

RESEARCH ARTICLE

# A Framework to Optimize Biodiversity Restoration Efforts Based on Habitat Amount and Landscape Connectivity

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## Abstract

The effectiveness of ecological restoration actions toward biodiversity conservation depends on both local and landscape constraints. Extensive information on local constraints is already available, but few studies consider the landscape context when planning restoration actions. We propose a multiscale framework based on the landscape attributes of habitat amount and connectivity to infer *landscape resilience* and to set priority areas for restoration. Landscapes with intermediate habitat amount and where connectivity remains sufficiently high to favor recolonization were considered to be intermediately resilient, with high possibilities of restoration effectiveness and thus were designated as priority areas for restoration actions. The proposed method consists of three steps: (1) quantifying habitat amount and connectivity; (2) using landscape ecology theory to identify intermediate resilience landscapes

based on habitat amount, percolation theory, and landscape connectivity; and (3) ranking landscapes according to their importance as corridors or bottlenecks for biological flows on a broader scale, based on a graph theory approach. We present a case study for the Brazilian Atlantic Forest (approximately 150 million hectares) in order to demonstrate the proposed method. For the Atlantic Forest, landscapes that present high restoration effectiveness represent only 10% of the region, but contain approximately 15 million hectares that could be targeted for restoration actions (an area similar to today's remaining forest extent). The proposed method represents a practical way to both plan restoration actions and optimize biodiversity conservation efforts by focusing on landscapes that would result in greater conservation benefits.

**Key words:** Brazilian Atlantic Forest, graph theory, landscape resilience, regional planning, restoration priorities.

## Introduction

Ecological restoration of degraded areas is commonly an expensive enterprise that can result in varying levels of biodiversity recovery (Rey Benayas et al. 2009). The outcomes of restoration actions depend on constraints (e.g. factors associated with local disturbance; Holl & Kappelle 1999) and feedback forces that may alternatively prevent or facilitate the recovery of degraded land (Suding et al. 2004). Identification of restoration constraints, in particular, is a prerequisite to distinguishing ecological systems that are capable to recover by autogenic processes from those that require external restoration actions (Hobbs 2007). The large areal extent of degraded lands that require restoration and the limited available financial resources for restoration activities combine to drive an

urgent need to establish strategies for restoration prioritization in order to optimize restoration efforts (Bottrill et al. 2008; Chazdon 2008).

Despite an extensive literature related to local restoration constraints, now there is a wide recognition that constraints can also operate at larger scales (Holl & Aide 2011). For biodiversity in general, parameters related to landscape connectivity (i.e. the capacity of the landscape to facilitate biological flows), such as proximity among patches (Martensen et al. 2008), the matrix permeability (Uezu et al. 2008), and corridors and stepping stones density (Boscolo et al. 2008), are important influences for (re)colonization dynamics (Jacquelyn et al. 2003) and consequently influence restoration effectiveness (Rodrigues et al. 2009).

Moreover, recent findings have associated landscape structure with resilience and management efficiency (Tscharntke et al. 2005; Pardini et al. 2010). Here, we consider *landscape resilience* as the capacity of the landscape-wide biota to recover from local species losses in individual patches through immigration at the landscape scale. In this study, we propose that landscapes with intermediate amounts of remaining habitat and that still maintain certain levels of connectivity should be the highest priority for restoration actions (Holl & Aide

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2011). These landscapes still shelter high levels of biodiversity, which has the potential to recolonize restored areas, but are also at higher risk for species extinctions from habitat loss and fragmentation (Pardini et al. 2010; Martensen et al. 2012).

In contrast, both highly degraded and well-preserved landscapes may be less ideal targets for restoration actions. In highly degraded landscapes with low landscape resilience, a large fraction of the species is already lost, thus demanding very large restoration investments with low chances of success (Calmon et al. 2011). On the other hand, landscapes with high habitat amounts are likely to have high landscape resilience, given abundant sources of propagules and dispersers and high degrees of connectivity (McLachlan & Bazely 2003). These high resilience landscapes have a high potential to maintain biodiversity and to recover by autogenic processes, thus reducing the need for restoration actions other than degradation suppression and land abandonment (Hobbs 2007).

All these aspects make incorporating landscape context in restoration planning a promising approach, although not widely adopted (Holl et al. 2003). In the few studies that incorporate landscape context or broader scale environmental constraints, detailed information on species distribution (Zhou et al. 2008; Thomson et al. 2009) or local site conditions (Cipollini et al. 2005) is usually required, though largely unavailable in tropical regions. Other restoration planning methods may have other limitations, such as little flexibility in the selection of local areas for restoration (e.g. Twedt et al. 2006) or prioritizing extremely degraded landscapes (e.g. Crossman & Bryan 2009).

In this study, we present a new methodological framework to define priority restoration areas, based on landscape structure in multiple scales. The primary goal is to optimize restoration efforts by enhancing landscape connectivity while reducing costs and, thus, improving the potential benefits for biodiversity conservation. At the local scale (i.e. a single landscape), we considered landscape resilience and management effectiveness based on habitat amount and connectivity, two metrics that can be used to identify landscapes with high chances of restoration success, defined as the best cost/benefit outcome. On a broader scale (i.e. regional scale composed of multiple landscapes) we rank these best cost/benefit landscapes in terms of their importance as corridors or bottlenecks for biological flows, based on a graph theory approach. To illustrate our protocol, we applied our approach to identify priority restoration landscapes in the Brazilian Atlantic Forest biome (approximately 150 million hectares), one of the world's top biodiversity hotspots (Myers et al. 2000).

## Methods

### Methodological Framework

The proposed framework is based on three main steps: the first two performed at the local scale and the third one at a broader scale: (1) calculating habitat amount and connectivity; (2) inferring landscape resilience from habitat amount and landscape connectivity measured in the first step; and (3)

performing habitat removal experiments to identify the key landscapes in which restoration will have the strongest effects on connectivity (Fig. 1a).

### Step 1: Habitat Amount and Landscape Connectivity

**Analysis.** Initially, the entire area under evaluation is divided into several equally sized hexagonal focal landscapes (FLs; Fig. 1b). Ideally, the size of a FL should be based on the scale at which the landscape context is known to influence the persistence of biodiversity. In the absence of this information, sensitivity analysis can be performed to test the effect of FL size on the selection of the restoration site.

In this step, each FL is individually analyzed according to its percentage of habitat remaining and landscape connectivity. We used a graph theory approach to evaluate landscape connectivity, due to its simplicity of representation, robustness, predictive power, and high potential to incorporate connectivity functional attributes (Urban & Keitt 2001). A graph is a set of nodes and links that connect these nodes (Urban & Keitt 2001). In the representation of a landscape as a graph, the habitat patches are the nodes, including their respective attributes, such as the patch area (or its biodiversity, biomass, or other relevant attribute), and a link connecting two nodes indicates a pair of functionally connected patches.

We suggest using the probability of connectivity (PC) index or, if the graph structure has more than 5,000 nodes, the integral index of connectivity (IIC; Saura & Pascual-Hortal 2007), more specifically the indices' numerator. Both indices use species dispersal capability to calculate functional connectivity, present a consistent behavior for analyzing landscape changes, and are considered robust for the evaluation of connectivity (Saura & Pascual-Hortal 2007). To calculate PC index and IIC, each FL is depicted as a graph in which habitat patches are the nodes, patch area is used as the node's attribute, and the biological information on organisms' dispersal capability is used to define the links between nodes, which represent the functional connectivity.

### Step 2: Identifying Landscapes with Intermediate Resilience.

Based on the results of the PC index and habitat amount, the FLs are classified into three categories (Fig. 1c): (1) *biodiversity sources*, which are the FLs with high habitat amount or intermediate habitat amount and high connectivity and, thus, with a great potential to maintain biodiversity, independent of restoration actions; (2) *intermediate resilience landscapes*, which are FLs with intermediate habitat amount and connectivity; and (3) *low resilience landscapes*, which are FLs with low habitat cover and connectivity.

We assumed that *low resilience landscapes* are biodiversity poor and that *biodiversity sources* should have high *landscape resilience* and are able to recover by autogenic processes. Finally, we considered that *intermediate resilience landscapes* present the best options (costs and benefits) for biological conservation (Tscharntke et al. 2005; Pardini et al. 2010). Even in favorable landscapes, the resilience can be influenced by local conditions; however, we did not consider local conditions, assuming that this should be considered in a further

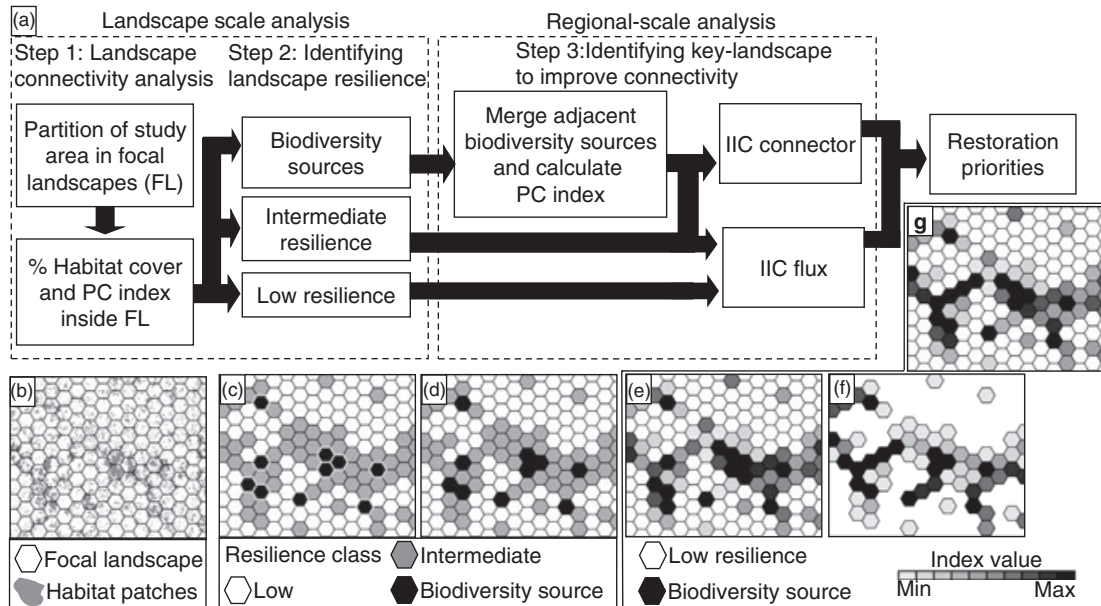


Figure 1. (a) Major steps of the proposed method, integrating the local-scale and broader scale analysis to set restoration priorities. (b) During the local-scale analysis, the study area is divided into FLs, which are classified into three resilience classes according to their habitat amount and PC index (c). The broader scale analysis begins by merging the contiguous *biodiversity source* FLs, creating larger biodiversity sources (d) and recalculating their PC indices. Then, the method has two subsequent analyses: (1) all FLs are used to calculate IICflux values to identify regions with great potential for organism flow (e), and (2) FLs with *intermediate resilience* and *biodiversity source* landscapes are used to calculate IICconnector values and identify possible bottlenecks for organism flows among FLs (f). The combination of the two indices indicates the priority FL for restoration actions (g). Refer to the text for detailed information about each calculation.

step of the restoration plan, after identifying the most adequate regions for restoration actions.

**Step 3: Identifying Key Landscapes to Improve Connectivity on a Broader Scale.** The broader scale analysis is undertaken to establish priorities among the *intermediate resilience landscapes* based on their importance as possible ecological corridors or bottlenecks. For this analysis, the entire study region is considered as a graph and the FLs as nodes, with the PC index calculated in the first step as node attribute.

Then, based on FLs removal experiments, the connectivity of the whole study region is calculated and the most important *intermediate resilience landscapes* to connect *biodiversity sources* are identified. In these experiments, the graph connectivity index is calculated before and after the removal of every FL, and the variation in the graph connectivity index for the entire analyzed region represents the importance of the FL in the graph structure. In this step, we suggest using the *flux* and the *connector* fractions of the PC or the IIC indices (Saura & Rubio 2010). During the FLs removal experiments, the variations in two fractions of the connectivity indices allow one to distinguish the importance of each FL for organism flow in the landscape (varPCflux or varIICflux) or as a key landscape for maintaining the connectivity in the whole graph (varPC-connector or varIICconnector; see Holvorcem et al. 2011 for a regional-scale case study). Higher variation in the indices fractions indicates FLs that must be prioritized for restoration actions owing to their importance in this broader scale.

#### Application in the Atlantic Forest

We illustrate how to deal with complex situations of a real-world selection process using the Brazilian Atlantic Forest as a case study. The Atlantic Forest originally covered an area of approximately 150 million hectares, extending from the south to the northeast of Brazil (Fig. 2), resulting in a very heterogeneous forest that harbors one of the world's most diverse biota (Metzger 2009). Today, the Atlantic Forest is severely threatened by habitat loss and fragmentation (Ribeiro et al. 2009). The biome can be divided into biogeographical subregions (BSRs) based on their environmental and biotic characteristics (Silva & Casteleti 2003), with different levels of habitat loss and fragmentation (Ribeiro et al. 2009, 2011). Despite the differences among BSRs, all of them present large extents of degraded and/or illegally occupied areas (Calmon et al. 2011; Ribeiro et al. 2011), such as riparian zones and high slope areas, which are defined as permanent preservation areas by a federal environmental law (the Brazilian Forest Act; Ferreira et al. 2012). This scenario represents great opportunities for restoration actions aimed at enforcing law compliance and promoting biodiversity conservation.

The analyses were based on the Atlantic Forest vegetation map (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais 2008), which we simplified in order to consider only two classes: forest and non-forest, considered here as habitat and non-habitat, respectively. This map is considered to be the best available information on forest cover for the entire Atlantic Forest biome (Ribeiro et al. 2009; refer to

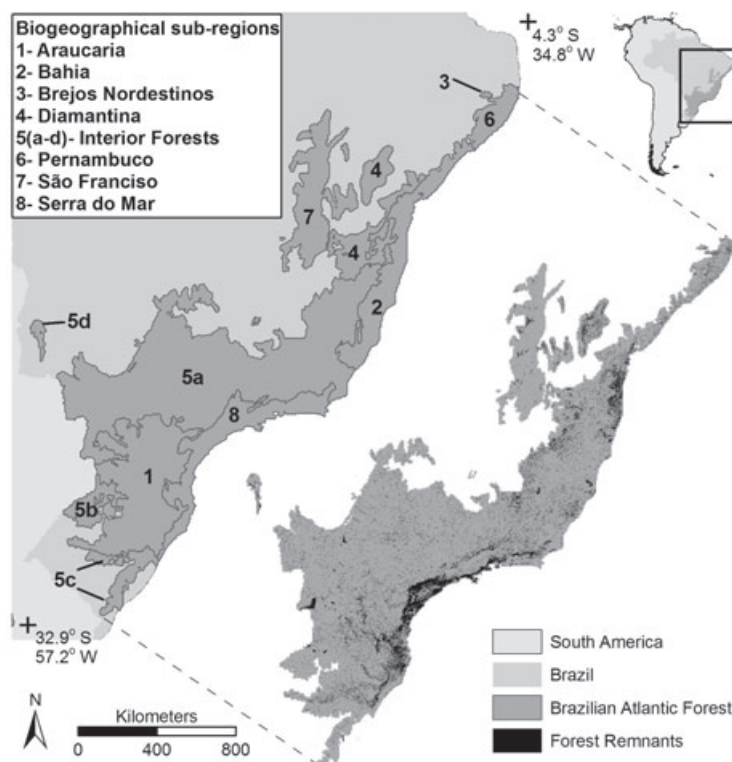


Figure 2. Distribution of the Atlantic Forest's BSRs (Silva & Casteleti 2003; modified by Ribeiro et al. 2009) and forest remnants (SOS Mata Atlântica and Instituto Nacional de Pesquisas Espaciais 2008).

Appendix S1, Supporting Information for more details and limitations of the forest cover map). The different BSRs (Silva & Casteleti 2003; modified by Ribeiro et al. 2009; Fig. 2) were analyzed separately to ensure that all subregions have priority areas, thereby optimizing the beta diversity in the whole system. Grasslands and other non-forest ecotypes that occur naturally in the region were not included in this vegetation map.

The study region was divided into 29,505 hexagonal landscapes of 5,000 ha each. Defining landscape size is a controversial issue. Jackson and Fahrig (2012) suggested that the ideal landscape size would have a radius between 4 and 9 times the mean dispersal distance or between 0.3 and 0.5 the maximum dispersal distance. Biological information about dispersal distances between habitat patches in the tropics is scarce. Bird species are better studied, and while some species have been shown to avoid forest edges, thus, not presenting any capacity to disperse between patches, others have shown longer dispersal capacity, up to 7 km. However, most of the studies have shown that understory birds can usually cross gaps of 50–100 m (Awade & Metzger 2008; Martensen et al. 2008). Thus, if we consider dispersal capacities varying between 100 m and up to 7 km, the landscapes would have size varying from 315 to 3,800 ha, sizes that have been used in some studies in the Atlantic Forest (Boscolo & Metzger 2009, 2011). However, other studies in the same region also identified influences of larger landscapes on species occurrence, for example, 10,000 ha (for birds, Martensen et al. 2008, 2012;

Banks-Leite et al. 2011; for small mammals, Pardini et al. 2010; for birds, small mammals, frogs and lizards, and trees, Metzger et al. 2009). Thus, after investigating different sizes, we adopted 5,000 ha landscapes in this study to represent an average landscape size for forest dwelling species.

**Local-Scale Analyses (Steps 1 and 2).** The PC index was calculated using patch area as node attributes and considering a 50% probability of crossing 50 m of non-forest areas. This dispersal capability was based on biological information obtained for some forest dwelling species in the Atlantic Forest, particularly understory birds and small mammals (Awade & Metzger 2008; Boscolo et al. 2008; Martensen et al. 2008; for a review, see Crouzeilles et al. 2010). Such species can be considered to be intermediately sensitive to forest loss and fragmentation, are not exclusively found in large mature continuous forests, and thus can survive in fragmented secondary forests, but they do not tolerate high levels of fragmentation (Martensen et al. 2008, 2012; Banks-Leite et al. 2011) or forest loss (i.e. >60%; Martensen et al. 2012). Thus, these species would be the first to be benefited by connectivity improvements (Martensen et al. 2012).

The *biodiversity source landscapes* were those with more than 60% forest cover or between 40 and 60% forest cover with a PC index value above the median PC index value for this forest cover interval (Fig. 3). This criterion was based on the percolation threshold, considering orthogonal and



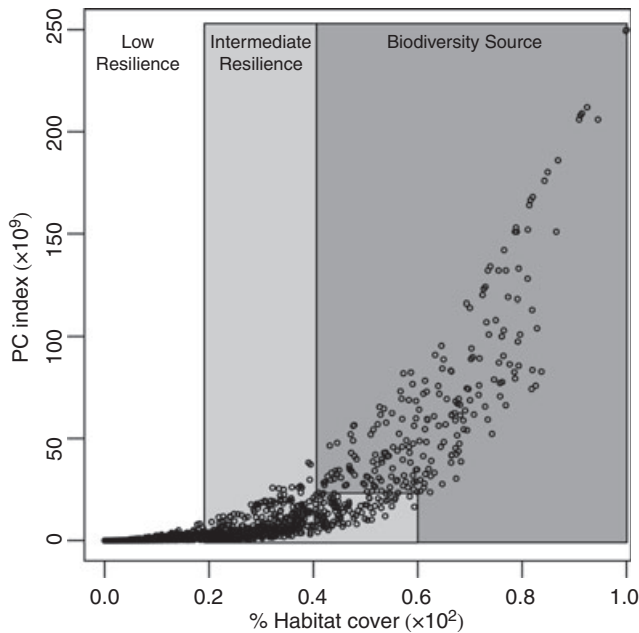


Figure 3. Distribution of focal landscapes (circles) according to the habitat cover and connectivity (PC index) in one of the BSRs of the Brazilian Atlantic Forest (Bahia). Dark gray polygon represents limits of *biodiversity source* landscapes; light gray polygon represents limits of *intermediate resilience* landscapes. *Low resilience* landscapes are those with less than 20% of habitat cover.

diagonal links (59.3 and 40.7%, respectively; Stauffer 1985). Random landscapes in this range of forest cover should have a 50% percolation probability, and are consequently likely to maintain good structural connectivity. The *intermediate resilience landscapes*, where restoration actions should be focused, were those with more than 20% forest cover (Fig. 3). Finally, *low resilience landscapes* were those with less than 20% forest cover.

The classification of landscape resilience also followed theoretical thresholds in landscape ecology (Andr n 1994; Fahrig 2003) and empirical studies in the Atlantic Forest that suggest landscapes with 10% forest cover as biodiversity poor with respect to forest dwelling species, especially intermediately and highly sensitive species (Martensen et al. 2012). Conversely, landscapes with 30% forest cover still sheltered high biodiversity levels (Pardini et al. 2010; Martensen et al. 2012), particularly for intermediately sensitive species (Martensen et al. 2012), and thus are the most likely to benefit from restoration actions (Pardini et al. 2010).

**Broader Scale Analyses (Step 3).** In this step, each BSR was considered as a graph in which each FL was a node, and the PC index was used as the attribute of the nodes.

First, all the contiguous *biodiversity source* FLs were merged to create larger *biodiversity sources* (Fig. 1d), and the PC index was calculated for these new FLs. The use of the numerator of the PC index instead of the PC index value (which is a normalized value) throughout the analysis results in higher attribute values and, consequently, greater

importance for these larger *biodiversity sources* during the next steps. In this case, the number of nodes was too large, and it was not possible to use the PC index owing to computational limitations. Thus, we adopted the IIC and its fractions IICflux and IICconnector.

Next, we conducted the forest removal experiments inside each FL to calculate the variation of the IICflux (varIICflux) and the IICconnector (varIICconnector) fractions (see Appendix S1 for details). The varIICflux considers the attributes of all functionally connected nodes in order to estimate the importance of each node for the potential flow of organisms. A focal node will have greater importance when it has higher attribute value and when it is also functionally connected to other nodes with high attribute values. The value of varIICconnector depends on the focal node's position in the graph and on the attributes of the other functionally connected nodes. The varIICconnector value will become higher as the removal of the focal node breaks the graph in two or more components with high node attributes, representing a break in the important connections of the graph.

The identification of bottlenecks in major dispersal routes among FLs is performed by removing all the *low resilience landscapes*, then calculating the varIICconnector value for each remaining FL in the graph (Fig. 1f). Only the immediate neighbors are considered to be functionally connected for the varIICconnector in order to detect the creation of possible gaps between two or more *intermediate resilience* or *biodiversity sources* FL. Higher values of varIICconnector indicate those FLs that represent the most probable alternatives for organisms to move among *biodiversity sources* and *intermediate resilience landscapes*. Finally, the varIICflux and the varIICconnector of *intermediate resilience landscapes* were normalized from 0 to 1 and, then, summed to obtain the final priority score for each BSR separately.

All connectivity analyses were performed with the freely available software Conefor Sensinode 2.5.8 command line version (Saura & Torne 2009) and the input files for Conefor Sensinode were generated using the freely available extension Conefor Inputs for ArcGis (www.jennessent.com). Spatial data generated by the authors during this study are available online (refer to Appendix S1 for data availability).

## Results

### Restoration Prioritization in the Atlantic Forest Region

The classification of FLs in each BSR according to their resilience status resulted in 85% of the Atlantic Forest landscapes being considered of *low resilience*, 10% as *intermediate resilience*, and 5% as *biodiversity sources* (Table 1; Fig. 4). The last two landscape categories contain almost 60% of the remaining forest cover, with 29.6% in an intermediate resilience condition, where restoration actions could be optimized.

The distribution is highly heterogeneous among subregions. The Serra do Mar BSR stands out as having a high representation of *biodiversity sources* and *intermediate resilience*

**Table 1.** Total number of focal landscapes (FL) and forest cover (100ha) according to the resilience class inside each Atlantic Forest biogeographical subregion (BSR).

| BSR                    | Low Resilience      |                       | Intermediate Resilience |                       | High Resilience (Biodiversity Source) |                       |
|------------------------|---------------------|-----------------------|-------------------------|-----------------------|---------------------------------------|-----------------------|
|                        | FL                  | Forest Cover          | FL                      | Forest Cover          | FL                                    | Forest Cover          |
| Araucaria              | 4,080 (82%)         | 13,394 (43.8%)        | 709 (14%)               | 10,762 (35.2%)        | 206 (4%)                              | 6,449 (21.1%)         |
| Bahia                  | 1,924 (73%)         | 6,308 (29.5%)         | 496 (19%)               | 7,940 (37.2%)         | 224 (8%)                              | 7,121 (33.3%)         |
| Brejos Nordestinos     | 23 (82%)            | 61 (44.9%)            | 4 (14%)                 | 53 (39.0%)            | 1 (4%)                                | 22 (16.2%)            |
| Diamantina             | 1,506 (80%)         | 4,679 (50.2%)         | 302 (16%)               | 4,595 (49.3%)         | 70 (4%)                               | 42 (0.5%)             |
| Interior               | 13,373 (94%)        | 33,263 (68.5%)        | 721 (5%)                | 10,295 (21.2%)        | 147 (1%)                              | 4,972 (10.2%)         |
| Pernambuco             | 635 (86%)           | 2,258 (59.6%)         | 95 (13%)                | 1,329 (35.1%)         | 7 (1%)                                | 204 (5.4%)            |
| São Francisco          | 2,405 (94%)         | 2,407 (47.6%)         | 125 (5%)                | 1,927 (38.1%)         | 26 (1%)                               | 723 (14.3%)           |
| Serra do Mar           | 1,110 (46%)         | 4,005 (9.9%)          | 619 (26%)               | 10,196 (25.2%)        | 697 (29%)                             | 26,257 (64.9%)        |
| <b>Atlantic Forest</b> | <b>25,056 (85%)</b> | <b>66,374 (41.7%)</b> | <b>3,071 (10%)</b>      | <b>47,097 (29.6%)</b> | <b>1,378 (5%)</b>                     | <b>45,789 (28.8%)</b> |

Values inside parentheses refer to the percentages of FL and forest cover in each BSR.

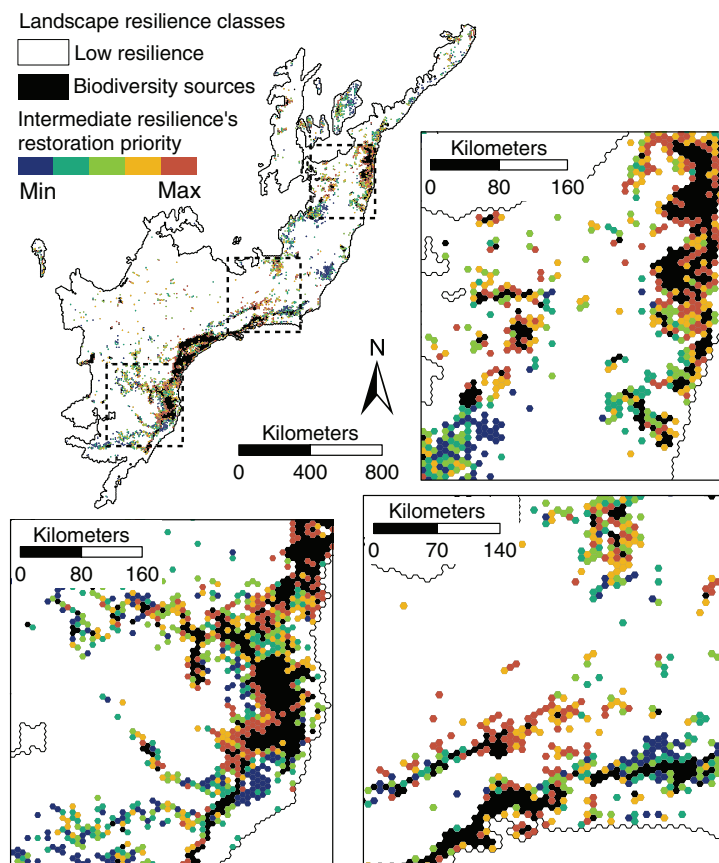


Figure 4. Spatial distribution of the three resilience classes of the Atlantic Forest focal landscapes (top left) and restoration priorities for the *intermediate resilience* landscapes. This figure appears in color in the online version of the article (doi: 10.1111/rec.12049).

landscapes, whereas the more deforested regions, such as the São Francisco and Interior BSRs, contain larger amounts of *low resilience landscapes* (Table 1). With the exception of these two last regions, all other BSRs had at least 13% of *intermediate resilience landscapes*.

The limitation of restoration priority areas to only 10% of the whole Atlantic Forest region can be seen as a strong restraint. However, in the 3,071 FLs of *intermediate resilience*, there are 4.7 million hectares of forest remaining, and,

thus, there are approximately 15 million hectares of non-forest areas that might be good candidates for restoration actions.

Values of varIICflux and varIICconnector obtained during regional-scale analyses presented complementary information that can be used to set restoration priorities (Fig. S1). The presence of FLs with high IICconnector and low IICflux highlights the value of FLs that may have reduced potential organism flow as a consequence of internal and surrounding

landscapes characteristics, yet act as dispersion bottlenecks within a given BSR.

## Discussion

The methodological framework presented here can be considered as a first step in restoration planning to optimize the relation between costs and benefits of a given restoration project, and used to solve a primary question in *Restoration Ecology*: where to restore in a scenario of millions of hectares of degraded lands and limited resources? Ideally, site, landscape, and regional scales should all be assessed within the prioritization process, especially in restoration projects aimed at recovering large areas and several ecosystem services (Holl & Aide 2011). Thus, a new set of parameters (such as soil degradation or suitability for forest regeneration) should be considered in a subsequent step on a site scale when planning the restoration.

This proposed approach is highly flexible. The definition of landscape connectivity can include a diversity of species with different dispersal abilities. Thus, prioritization can be performed for different umbrella or focal species (Lambeck 1997), which can then be compared and integrated to identify areas that can benefit species with different ecological requirements. Similarly, the definition of size and shape of the FLs can vary according to the ecological process under investigation. Additionally, a sensitivity analysis can be performed to test the effects of different landscape extents and spatial arrangements on prioritization results.

Another important advantage of the proposed method is that it does not demand extensive biological knowledge. The graph theory approach allows analysis of landscape connectivity with little biological data (Minor and Urban 2007) or even considering only “virtual species.” However, when the information is available, this approach can integrate a large quantity of information, such as matrix permeability, corridor effects, habitat quality, and local species richness (potentially obtained from species distribution models, or field data). Furthermore, in the absence of biological information, the criteria for defining landscape resilience classes can rely only on theoretical thresholds, such as the percolation and fragmentation thresholds (Stauffer 1985; Andr  n 1994). Finally, the ability to independently analyze different subregions, with different community composition or pool of endemic species, with later integration in the final results, allows this method to be applied to heterogeneous regions for broad-scale regional restoration plans.

Focusing restoration efforts on intermediate resilient landscapes can be a controversial issue. Some authors have suggested that all landscapes (and particularly the most degraded ones) deserve to be restored (Crossman & Bryan 2009). However, some prioritization is necessary for efficient allocation of resources toward conserving biodiversity (Bottrill et al. 2008). A focus on intermediate habitat amount landscapes can avoid the imminent extinctions of species due to habitat loss and also facilitate the recolonization of naturally regenerated areas (Pardini et al. 2010; Lira et al. 2012). For instance,

in resilient landscapes with high forest cover and connectivity, less costly actions based on the protection of degraded areas to allow natural forest recovery or species enrichment of degraded patches may be sufficient (Rodrigues et al. 2009). At the other extreme, in landscapes with low habitat cover and connectivity, more costly actions would be necessary, but the benefits for biodiversity conservation will most likely be very low compared to the effort involved (Hobbs et al. 2009). However, restoring areas with low priority within a biodiversity perspective can be highly important for other ecosystem services, such as regulation of water flow, and reduction of soil erosion, nutrient leaching, and greenhouse gases emission. Planning restoration for these services would require a complete different set of variables and criteria, and would probably result in trade-offs owing to a lack of spatial congruence in the optimal allocation of restoration actions for biodiversity and other ecosystem services (Mason et al. 2012). Moreover, the improvement of connectivity can also be a potential advantage in the future if climate changes obligate species to move throughout the region to find suitable environmental conditions (Dunwiddie et al. 2009). Planning multifunctional landscapes with the integration of biodiversity with different ecosystem services remains an open and stimulating challenge.

The application of the proposed approach in the Atlantic Forest region showed the potential of this framework, even considering a simplified example with only one species profile and FL size. Even if only 10% of the entire Atlantic Forest region was classified as *intermediate resilience*, the 15 million hectares of non-forest in this condition is almost equivalent to the present forest cover in the Atlantic Forest region (15.7 million hectares; Ribeiro et al. 2009). This methodological framework was developed in response to a demand from the Brazilian Environmental Ministry, which demands a robust framework with which to plan large-scale restoration actions and indicate favorable locations where restoration can be performed with relatively low costs and with clear biological benefits.

Finally, this methodological framework can be used to delineate new experiments on restoration effectiveness and to evaluate the results of past restoration projects, considering not only the local site resilience but also the landscape and regional contexts. The restoration constraints occurring at these different scales appear to influence the results of restoration actions in different manners (Matthews et al. 2009); however, there is still a lot to understand about the effects of management strategies according to local and regional conditions (Cunningham et al. 2007). The need to strengthen the links between ecological restoration and landscape ecology has long been recognized as an important strategy to improve the theoretical basis of both fields (Bell et al. 1997; Cunningham et al. 2007) as well as supporting improved restoration and management decisions (Holl & Aide 2011). This proposed approach represents a novel contribution to strengthening these links in a robust, replicable, and applicable manner.

### Implications for Practice

- Landscapes with intermediate resilience present a high potential for management effectiveness and should be the primary focus of restoration actions to conserve biodiversity.
- The application of graph theory is a useful approach to evaluate connectivity within a multiscale approach, considering regional, landscape, and local habitat characteristics.
- In making the spatial data from this study available to the public, practitioners will be able to replicate the analysis and better understand the method.
- The application of this method, with different data sets and in different regions, can contribute to increase the comprehension of landscape structure effects on the recovery of ecosystems.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Detailed information about forest cover map, regional analysis, and data availability.

**Figure S1.** Importance of each focal landscape (FL) for biological flow among FLs (multiscale varIICflux, refer to *Calculation of the IICflux* in Appendix S1 for details) and as key elements for maintaining connectivity among FLs (varIICconnector) in biogeographical subregions (BSRs) in the Atlantic Forest (refer to text for detailed information on variable definitions and calculation). FLs with higher values of varIICconnector and lower values of multiscale varIICflux highlight the importance of some FLs that do not have high internal connectivity and high biological flow among surrounding landscapes but are very important for maintaining the biological flux in the BSR. FLs with lower varIICconnector and higher multiscale varIICflux indicate FLs that have high internal connectivity but are not bottlenecks because there are other surrounding landscapes with high connectivity that might act as alternative routes.