodin and Saura, 2010). To calculate *IIC* (eqn (1)), we used forest remnants' size (patch attribute), Euclidean distance between two forest remnants (distance attribute) and species' dispersal distances as thresholds. Due to a lack of data on dispersal ability for species that occur in the Atlantic Forest (Crouzeilles et al., 2010), we simulated three hypothetical species representing Atlantic Forest animals with "poor" (10 m), "intermediate" (700 m) and "good" (3000 m) dispersal abilities (based on Crouzeilles et al., 2010; 2014; Almeida-Gomes et al., 2016). That is, each dispersal ability value represents a threshold dispersal distance below which two patches are considered unconnected.

The *IIC* was calculated as follows:

$$IIC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i a_j / \left(1 + nL_{ij}\right)}{A_L^2} \tag{1}$$

where n is the number of patches, a_i and a_j are attributes of the patches i and j, A_L^2 is total landscape area, and nL_{ij} is the number of links present in the shortest path between patches i and j. Whenever interpatch distance was shorter than the threshold dispersal distance, a link was assigned between that pair of patches. *IIC* ranged from 0 (no habitat available) to 1 (entire landscape is occupied by habitat) (Pascual-Hortal & Saura, 2006).

Step 3 was to quantify environmental debts within each property. According to the Native Vegetation Protection Law, landholders must protect native vegetation in "Areas of Permanent Preservation" (APP) and "Legal Reserve" (LR) (Law N° 12.651/2012). The APP is set to preserve ecosystem services, such as forests along rivers for water quality and forests on steep slopes to avoid landslides. The width of the APP to be kept along rivers depends on river width and property size (see Supplementary Material). The LR, on the other hand, is set to preserve forest itself, claiming a specific percentage of a rural property depending on the biome in which it is located, i.e. 20% in the Atlantic Forest biome. The amount of APP is included in the 20% of native vegetation required for LR. Small properties, i.e. measuring up to four "fiscal modules" (area measurement unit fixed by county and calculated based on its predominant agriculture), are exempt from preserving or restoring LR. The law also requires landholders to achieve environmental compliance within a 20 year time frame, restoring a minimum of 1/10th of their environmental debt every 2 years (see Zakia & Pinto (2013) for more details on the Native Vegetation Protection Law).

Following the regulations above (but see Supplementary Material for further details), we used the Rural Environmental Registry, forest remnants cover, stream network, and counties division maps to calculate the number of planning units that must be restored within each property, and specifically within APP and RL, if environmental debt exists, every two years (i.e. 1/10th of total environmental compliance every two years). That is, for each property within each one of the three landscapes, we calculated the number of planning units that should be restored every two years up to the 20-year restoration practice as required by Brazilian legislation.

Step 4 was to quantify the potential for natural regeneration and restoration costs in each planning unit. Natural forest regeneration is the spontaneous or assisted recovery of forests established on abandoned lands (Shono et al., 2007; Zahawi et al., 2014). Locations with higher probability for natural regeneration tend to demand less human intervention, which may reduce restoration implementation costs (Chazdon & Guariguata, 2016; Crouzeilles et al., 2017). Thus, for strategies focused on lowering implementation cost, we used the map of probability for natural regeneration in the Atlantic Forest provided by Crouzeilles et al. (Under review). This map ranges from 0 (natural regeneration is unlikely) to 1 (highest probability of natural regeneration), where probability is higher in non-forest pixels that are closer to existing forest remnants (distance to existing forest was the most important variable in the model, totaling 72% of 78% of models' accuracy to predict natural regeneration) (see Supplementary Material for more details). Thus, strategies that include minimizing implementation cost as at least one of its targets (e.g. minimizing transition cost) are indirectly accounting for biodiversity benefits through the selection of areas that are closer to existing forest remnants, which increases connectivity and average forest patch size and, consequently, habitat availability.

To estimate the costs for restoration implementation we assumed that it was linearly and negatively related to the probability for natural regeneration (following Strassburg et al., 2019). That is, when probability for natural regeneration is 1 there is no costs for restoration implementation and when the probability for natural regeneration is 0 then implementation cost is equal to the cost of full tree-planting (the most expensive type of active restoration). The restoration implementation costs were based on the full tree-planting cost (Fig. 2A), provided by the Onda Verde NGO (www.ondaverde.org.br), which is the main NGO carrying out restoration projects in the study area (see Supplementary Material for more details). The opportunity cost (Fig. 2B) was calculated based on Net Present Value for each rural activity (i.e. cash flow of an activity with a discount rate or decrease in capital opportunity cost), based on the counties' average production yield for each type of agricultural crop and livestock (IBGE, 2014), average cost of agricultural crops estimates (Conab, 2016; EMBRAPA, 2004), and agricultural prices (IEA, 2016; Cepea, 2016). In this study, we considered a discount rate of 8% per year, which is the minimum interest rate practiced by the main rural credit lines in Brazil, such as the ABC credit. The time horizon was 20 years, the period determined by the law for landholders to complete forest restoration on their properties. Thus, opportunity cost represents the mean Net Present Value for agricultural crop or livestock in areas available

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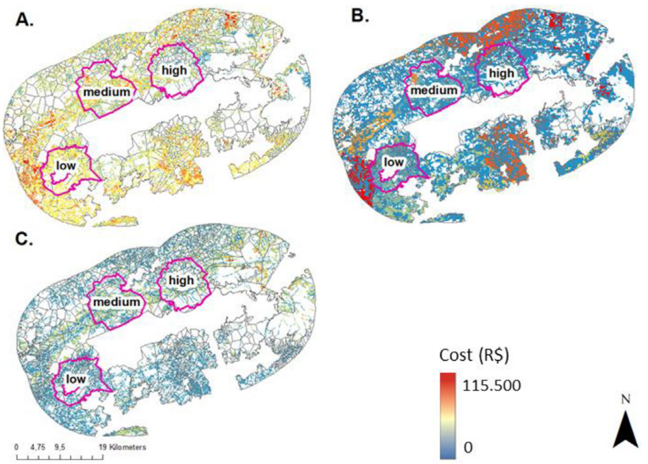

Fig. 2. Costs in restorable areas. A) Restoration implementation cost, B) Opportunity Cost, and C) Transition cost. Colors represent financial value in Brazilian Reais. Blank depicts non-restorable areas (urban areas, forest and highways). Boundaries of the three study landscapes are shown in purple. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

for restoration (agricultural and pastureland areas in the land use map; see Supplementary Material).

We then calculated the transition cost (Fig. 2C, eqn (2)) based on the probability for natural regeneration, costs for restoration implementation, and opportunity cost. The transition cost was calculated as follows:

$$TC = OC + (1 - -PNR) \times RIC \tag{2}$$

where TC is the transition cost, OC is the opportunity cost, PNR is the probability for natural regeneration, and RIC is the restoration implementation costs with full tree-planting. Cost values were converted from Brazilian Reais to American dollars (US$) using an exchange rate of 3.8.

Step 5 was to quantify the contribution of each potentially restored planning unit to habitat availability (eqn (3)). We calculated the individual contribution of each planning unit available for restoration (i.e. agricultural and pastureland areas) to the increase in habitat availability in a landscape through an individual habitat restoration experiment (Saura & Rubio, 2010). Each pixel was transformed from non-forest to forest at independent times and at each, contribution to habitat availability was calculated as:

$$\Delta IIC_k = IIC_{add,k} - -IIC \tag{3}$$

where ΔIIC_k is the contribution of the new habitat patch $_k$ (i.e. restored planning unit), IIC is the current habitat availability value, and $IIC_{add,k}$ is the habitat availability value after the addition of the patch $_k$ in the landscape.

The individual habitat restoration experiment allows for the detection of planning units where restoration would increase habitat availability for each species the most. In this step, in order to include the effects of the REBIO Tingua as a source of species, we kept its original area of habitat, i.e. the forested area within the 10,000 ha landscape plus the total forested area within REBIO Tingua. In addition, we also included an extra 5-km buffer around each 10,000 ha landscape for strategies that target increasing habitat availability. We did so in order to account for the influence of surrounding forest remnants on planning unit contributions to habitat availability, particularly relevant for units located at the boundary of a landscape. We excluded REBIO Tingua and the 5-km buffer area, however, when calculating post-restoration increments in habitat availability (Step 7, eqn (4)), because our aim was to calculate the post-restoration contribution of restored areas to the 10,000 ha landscape only (i.e. over the initial forest cover of 13%, 24% and 44%). Including surrounding forest and the REBIO Tingua would boost initial amounts of forest cover in our landscapes, which would interfere with the model and diminish the estimated gains in post-restoration habitat availability. Moreover, by doing so we would not be able to compare the results with the other strategies, which do not include neither the buffer nor the REBIO.

Step 6 was to prioritize planning units for restoration under different strategies. We contrasted five strategies: 1) minimizing opportunity cost, 2) minimizing transition cost, 3) maximizing habitat availability, 4) maximizing habitat–availability-to-transition-cost ratio, and 5) random restoration. To do so, within each property in each one of the three study landscapes (and within APP if debt existed), we sorted planning units available for restoration (up to reaching the total environmental debt within each property) by increasing value of opportunity or transition costs (strategies 1 and 2, respectively), decreasing value of the contribution to habitat availability (strategy 3), or decreasing value of the ratio between potential contribution to habitat availability and transition cost (strategy 4). For strategy 5, the selection of planning units for restoration was random and not constrained to APP, if debt existed.

Finally, Step 7 was the restoration simulation of priority planning units for each strategy, followed by the quantification of the sum of costs for restoring the landscape (in this study: the sum of transition cost) and post-restoration habitat availability. We performed 10 restoration events (i.e. time-steps) following the number of planning units that should be restored every two years (Step 2) in each one of the three study landscapes. Selected planning units were restored, successively, by changing pixels' values from 0 (agricultural and pastureland pixels) to 1 (forest), according to each strategy. After each time-step (1/10th of total environmental compliance), we calculated transition cost and post-restoration habitat availability for each species. Additionally, we performed these successive simulations another 30 times in all landscapes and under all strategies, because different planning units may have the same value of cost or contribution to habitat availability and, consequently, prioritization solution may change across space and time. After repeating the process 30 times, we calculated the mean values of the sum of transition cost (eqn (2)) and post-restoration habitat availability (eqn (4)) for each species within each study landscape. We then calculated cost-effectiveness as the improvement of habitat availability per cost for each restoration event, under each strategy, and for each species in each landscape.

The increment in habitat availability was calculated under each strategy and for each species in each landscape as:

$$IIC_i = \frac{(IIC_{t20} - IIC_{t0}) \times 100}{IIC_{t0}} \tag{4}$$

where IIC_{t0} is the value of IIC at year 0 (i.e. current habitat availability), IIC_{t20} is the value of IIC after 20 years (i.e. post-restoration habitat availability), and the increment in habitat availability IIC_i is expressed as a percentage of IIC_{t0}.

To test for the significance in the difference of cost-effectiveness among different strategies, we used the Kruskal-Wallis test, followed by a post-hoc modified Mann-Whitney U test, on final post-restoration cost-effectiveness values for each species within each landscape. Normality and homoscedasticity of data were tested using Shapiro Wilk and Fisher tests, respectively. All analyses were performed in R 3.3.0 (R Development Core Team, 2016) and ArcGIS 10.3.1 (ESRI, 2015).

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3. Results

We estimated an environmental debt varying from 803 ha to 411 ha, from the landscape with the lowest initial forest cover to the one with the highest initial forest cover (Table 1). In general, our strategies tended to result in the creation of forest corridors (all strategies, except the "random restoration"), stepping stones (e.g. the "opportunity cost" strategy due to high auto-spatial correlation) and/or the enlargement of existing forest remnants (e.g. "maximizing habitat availability" and "minimizing transition cost"; Fig. 3). These results reflect the spatial constraints imposed by the Brazilian environmental law, which determines that restoration should focus on APP along rivers, creating forest corridors, and Legal Reserves, which focused on sites around existing forest patches. The "random restoration" strategy resulted in numerous small and isolated forests scattered across each landscape (Fig. 3). The biodiversity benefits, restoration costs and cost-effectiveness of each restoration strategy varied among landscapes and species.

