



What makes ecosystem restoration expensive? A systematic cost assessment of projects in Brazil[☆]

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ABSTRACT

Limited funding is a major barrier to implementing ambitious global restoration commitments, so reducing restoration costs is essential to upscale restoration. The lack of rigorous analyses about the major components and drivers of restoration costs limit the development of alternatives to reduce costs and the selection of the most cost-effective methods to achieve restoration goals. We conducted detailed restoration cost assessments for the three most widespread biomes in Brazil (Amazon, Cerrado, and Atlantic Forest) and estimated the restoration costs associated with implementing Brazil's National Plan for Native Vegetation Recovery (12M hectares). Most surveys (60–90%) reported using the costly methods of planting seedlings or sowing seeds throughout the site, regardless of the biome. Natural regeneration and assisted regeneration approaches were an order of magnitude cheaper but were reported in < 15% of projects. The vast majority of tree planting and direct seeding costs were incurred during the implementation phase, and nearly 80% of projects ended maintenance within 30 months. We estimated a price tag of US\$0.7–1.2 billion per year until 2030 to implement Brazil's restoration plan depending on the area that recovers through natural regeneration. Our results offer valuable insights for developing strategies to make restoration cheaper and to increase its cost-effectiveness for achieving diverse benefits in Brazilian ecosystems. Our survey also provides a starting point for sound assessments of restoration costs and their drivers in other biomes, which are needed to reduce the financial barriers to scaling up restoration at a global scale.

1. Introduction

Regional and international commitments have mobilized unprecedented political support to restore hundreds of millions of hectares throughout the globe, mainly where biodiversity persistence and human wellbeing have been threatened by degradation and unsustainable use of natural resources (Menz et al., 2013; Holl, 2017). The knowledge base to support large-scale restoration programs is expanding rapidly and provides evidence of the benefits and limitations of restoration to recover species and ecosystem services (Benayas et al., 2009; Maron et al., 2012; Moreno-Mateos et al., 2017); the pros and cons of different restoration approaches (Shoo et al., 2016; César et al., 2017; Crouzeilles et al., 2017); the importance of landscape planning to

maximize outcomes (Birch et al., 2010; Brancalion et al., 2019; Strassburg et al., 2019); and the key role of governance for successful programs (Guariguata and Brancalion, 2014; Budiharta et al., 2016). Despite these advances, restoration advocates are still unable to answer one of the first and most important questions that policy makers and investors ask: How much does it cost?

Discussions of the costs and benefits of ecosystem restoration have advanced in recent years (e.g. De Groot et al., 2013; Iftekhhar et al., 2017; Rohr et al., 2018). Most previous studies, however, are based on generic restoration cost estimates and lack detailed analyses of the components and drivers of restoration costs. Restoration is a complex activity involving several costs components. The total amount needed is difficult to quantify and predict (Holl and Howarth, 2000), given that

[☆] We estimated a price tag of US\$0.7–1.2 billion per year to implement Brazil's plan to restore 12M hectares of native ecosystems

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restoration projects rarely go exactly as planned so contingency funds are needed to undertake corrective actions. Restoration implementation costs vary widely, especially between passive (e.g. natural regeneration) and active (e.g. tree planting) restoration approaches (Holl and Aide, 2011; Brancalion et al., 2016b). The way these restoration approaches are implemented also affects costs, depending on the operational procedures (e.g. mechanized or manual site preparation, use of herbicides), species used (e.g. easily produced pioneer species or high conservation value species with expensive seeds; Brancalion et al., 2018), extent of site preparation needed to improve degraded biophysical conditions (Chazdon, 2008), and duration of ongoing project maintenance. Despite the challenges of estimating restoration costs, robust financial information is essential to support program planning and management for the aforementioned commitments, as well to attract investments from the private sector (Brancalion et al., 2017). Whereas high restoration costs are commonly cited as a primary barrier to scaling up restoration, the lack of rigorous analyses about the major components and drivers of restoration costs limit efforts to develop and implement more cost-effective alternatives (Holl and Howarth, 2000).

Here, we provide a country-wide analysis of terrestrial restoration costs across diverse ecosystems and degradation conditions in Brazil, the fifth largest and the most biodiverse country in the world. We quantified the costs to restore the largest Brazilian biomes, which encompass a range of biophysical and socioeconomic conditions. In addition, we estimated the restoration costs associated with implementing Brazil's National Plan for Native Vegetation Recovery (PLANAVEG, acronym in Portuguese), which aims to restore 12 million hectares by 2030. Although restoration costs vary substantially from country to country, our assessment provides valuable insights on the major components and drivers of restoration costs, which in turn helps to develop innovations and policies to make restoration more cost-effective (Brancalion and van Melis, 2017) and to prioritize where to spend limited restoration funds (Torrubia et al., 2014).

2. Methods

2.1. Gathering information on restoration methods, activities, and inputs

In order to obtain a comprehensive overview of restoration costs, we first characterized the methods used to restore terrestrial ecosystems in Brazil along with the associated activities and inputs (Fig. S1). This characterization was based on an online survey of restoration practitioners who plan and manage restoration projects in all Brazilian biomes (Appendix S1). Given the low representation of some biomes in the initial responses (Pampas/grassland = 1; Pampas/forest = 1; Pantanal = 1; Caatinga = 3), we focused our analyses in the Atlantic Forest (32), Cerrado (Savanna = 12, Forest = 7), and Amazon (7) biomes (Fig. S2), which account for 86.2% of the Brazilian territory. We disseminated the online survey in two campaigns on the Facebook page of the Brazilian Network of Ecological Restoration (Isernhagen et al., 2017), which had 612 members at the time, and announced it on the institutional webpages and e-mail lists of The Nature Conservancy Brazil and The Atlantic Forest Restoration Pact. We also compiled a list of professionals, organizations, and companies doing restoration based on information from The Nature Conservancy, the Ministry of Environment, the Brazilian Agricultural Research Corporation (EMBRAPA, 1997), and the Institute for Applied Economic Research (Ipea). This list was complemented by using a "snowball" approach; a total of approximately 500 e-mails were sent and 100 phone calls made to directly apply the survey to selected people.

Responses to most survey questions consisted of a pre-established list of options with an "other" category allowing respondents to add to the list. Questions covered: (1) general characteristics of the project such as location, project size (< 5, 5–15, > 15 ha), biome, and ecosystem (e.g. forest, savanna); (2) predominant restoration method: i) natural regeneration, ii) assisted regeneration (e.g., clearing around

naturally establishing trees), iii) enrichment planting (using seeds or seedlings) of species that do not colonize natural regeneration sites, iv) direct seeding; v) seedling planting, and vi) topsoil translocation); 3) main activities in the implementation and maintenance phases (see Table S1 for full list), which we aggregated into four groups: site protection against disturbances, soil preparation, control of weeds and other pests, and reintroduction of plants; (4) duration of the maintenance phase (six time classes ranging from 1 to 3 months to > 60 months); and (5) description and quantification of inputs during the implementation and maintenance phases (e.g. quantity of herbicide, fertilizers, and seedlings).

We received 56 responses from restoration practitioners who work for education and/or research organizations (27), government agencies (3), private companies (18), and non-governmental organizations (8). Two of the respondents filled out the survey twice for different projects for a total of 58 completed surveys (Amazon = 7; Atlantic Forest = 32; Cerrado forest = 7, Cerrado savanna = 12). We present the relative frequency of restoration methods, activities, and inputs used for each biome considering individual surveys as the sample unit.

2.2. Estimating restoration costs

We compiled a list of the most common restoration methods, activities, and inputs based on responses to the initial survey (Fig. S1) and then assessed the costs of each in three ways. First, we sent a follow-up survey (Table S3) to the same contact list of restoration practitioners described above with questions about costs of the main restoration activities and inputs for the restoration projects included in the first survey and received 40 responses (Figure S1; Atlantic Forest 23; Amazon 5; Cerrado 12). Second, we created an additional survey focused on gathering general market costs for the most common restoration activities and inputs assessed above (Table S4) without considering a specific restoration project. We contacted restoration companies and stores selling products for agriculture and forestry through ~600 e-mails and ~200 phone calls and received 66 responses (Figure S1; Atlantic Forest 46; Amazon: 7; Cerrado: 13). Third, we extracted detailed costs of restoration activities and inputs from 27 budget worksheets (Figure S1 and Table S4; Atlantic Forest 13; