A framework to optimize biodiversity restoration efforts based on landscape cover and connectivity

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Abstract

The effectiveness of ecological restoration actions to conserve biodiversity depends on local and landscape constraints. Despite an extensive literature on local constraints, few studies consider the landscape context when planning restoration actions. We propose a multi-scale framework based on landscape cover and connectivity to infer landscape resilience and to set priority areas for restoration. Landscapes with intermediate habitat cover and where habitat connectivity is still high enough to favor recolonization dynamics were considered to be intermediately resilient, with a high chance of restoration effectiveness, and thus were designated priority areas for restoration actions. The proposed methodology consists of three steps: i) quantifying landscape cover and connectivity; ii) using landscape ecology theory to identify intermediate resilience landscapes; and iii) identifying landscapes that could act as corridors or bottlenecks for biological flows on a broader scale. We adopted a graph theory approach to evaluate landscape connectivity and to identify landscapes that act as corridors or bottlenecks. We present a case study of the Brazilian Atlantic Forest (~150 million hectares). Landscapes with high restoration effectiveness represent only 10% of the Atlantic Forest, but contain approximately 15 million hectares of non-forest areas that should be the focus of restoration actions. This area is almost equivalent to the present forest cover and is just below the non-conformity area with respect to the current environmental laws (~18 million hectares). The proposed methodology represents a practical way to plan restoration actions and optimize efforts by focusing on landscapes that would result in greater benefits to biodiversity conservation.

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Introduction

Ecological restoration of degraded areas is usually an expensive enterprise and results in varying levels of biodiversity recovery (Rey Benayas et al. 2009). The amount of resources needed and the results of restoration actions depend on the constraints and feedback forces that prevent the recovery of degraded land (Suding et al. 2004; Briske et al. 2008). Therefore, it is necessary to identify the constraints that limit or impede restoration success in order to distinguish systems that are capable of recovery by autogenic processes from those that require external restoration actions (Hobbs 2007). Moreover, because of the extensiveness of degraded lands, the environmental constraints for biodiversity recovery, and the limited financial support available, there is an urgent need to establish strategies to prioritize areas in order to optimize restoration efforts and to achieve the expected results (Bottrill et al. 2008; Chazdon 2008).

Despite an extensive literature related to local constraints (usually factors associated with the local disturbance level; Holl & Kappelle 1999), there is now wide recognition that constraints can operate at larger scales as well (Holl & Aide 2011). For biodiversity, of particular importance are the parameters related to landscape connectivity (i.e., the capacity of the landscape to facilitate biological flows), such as the proximity of patches (Holvorcem et al. 2011), the matrix permeability (Uezu et al. 2008) and the density of corridors and stepping stones. Those parameters can influence (re)colonization dynamics (Jacquemyn et al. 2003) and, thus, may have important implications in restoration effectiveness (Rodrigues et al. 2009).

Moreover, recent findings have associated landscape structure to landscape resilience and management efficiency (Tscharntke et al. 2005; Pardini et al. 2010). Landscape resilience is the capacity of the landscape-wide biota to recover from local species losses in individual patches through immigration on the landscape scale (Pardini

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et al. 2010). In this study, we propose that landscapes with intermediate habitat loss and that still maintain certain levels of connectivity would be the most highly indicated for restoration actions (Holl & Aide 2011). These landscapes still shelter high levels of biodiversity with the potential to recolonize restored areas but are close to suffering extinctions due to habitat loss and fragmentation (Pardini et al. 2010), thus showing a high potential for effective management for biodiversity conservation. In contrast, highly degraded landscapes, as well as well-preserved ones, would be less ideal targets for restoration actions. In highly degraded landscapes, the remaining habitat areas have already lost a large fraction of the species, thus demanding very large investments with low chances of success (Calmon et al. 2011; Rodrigues et al. 2011). Although these degraded landscapes can be considered to be in an alternative and resilient state with low biodiversity levels (Suding et al. 2004), we will consider this an undesirable state for biodiversity conservation (Gunderson 2000). In contrast, landscapes with high habitat cover present high resilience because propagule sources are abundant, and dispersion is facilitated by the landscape configuration (e.g., low isolation, high degree of connectivity) and by the presence of dispersers (Mclachlan & Bazely 2003). Those landscapes, therefore, have a high potential to maintain biodiversity and to recover by autogenic processes, thus reducing the need for restoration actions other than land abandonment (Hobbs 2007).

All these aspects make incorporating the landscape context in restoration planning a promising approach that has been performed only tentatively in recent years (Aronson et al. 1998; Rannap et al. 2009; Aviron et al. 2011). In the few studies that have tried to incorporate the landscape context and/or environmental constraints in regional restoration planning, most required detailed information on species' distribution (Crossman & Bryan 2006; Zhou et al. 2008; Butler 2009; Thomson et al.

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2009) or local site conditions (Cipollini et al. 2005), which are rarely available in tropical areas. Other methods do not require precise biological information but may have other limitations, such as little flexibility in the selection of local areas for restoration (Twedt et al. 2006) or prioritizing extremely degraded landscapes (Crossman & Bryan 2009).

In this study, we present a new methodological framework to define priority restoration areas while considering the landscape structure on multiple scales. The primary goal is to enhance landscape connectivity and optimize restoration efforts by reducing their costs and improving the potential benefits for biodiversity conservation. On a more local scale, we use models and landscape theories to infer landscape resilience and management effectiveness based on habitat cover and connectivity, which can be used to identify landscapes with a high chance of restoration success (best cost/benefit ratio). On a broader scale, we rank those identified landscapes in terms of the priority inferred from their importance as corridors or bottlenecks for biological flows. As an illustrative case, we applied this method to the identification of priority restoration landscapes in the entire Brazilian Atlantic forest biome, which is one of the world's top biodiversity hotspots (Myers et al. 2000), although only 12-16% of the original habitat remains covered by forests, and this remainder is primarily distributed in fragments of < 50 ha (Ribeiro et al. 2009). Thus, the Atlantic forest contains a tremendous number of degraded areas that need to be restored in order to effectively conserve biodiversity. It is therefore essential to develop efficient methods to reduce costs and optimize the biological benefits.

Methodological framework

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The proposed framework is based on three main steps, the first two performed on a more local scale, and the third one on a broader scale: i) calculating habitat cover and connectivity; ii) inferring landscape resilience from habitat cover and connectivity measured in the first step; and iii) performing habitat removal experiments to identify the key landscapes in which restoration will have the strongest effects on connectivity on a broader scale (Fig. 1a).

Step 1: landscape cover and connectivity analysis

Initially, the entire area under evaluation is divided into several equally sized hexagonal focal landscapes (FLs), as shown in Figure 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 cover 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 functional attributes of connectivity (Urban & Keitt 2001; Martensen et al. 2008; Awade et al. 2012). A graph is a set of nodes and links that connects 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.

On this scale, we adopted the Probability of Connectivity Index (Saura & Pascual-Hortal 2007), more specifically the numerator of the PC index (PC). This probabilistic index uses the dispersal capability to calculate functional connectivity in

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landscapes. This index presents a consistent behavior for analyzing landscape changes and is considered one of the best indices for the evaluation of connectivity (Saura & Pascual-Hortal 2007).

To assess the PC, each FL is depicted as a graph in which habitat patches are the nodes and the patch area is used as the node's attribute, whereas 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 and habitat cover, the FLs are classified into three categories (Fig. 1c): 1-*biodiversity sources*, which are the FLs with very high habitat cover (for example, above the percolation threshold of 0.5829; Stauffer 1985) or intermediate habitat cover and high connectivity that results in a high resilience landscape with high structural connectivity and thus with a great potential to maintain biodiversity, independent of restoration actions; 2- *intermediate resilience landscapes*, which are FLs with intermediate habitat cover and connectivity that still shelter high biodiversity and would permit the recolonization of restored areas; and 3- *low resilience landscapes*, which are FLs with low habitat cover and connectivity, thus presenting low potential for sheltering biodiversity and for the recolonization of restored areas.

We assumed that *biodiversity sources* should have high *landscape resilience*, i.e., the landscape structure should facilitate species movement and thus the arrival of colonizers in areas to be restored, which are therefore able to recover by autogenic processes. Although the costs of restoration in these landscapes are likely low, the benefits for biodiversity conservation would also be low due to the already high habitat cover and connectivity. We also assume, following Tscharntke et al. (2005) and Pardini

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et al. (2010), that landscapes with intermediate habitat cover and connectivity, classified here as *intermediate resilience*, present the best ratio of restoration cost to benefits for biological conservation. Even in favorable landscapes, the resilience can be altered due to local disturbances, which can strongly affect the structure and quality of the habitat. In this framework, we have ignored those local habitat quality variations, assuming that local conditions should be incorporated in a further 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 performed 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 to be a graph, but instead of using each habitat patch as a graph node, the FLs are the graph nodes, and the node attributes are the PC index calculated during the proximate scale analysis.

The second step of the broader scale analysis consists of calculating the connectivity of the whole study region and performing habitat removal experiments to identify the most important *intermediate resilience landscapes* to connect *biodiversity sources*. In these experiments, the graph connectivity index is calculated before and after the removal of all habitats present in each FL, and the variation in the graph connectivity index represents the importance of the FL for the graph structure of the entire analyzed region.

Higher variation in the graph connectivity index indicates FLs that must be prioritized for restoration actions due to their internal habitat cover and connectivity, representing probable routes of organism flow that offer good chances of recolonization and have great importance for biodiversity conservation.

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Application in the Atlantic Forest

The application of the methodological framework in a real situation is not a trivial task because it involves critical, and not always obvious decisions, especially when basic biological information is lacking, such as setting FL sizes, defining dispersal capabilities and choosing habitat threshold levels. We illustrate how we dealt with these assignments using a case study of the Brazilian Atlantic Forest. The Atlantic Forest originally covered an area of approximately 150 million hectares, extending from the southern to the northeastern regions of Brazil (Fig. 2), resulting in a very heterogeneous forest that harbors one of the world's most diverse biota (Metzger 2009). The biome can be divided into eight biogeographical sub-regions (BSRs) based on their environmental and biotic characteristics (Silva & Casteleti 2003), which currently present different levels of habitat loss and fragmentation (Ribeiro et al. 2009; Ribeiro et al. 2011). Despite the differences among BSRs, none present the minimum forest cover demanded by the Brazilian Forest Act, resulting in great opportunities for restoration of the degraded and/or illegally occupied lands (Calmon et al. 2011; Ribeiro et al. 2011). Due to the extent of this biome and the amount of area that can be restored, the proposed method was applied to the whole Brazilian Atlantic Forest to identify the priority regions for forest restoration actions.

The different BSRs (Silva & Casteleti 2003; modified by Ribeiro et al. 2009; Fig. 2) were analyzed separately to guarantee that all sub-regions have priority areas, avoiding the prioritization of only the most preserved regions of the Atlantic Forest (see Ribeiro et al. 2011), thereby optimizing the beta-diversity in the whole system.

The analyses were based on the Atlantic Forest vegetation map (SOS Mata Atlântica/INPE 2008), which considers only two classes: forest and non-forest.

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Grasslands and other pioneer or non-forest ecotypes that occur naturally in the region were not included in this vegetation map. Despite previously observed commission and omission errors, this map is considered to be the best information on forest cover for the entire Atlantic Forest biome (Ribeiro et al. 2009; refer to the supplementary material for more details and limitations of the forest cover map).

The whole study region was divided in to 29,505 hexagonal landscapes of 5,000 ha each. The area adopted for the FLs is on a suitable scale for studying the effects of forest fragmentation for several taxonomic groups in the Atlantic Forest biome (Martensen et al. 2008; Boscolo & Metzger 2009; Metzger et al. 2009; Pardini et al. 2010; Banks-Leite et al. 2011; Martensen et al. in press).

Local scale analyses (Steps 1 and 2)

For the local scale analysis, the PC index was calculated using the patch areas as node attributes and considering a 50% probability of crossing 50 m of non-forest areas. This dispersal capability was based on the functional connectivity parameters observed for some forest dwelling species in the Atlantic Forest (Uezu et al. 2005; Awade & Metzger 2008; Boscolo et al. 2008; Hansbauer et al. 2008; Martensen et al. 2008; and for a review, see Crouzeilles et al. 2010). Such species can be considered to be intermediately sensitive to forest loss and fragmentation: they are not exclusively found in large mature continuous forests (they can survive in secondary forests in some fragmented landscapes), but they do not tolerate high levels of forest loss (>60% of deforestation; Martensen et al. in press) and fragmentation (Hansbauer et al. 2008; Martensen et al. 2008; Banks-Leite et al. 2011). We are of the opinion that these species would be the first to be benefited by improved landscape connectivity (Martensen et al. in press).

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The *biodiversity source landscapes* were those with more than 60% forest cover or between 40-60% forest cover with a PC value above the median PC value for this forest cover interval (Fig. 3). This criterion was based on the percolation threshold, considering orthogonal links (59.3%) and diagonal links (40.7%), according to Stauffer (1985). Random landscapes with these amounts of forest cover should have a 50% percolation probability, which means that landscapes within this habitat range and with high PC values likely maintain good structural connectivity. Thus, even for species that do not move through a non-forest matrix, connectivity should still be high in this condition.

The *intermediate resilience landscapes*, where restoration actions should be focused, were those with above 20% forest cover and not classified as biodiversity sources (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 (Andrén 1994; Fahrig 2003) and empirical studies in the Atlantic Forest, indicating that landscapes with 10% forest cover were biodiversity-poor with respect to forest dwelling species, especially intermediately and highly sensitive species. Conversely, landscapes with 30% forest cover still shelter high biodiversity levels (Pardini et al. 2005, 2010; Martensen et al. in press), particularly for intermediately sensitive species (Martensen et al. in press), and thus, are the most indicated for 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 node.

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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 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.

On this scale, if the number of nodes is too large, it is no longer possible to use the PC due to computational limitations. In this situation, we suggest using a second connectivity index, the Integral Index of Connectivity (IIC), and its fractions, IICflux and IICconnector (Bodin & Saura 2010; Saura & Rubio 2010), which is also considered to be a robust index (Pascual-Hortal & Saura 2006; Saura & Pascual-Hortal 2007). Moreover, during the forest removal experiments, the variations in two fractions of the IIC allow one to distinguish the importance of each FL for organism flow in the landscape (varIICflux) or as a key landscape for maintaining the connectivity in the whole graph (varIICconnector; for detailed information on the index fractions refer to Saura & Rubio 2010; see Holvorcem et al. 2011 for a case study on a regional scale).

The varIICflux considers the node attributes of all functionally connected nodes 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 values and when it is also functionally connected to other nodes with high attribute values. The varIICflux was calculated to identify biological corridors in the BSRs of the Atlantic Forest (refer to supplementary material for details).

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

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more components with high node attributes, representing a break in the important connections of the graph.

This identification of bottlenecks in major dispersal routes among FLs is performed by removing all the *low resilience landscapes* from the study area graph, 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).

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 *low resilience*, and only 10% as *intermediate resilience* and 5% as *biodiversity sources* (Table 1; Fig. 4). However, these last two landscapes categories contain almost 60% of the remaining forest cover, with 29.6% in an intermediate resilience condition, where restoration actions could be optimized.

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The distribution is highly heterogeneous among sub-regions. Particularly, Serra do Mar BSR stands out as having a high representation of *biodiversity sources* and *intermediate resilience landscapes*, while the more deforested regions, such as the São Francisco and Interior BSR, contain a large amount of *low resilience landscapes*. With the exception of these two last regions, all other BSRs had at least 13% *intermediate resilience landscapes*.

The limitation of restoration priority areas to only 10% of the whole Atlantic Forest region can be seen as a strong restriction. However, in the 3,071 FLs of *intermediate resilience,* there are 47,097 km² of forest, and, thus, there are approximately 15 million hectares of non-forest areas that might be good candidates for restoration actions.

Values of multi scale varIICflux and varIICconnector obtained during regional scale analyses presented complementary information for setting restoration priorities (Fig. 5). The presence of several FL with high IICconnector and low IICflux highlights the importance of some FLs that are not the most important when considering potential flow due to internal and surrounding landscapes characteristics but are key landscapes that may act as dispersion bottlenecks in the BSRs.

Discussion

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) and for better supporting restoration and management decisions (Hobbs & Norton 1996; Holl & Aide 2011). However, most of the previous studies have performed *a posteriori* analyses, i.e., considering the influence of the landscape context on the restoration effectiveness after

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carrying out the restoration action (Shono et al. 2006; Cunningham et al. 2007; Matthews et al. 2009).

The proposed methodological framework can be considered as a first step in restoration planning to optimize the costs/benefit ratio of any restoration project and might also help to solve one of the primary questions in the field of restoration ecology: where to restore in a scenario of millions of hectares of degraded lands and limited resources? Obviously, 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. Ideally, site, landscape, and regional scales should all be assessed, especially in restoration projects aimed at recovering large areas and several ecosystem services (Holl & Aide 2011).

Moreover, the proposed approach presents a high flexibility. The definition of landscape connectivity can include a large range of species profiles with different dispersal abilities and, therefore, with different functional connectivities. Thus, prioritization can be performed for different umbrella or focal species (Lambeck 1997), which can then be compared and integrated to identify which areas can benefit species with different ecological requirements. Similarly, the size, shape and disposition of the focal landscapes can vary according to functional characteristics of the landscapes under investigation, or 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 approach is that it does not demand extensive knowledge of biodiversity or species occurrence, as would be necessary with previous approaches. 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

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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). Furthermore, the criteria for defining landscape resilience classes can rely only on theoretical thresholds, such as the percolation and theoretical fragmentation thresholds (Stauffer 1985; Andrén 1994), if no other specific biological information exists for the system under investigation. Finally, the ability to independently analyze different sub-regions, with different community composition or endemic species, with greater integration in the final results allows this method to be applied to heterogeneous regions for broad scale regional restoration plans.

The proposed approach can optimize restoration effectiveness and help maintain biodiversity by focusing on improving the connectivity of resilient landscapes with intermediate habitat cover and connectivity, which is particularly important for biodiversity conservation in fragmented regions (Tabarelli et al. 2010; Ribeiro et al. 2011). Focusing on intermediate resilient landscapes can be a controversial issue for some stakeholders who hold the view 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 if we want to successfully conserve biodiversity (Bottrill et al. 2008). Inferring landscape resilience can be useful in planning different actions in areas of differing habitat degradation (Hobbs 2007; Chazdon 2008). For instance, in landscapes with low habitat cover and connectivity, more costly actions would be necessary to restore some ecosystem services, but the benefits for biodiversity conservation will most likely be very low compared to the effort involved (Hobbs et al. 2009). At the other extreme, in resilient landscapes with high forest cover and connectivity, cheaper actions based on the protection of degraded

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areas to allow natural recovery or species enrichment of degraded patches may be sufficient to recover degraded areas (Rodrigues et al. 2009).

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 area is also very close to the approximately 18 million hectares of non-conformity areas required according to Brazilian environmental law (the Forest Act; Metzger et al. 2011). This methodological framework was developed in response to a demand from the Brazilian Environmental Ministry, which needs a solid framework to plan large-scale restoration actions in the Atlantic Forest region. The application of the proposed methods in the Atlantic Forest shows that there are favorable situations where restoration can be performed with relatively low cost and potentially with clear biological benefits, allowing the regularization of non-conforming land use situations and a substantial increase in the forest cover if adequate restoration policies are applied.

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. Although the constraints presented by these different scales appears to influence the results of restoration actions in different manners (Matthews et al. 2009), there is still a lot to understand about the effects of management strategies according to local and regional conditions (Cunningham et al. 2007). The proposed

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approach would thus contribute to improving the knowledge of and strengthening the link between landscape and restoration ecology.

Implication for Practice

- Incorporating inferred resilience based on landscape cover and connectivity in restoration planning may have great potential for maximizing restoration benefits for biodiversity conservation.
- Landscapes with intermediate habitat cover and connectivity should be the primary focus of restoration actions to conserve biodiversity because those landscapes still shelter high levels of biodiversity and have great potential for the recolonization of restored areas and, therefore, present a high potential for management effectiveness.
- Restoration in landscapes with intermediate habitat cover and connectivity should be combined with local and more intensive interventions in highly degraded landscapes and with regeneration facilitation in landscapes with high habitat cover.
- The application of graph theory within a multi-scale approach has a huge potential for the identification of important landscapes for organism flows based not only on focal landscape characteristics but also on neighboring landscape conditions.

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Tables and Figures:

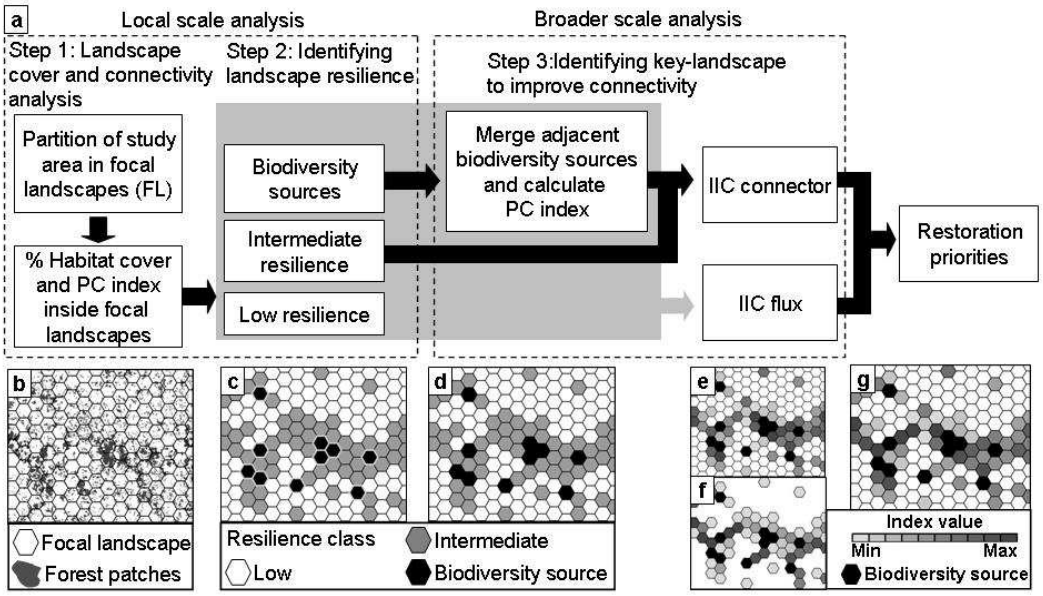

Figure 1. a) Major steps of the proposed methodology, integrating the local-scale and broader-scale analysis to set restoration priorities. b) During the local-scale analysis, the study area is divided into focal landscapes (FLs), which are classified into 3 resilience classes according to their forest cover and probability of connectivity (PC) index (c). The broader scale analysis begins by merging the contiguous *biodiversity source* FLs and recalculating their PC indices (d) and is followed by two subsequent steps: (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.

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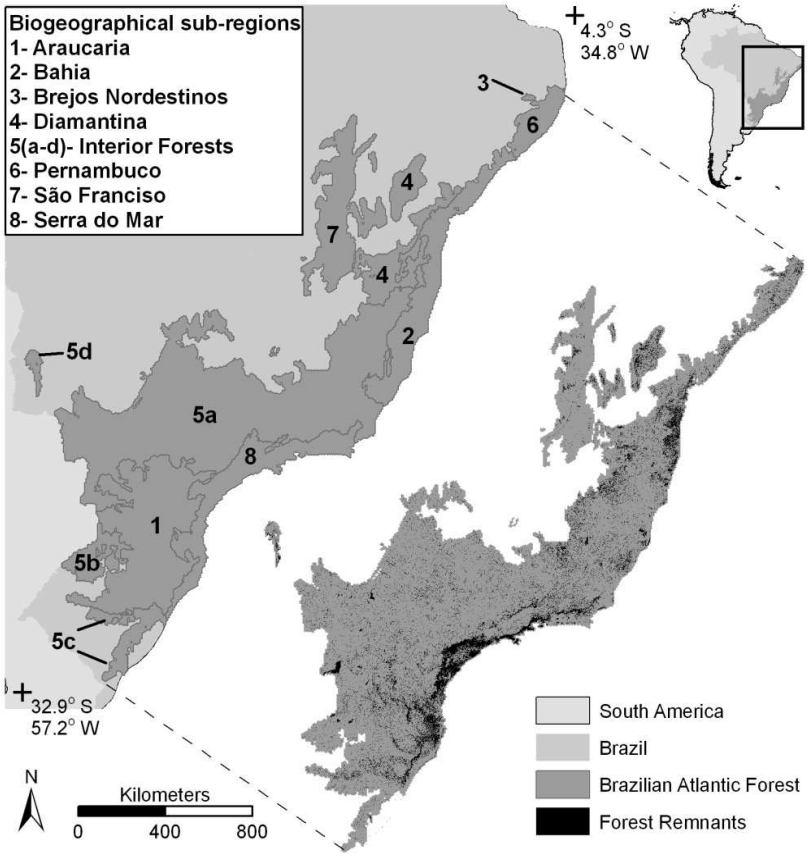

Figure 2. Distribution of the Atlantic Forest's biogeographical sub-regions (Silva & Casteleti 2003; modified by Ribeiro et al. 2009) and forest remnants (SOS Mata Atlântica/INPE 2008).

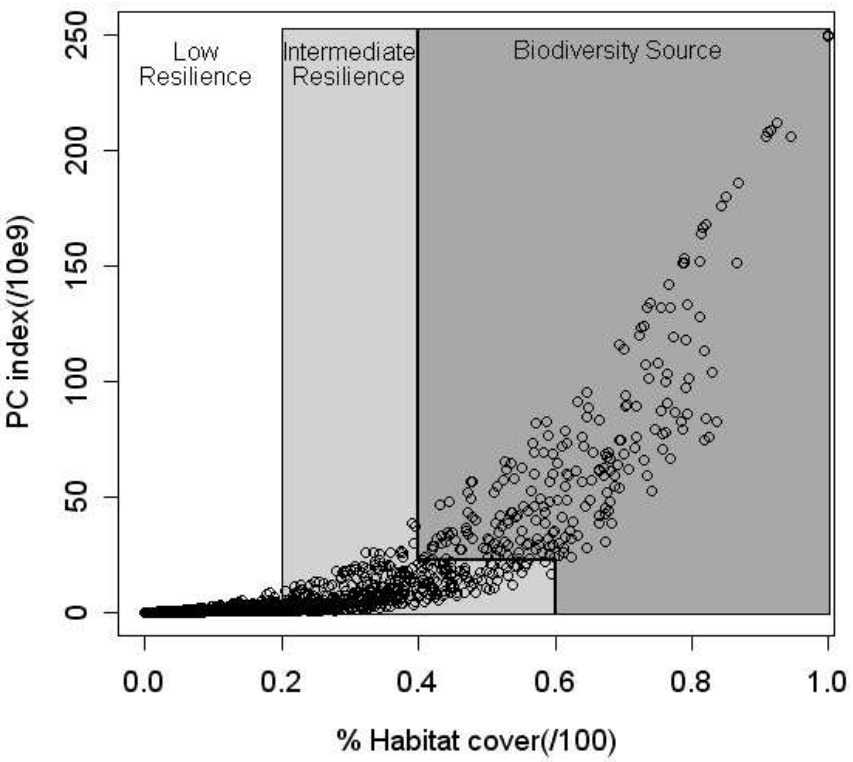

Figure 3. Distribution of focal landscapes (circles) according to the habitat cover and connectivity (PC index) in one of the biogeographical sub-regions of the Brazilian Atlantic Forest (Bahia). The dark gray polygon represents the limit of *biodiversity source* landscapes, the light gray polygon represents the limits of *intermediate resilience* landscapes, and *low resilience landscapes* are those with less than 20% of habitat cover.

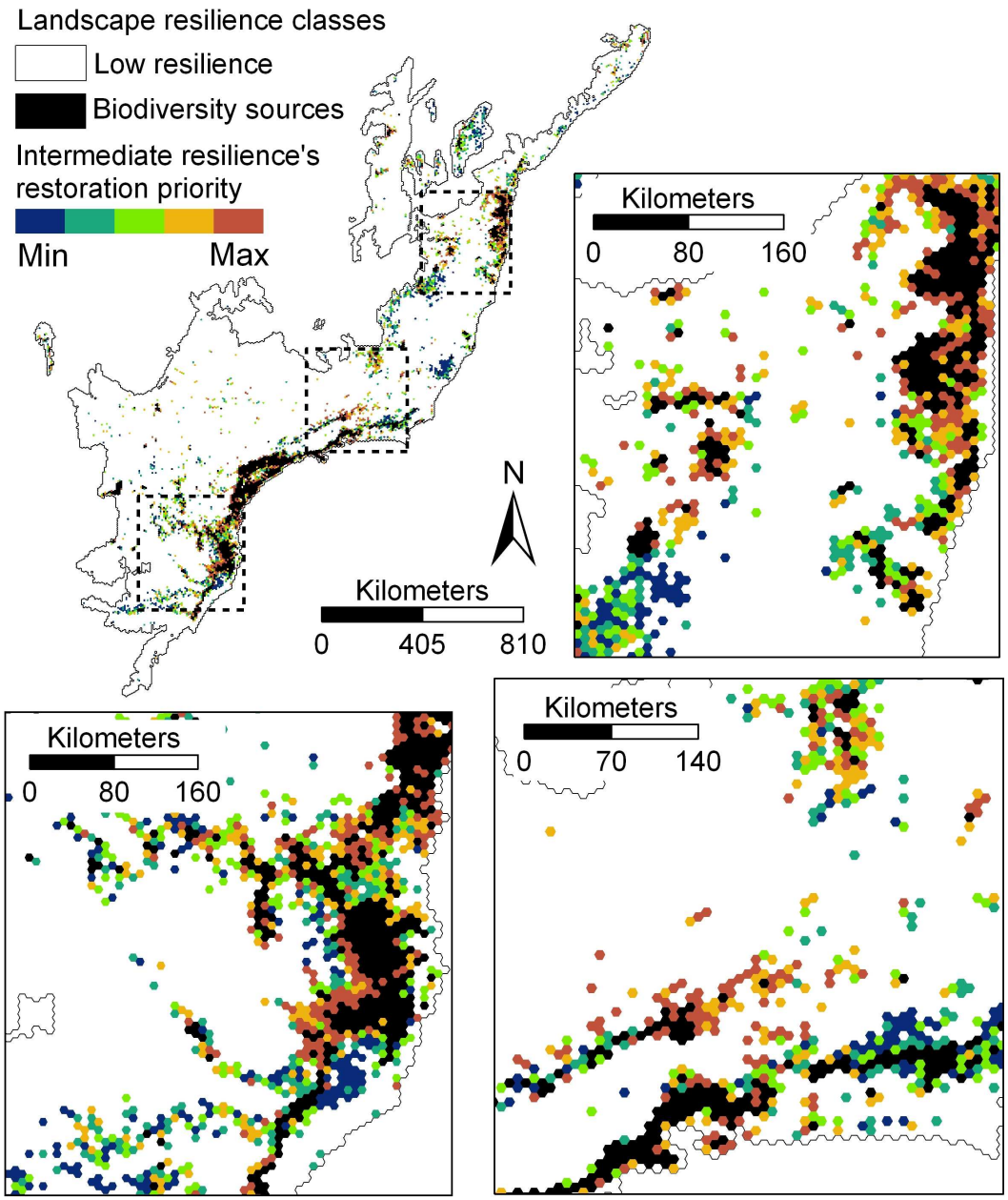

Figure 4. Spatial distribution of the three resilience classes of the Atlantic Forest focal landscapes (top left) and restoration priorities for the *intermediate resilience* landscapes.

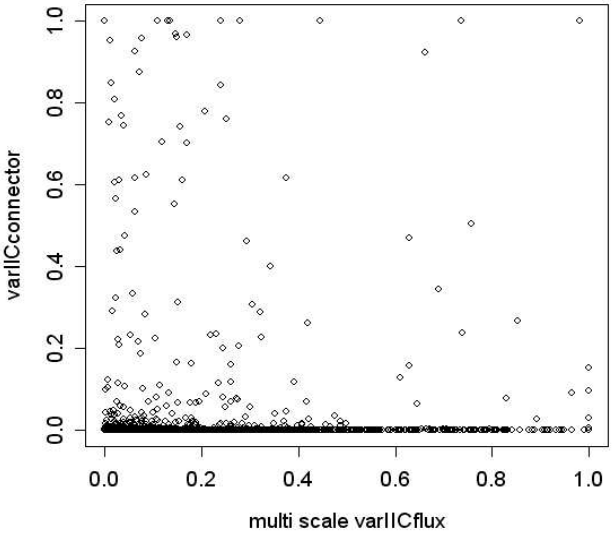

Figure 5. Importance of each focal landscape (FL) for biological flow among FLs (multi-scale varIICflux) and as key elements for maintaining connectivity among FLs (varIICconnector) in biogeographical sub-regions in the Atlantic Forest (refer to text for detailed information on variables definitions and calculation).

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Table 1. Total number of focal landscapes (FL) and forest cover (km^2) according to the resilience class inside each Atlantic Forest biogeographical sub-region (BSR). Values inside parentheses refer to the percentages of FL and forest cover in each BSR.

	Low resilience		**Intermediate resilience**		**High resilience (Biodiversity source)**	
BSR	**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%)
Atlantic Forest	**25,056 (85%)**	**66,374 (41.7%)**	**3,071 (10%)**	**47,097 (29.6%)**	**1,378 (5%)**	**45,789 (28.8%)**

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Supplementary Material

Details and limitations related to the forest cover map

The forest cover map was constructed through visual interpretation of TM5-Landsat and CCD/CBERS-2 images on a 1:50,000 mapping scale. The forest class includes different types of forests (e.g., coastal forests, Araucaria mixed forests, semi-deciduous forests, mangroves and restingas), with a predominant arboreal structure in the images that were used for the classification. Due to the characteristics of the images and the methods of classification, the forest class includes secondary forests in intermediate and advanced successional stages and might also include agroforestry patches, especially in the northeast region.

The heterogeneity of the matrix was not considered in this analysis due to the lack of an accurate land-use map for the whole Atlantic Forest region. Because different matrix permeabilities can affect the landscape connectivity, it is recommended to include this information when possible. Moreover, due to the spatial resolution of the satellite images, the forest cover map does not present isolated trees in the matrix that might act as stepping stones, increasing functional connectivity.(for more details refer to Ribeiro et al. 2009).

Details about the Atlantic Forest biogeographical sub-regions analysis

Due to the high heterogeneity, each biogeographical sub-region (BSR) was analyzed separately during the classification of FLs in resilience categories and also for the broader scale connectivity analysis.

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During the broader scale connectivity analysis we used a buffer that was three FLs wide for each BSR to incorporate FLs that were in neighboring BSRs and to consider the potential organism flow between BSRs.

Due to the large extent of the Interior Forests sub-region (14,421 FL) and its naturally discontinuous distribution and, thus, its environmental heterogeneity, this sub-region was divided into 4 smaller and continuous sub-regions (Fig. 2), which also helped to overcome computational limits for the indices calculation.

Calculation of the IICflux

During the calculation of the IICflux for each BSR, we decided to conduct three separate analyses, considering 1, 2 and 3 neighboring landscapes as functionally connected (3, 9 and 17 km for 5,000 ha hexagonal FL). The average of the three varIICflux values for each FL was calculated to obtain a multi-scale value of varIICflux. This average varIICflux value was used during the next steps of the case study.

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