As expected, the strategies that resulted in the highest values of habitat availability often included the explicit target of maximizing habitat availability (Table 2, Fig. 4). The "maximizing habitat availability" strategy was generally the most important for incrementing habitat availability (five times in nine cases). This strategy resulted in the highest habitat availability, especially in the landscape with low initial forest cover. In addition, strategies that explicitly included habitat availability as one of the targets generally out-performed other strategies at the early stages of the restoration process, especially for species with poor dispersal ability (Fig. 4). Still, it is important to note that in five instances, the strategies that most improved habitat availability involved minimizing transition and/or opportunity costs (Table 2). Consistently, for all species in all landscapes, the "random restoration" strategy led to the smallest final improvement in habitat availability (Table 2, Fig. 4).

As expected, habitat availability after restoration decreased with decreased initial amount of forest cover in the landscape (Table 2). The increment in habitat availability (as opposed to gain in habitat availability per se), on the other hand, did not follow a clear pattern (Table 2). As expected, the gain in habitat availability after restoration in the landscape with a medium amount of initial forest cover was lower than in the landscape with low initial forest cover (Table 2). The increment in habitat availability (%), however, was higher, especially for species with poor dispersal ability (Table 2). This means that, in areas with very low initial forest cover, the forest gain after reforestation might not be enough to truly increase habitat availability (a measure that incorporates both habitat amount and connectivity). At the landscape with low initial forest cover, a 8% increase in forest cover after restoration increased habitat availability from 18% (random restoration) to 159% (maximizing habitat availability) (Table 2). At the landscape with medium initial forest cover, a 6% increase in forest cover increased habitat availability from 13% (random restoration) to 160% (maximizing habitat-availability-to–transition-cost ratio) (Table 2). Finally, at the landscape with high initial forest cover, a 4% increase in forest cover increased habitat availability from 9% (random restoration) to 27% (maximizing habitat availability) (Table 2).

Table 1
Environmental debt (ha) in landscapes with differing initial amounts of forest cover (low = 13%, medium = 24% and high = 44%). APP = Permanent protected areas and LR = Legal Reserves, required under the Brazilian Native Vegetation Protection Law.

Initial Forest Cover	APP (ha)	LR (ha)	Total (ha)
Low	281	522	803
Medium	472	133	605
High	375	36	411

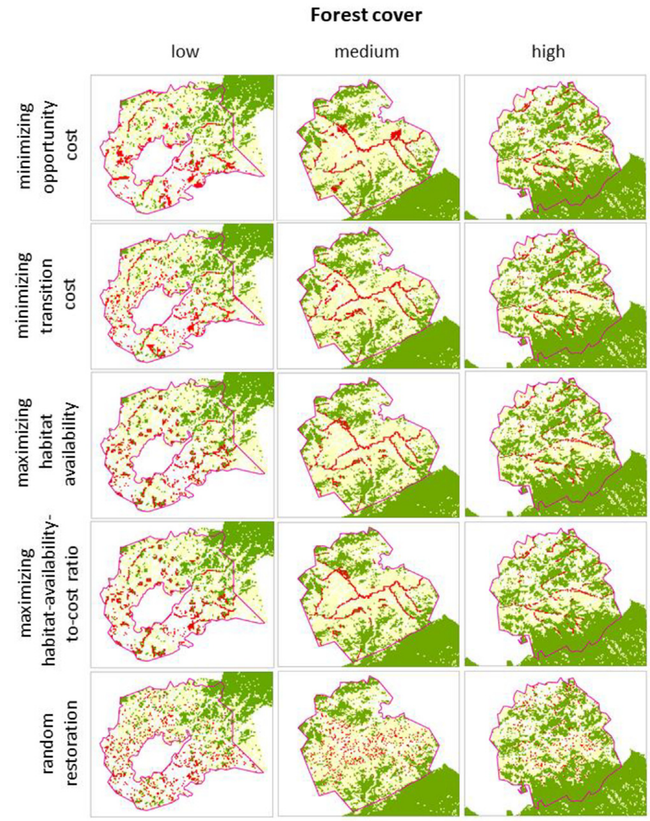

Fig. 3. Forest cover configuration at three outlined study landscapes with different initial amounts of forest cover: low (13%), medium (24%) and high (44%), after complete restoration under different prioritization strategies for species with poor dispersal ability (10 m). Green: current forest cover, Yellow: restorable areas (i.e. agriculture and pastureland), Red: restored forest cover after 20 years; and Blank: non-restorable areas (i.e. urban areas, rivers and roads). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Transition cost varied from US$34.7 million to US$100 million depending on landscape and strategy (Table 3). As expected, in all landscapes the restoration strategy that reduced transition cost the most was "minimizing transition cost". The difference in cost between this strategy and the second cheapest strategy (always "maximizing habitat availability to transition cost ratio"), however, was very small (Table 3). The "random restoration", on the other hand, was generally the most expensive strategy (except for the landscape with low initial forest cover, where "maximizing habitat availability" was a little more expensive) (Table 3). In most cases "random restoration" was the strategy with the lowest value of restoration implementation costs, followed by "minimizing transition cost", except in the landscape with medium forest cover, where "minimizing transition cost" achieved the lowest restoration implementation costs.

Cost-effectiveness decreased across time for all strategies, landscapes and species (Fig. 5). Generally, strategies that explicitly included minimizing transition costs or maximizing habitat availability as at least one target were the most cost-effective for all species in all landscapes (Fig. 3). Differences in final cost-effectiveness (i.e. *IIC* per transition cost after 20 years of restoration) were generally statistically significant (Df = 4, $p < 0.05$) between all strategies in all landscapes and for all species (the only exception was the difference between strategies 3 and 4 for species with poor dispersal ability in the landscape with low initial forest cover (Df = 4, $p = 0.35$)).

Table 2
Habitat availability (*IIC*) and increment in habitat availability (%) for each restoration strategy, landscape and hypothetical species. The increment in habitat availability was calculated as a percentage of current habitat availability. Landscapes have differing initial amount of forest cover: low (13%), medium (24%) and high (44%). Hypothetical species have different dispersal abilities: poor (10 m), intermediate (700 m) and good (3000 m). Restoration strategies: Minimizing opportunity cost (Min. Opp. Cost), Minimizing transition cost (Min. Trans. Cost), Maximizing habitat availability (Max. Hab.), Maximizing habitat-availability-to-transition-cost ratio (Max. Hab./Min. Trans. Cost), Random restoration (Random). Current: habitat availability in the beginning of the restoration process (not a strategy).

		Habitat Availability (*IIC*)			Increment in *IIC* (%)		
		poor dispersal	interm. dispersal	good dispersal	poor dispersal	interm. dispersal	good dispersal
	Low initial forest cover						
Strategy	Current	.0008	.0044	.0072	-	-	-
	Min. Opp. Cost	.0012	.0101	.0184	60.1	132.3	155.8
	Min. Trans. Cost	.0011	.0100	.0182	48.5	129.3	153.6
	Max. Hab.	.0013	.0107	.0187	77.0	145.6	159.5
	Max. Hab./Min. Trans. Cost	.0013	.0102	.0184	75.6	134.9	155.6
	Random	.0009	.0096	.0178	18.3	120.4	147.8
	Medium initial forest cover						
Strategy	Current	.0039	.0149	.0237	-	-	-
	Min. Opp. Cost	.0095	.0299	.0400	141.8	100.2	68.7
	Min. Trans. Cost	.0067	.0258	.0377	71.7	72.8	59.2
	Max. Hab.	.0086	.0297	.0379	119.5	99.3	59.8
	Max. Hab./Min. Trans. Cost	.0102	.0283	.0397	159.8	90.0	67.5
	Random	.0044	.0212	.0349	13.0	42.1	47.3
	High initial forest cover						
Strategy	Current	.0466	.0883	.1125	-	-	-
	Min. Opp. Cost	.0566	.1120	.1338	21.4	26.9	18.9
	Min. Trans. Cost	.0572	.1121	.1338	22.6	26.9	18.9
	Max. Hab.	.0543	.1122	.1425	16.5	27.0	26.6
	Max. Hab./Min. Trans. Cost	.0526	.1117	.1335	12.8	26.5	18.7
	Random	.0508	.1032	.1287	8.9	16.8	14.3

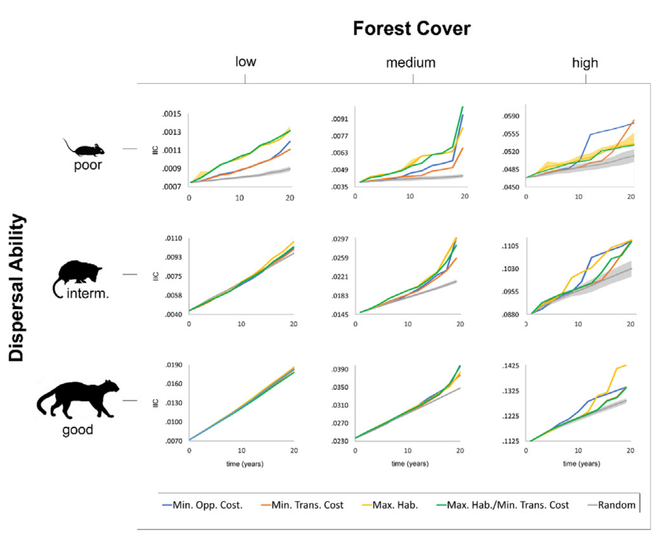

Fig. 4. Habitat availability (IIC) through time for each restoration strategy, landscape and hypothetical species. Landscapes have different initial amounts of forest cover: low (13%), medium (24%) and high (44%). Hypothetical species have different dispersal abilities: poor (10 m), intermediate (700 m) and good (3000 m). Restoration strategies: Minimizing opportunity cost (Min. Opp. Cost), Minimizing transition cost (Min. Trans. Cost), Maximizing habitat availability (Max. Hab.), Maximizing habitat-availability-to-transition-cost ratio (Max. Hab./Min. Trans. Cost), Random restoration (Random). Colored bands represent the standard deviation of the mean values of the 30 repetitions.

4. Discussion

We present, for the first time, an analytical framework that incorporates spatial planning for forest restoration within private land holdings with conservation co-benefits at the landscape scale. This framework is useful for planning and optimizing restoration actions within rural properties, while considering local restoration costs and ecological processes, such as habitat availability, which may allow species recovery and persistence in the long-term. Our results have special relevance considering the ecological importance of restoring Legal Reserves in Brazil and the current need to perform cost-effective ecological restoration (Metzger et al., 2019).

To our knowledge, no studies have shown and compared the trajectory of the increase in habitat availability through time among different restoration strategies within private land holdings. Spatially planed restoration in private lands increased habitat availability up to 8, 12 and 3 times more than random restoration in landscapes with low, medium and high initial amounts of forest cover, respectively. In general, strategies targeting habitat availability showed a more pronounced increment in habitat availability at early stages of the restoration process, when compared to strategies that do not. This is especially true for species with limited dispersal abilities (poor to intermediate), which are more strongly affected by landscape configuration compared to more mobile species (e.g. Awade et al., 2012; Martensen et al., 2012). Therefore, spatially planned restoration in landscapes with > 10% forest cover (where connectivity was not yet eroded) and < 50% (where forest remnants are already highly connected) can hasten benefits for species with limited dispersal abilities.

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Table 3
Implementation cost, opportunity cost, transition cost (US$) and cost-effectiveness (*IIC*/US$) for each restoration strategy, landscape and hypothetical species. Cost-effectiveness was calculated as post-restoration *IIC*/transition cost.). Landscapes have differing initial amount of forest cover: low (13%), medium (24%) and high (44%). Hypothetical species have different dispersal abilities: poor (10 m), intermediate (700 m) and good (3000 m). Restoration strategies: Minimizing opportunity cost (Min. Opp. Cost), Minimizing transition cost (Min. Trans. Cost), Maximizing habitat availability (Max. Hab.), Maximizing habitat-availability-to-transition-cost ratio (Max. Hab./Min. Trans. Cost), Random restoration (Random).

		Costs (million US$)			cost-effectiveness (*IIC*/cost)		
		Implem.	Opport.	Trans.	poor dispersal	Interm. dispersal	good dispersal
	Low initial forest cover						
Strategy	Min. Opp. Cost	83.12	9.68	99.89	.0012	.0101	.0184
	Min. Trans. Cost	77.14	10.26	96.61	.0012	.0103	.0189
	Max. Hab.	78.68	10.53	100.83	.0013	.0106	.0184
	Max. Hab./Min. Trans. Cost	78.62	10.44	98.39	.0013	.0104	.0183
	Random	76.93	10.48	100.27	.0009	.0096	.0178
	Medium initial forest cover						
Strategy	Min. Opp. Cost	79.49	11.81	71.54	.0132	.0417	.0559
	Min. Trans. Cost	72.87	12.25	62.85	.0099	.0386	.0570
	Max. Hab.	74.91	12.22	72.54	.0112	.0410	.0522
	Max. Hab./Min. Trans. Cost	73.19	12.21	67.04	.0115	.0424	.0600
	Random	79.14	12.30	77.34	.0057	.0272	.0451
	High initial forest cover						
Strategy	Min. Opp. Cost	44.65	9.90	36.95	.1532	.3032	.3620
	Min. Trans. Cost	43.45	10.01	34.73	.1647	.3226	.3852
	Max. Hab.	44.16	10.02	36.84	.1440	.3057	.4066
	Max. Hab./Min. Trans. Cost	44.01	10.02	35.23	.1463	.3191	.3844
	Random	38.91	10.09	39.37	.1288	.2612	.3262

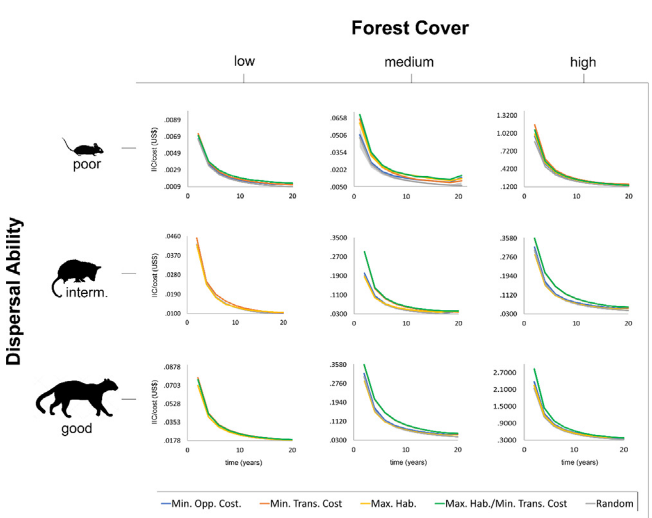

Fig. 5. Cost-effectiveness (IIC/US$) through time for each restoration strategy, landscape and hypothetical species. Landscapes have differing initial amounts of forest cover: low (13%), medium (24%) and high (44%). Hypothetical species have different dispersal abilities: poor (10 m), intermediate (700 m) and good (3000 m). Restoration strategies: Minimizing opportunity cost (Min. Opp. Cost), Minimizing transition cost (Min. Trans. Cost), Maximizing habitat availability (Max. Hab.), Maximizing habitat-availability-to-transition-cost ratio (Max. Hab./Min. Trans. Cost), Random restoration (Random). Colored bands represent the standard deviation of the mean values of the 30 repetitions.

Our results are especially meaningful considering the severe spatial constraints imposed by Brazilian environmental law (e.g. required restoration of specific APP areas). Basically, the higher the number of constraints included in spatial prioritization, the more limited the number of solutions, which consequently reduces optimization performance (e.g. Crouzeilles et al., 2015). This was evident in the low standard deviations found for the 30 repetitions, partially because of constraints to APP, and partially because cost values did not show high spatial variation in our landscapes. That is why, in general, only strategies that did not focus on minimizing costs showed higher standard deviation (e.g. maximizing habitat availability). For instance, final landscape configuration in this study showed small variation between prioritized strategies, generally resulting in forest corridors (because APPs are along rivers) and stepping stones. While Legal Reserves are important to maintain minimum habitat conditions for biodiversity, APP and stepping stones increase landscape permeability (i.e. a configuration that facilitates animal movement in the landscape), allowing species to move between forest fragments and reducing local extinctions (Metzger et al., 2019).

The cost-effectiveness of a strategy, however, depends not only on the increment in habitat availability, but also on the transition cost. We show that cost-effectiveness is generally very high in the first few years but decreases exponentially with time. Although this trend has never been reported before (to our knowledge), it is quite intuitive. It is important to highlight that this does not mean that restoration is not a cost-effective affaire. In fact, through the restoration process the amount of area available to be restored decreases and the cumulative transition cost increases and, therefore, the increment in habitat availability per cost decreases. That is why strategies that focused on, at least, minimizing transition cost were in general the most cost-effective. It is also important to highlight that these strategies also target (explicitly or not) an increase in habitat availability. The "minimizing transition cost" strategy explicitly incorporates the probability for natural regeneration (Strassburg et al., 2019), which is strongly driven by distance to forest remnants (Crouzeilles et al., Under review). This results in

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solutions focused on enlarging (and connecting) existing forest remnants instead of creating new ones (as in the "random restoration" strategy, for example), which considerably increases habitat availability (Saura & Pascual-Hortal, 2007). The cost-effectiveness of forest restoration strategies depends upon a landscape's initial amount of forest cover and the species of concern, but "minimizing transition costs" and "maximizing habitat availability to transition cost ratio" are no-regret strategies that can provide the best return on investments.

Our results show that any spatially planned restoration strategy can achieve high cost-effectiveness in landscapes with medium to high initial amounts of forest cover for four main reasons. First, these landscapes already have high initial connectivity and less available area for restoration. Landscapes with high connectivity (>50% forest cover) - and consequently habitat availability - are less affected by landscape configuration (Crouzeilles et al., 2014), thus, restoration strategies focused on maximizing habitat availability may not result in substantial increments in habitat availability. Second, in our study, forest restoration was severely constrained to APP along rivers, strongly restricting the choice of places to restore and, consequently, compromising the performance of a strategy explicitly focused on maximizing habitat availability. Third, we conducted a sequential restoration prioritization, as opposed to a dynamic one (i.e. re-running the entire framework after each individual planning unit was restored), which was impossible due to computational limitations. However, restoration is an interactive process, which means that restoring a planning unit influences the connectivity of all other planning units available for restoration (Crouzeilles et al., 2015). Fourth, the algorithm is focused on an individual planning unit's contribution to habitat availability (Saura & Rubio 2010), but does not know *a priori* the total area that should be restored, i.e. it is unable to properly choose between connecting patches or increasing patch size when targeting to increase habitat availability. This means that, at some point, the algorithm may not have enough area available to connect patches and thus performance will decrease. These limitations constrain our maximization exercise and enable other strategies that do not target for habitat availability to outperform the ones that do so, especially in landscapes with medium to high initial amounts of forest cover. Finally, we acknowledge that habitat availability may also depend upon vegetation type, age and structure. For simplification, our analysis assumes that all forest is of equal quality.

Despite these methodological limitations, our results corroborate previous studies showing that forest restoration based on spatial prioritization reaches the most cost-effective solutions (e.g. Crouzeilles et al., 2015; Strassburg et al., 2019). Our results build on previous studies revealing that spatial planning within private lands increases biodiversity benefits up to 12 times compared to random restoration and reduces the costs of restoration efforts performed by private landholders. Through our framework it is possible to account for multiple targets and demands, and to inform on the most appropriate way of conducting restoration within private lands. We emphasize the importance of including habitat availability as a target, especially in landscapes with low initial forest cover. By doing so we achieved higher conservation gains at low additional cost even under severe spatial constraints, such as those imposed by the Brazilian environmental law. Despite these spatial constraints, our results highlight some important outcomes of spatially planned restoration focusing on the Brazilian environmental law, such as the potential to increase landscape permeability through forest corridors and stepping stones. Still, restoration within private land holdings should be complemented by the conservation and protection of the remaining areas of native vegetation to increase forest cover and to achieve international commitments (Rother et al., 2018).

Our study demonstrates how different decisions influence the outcome and cost of restoration actions within private land holdings. It highlights the importance of incorporating the analysis of cost-effectiveness into spatial prioritization for forest restoration within private lands considering the ecological processes that occur at the landscape scale. Our framework should be used to plan restoration in Brazilian private land holdings and can be customized for other regions worldwide, targets, and additional restoration outcomes and costs.

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.scitotenv.2019.135262.

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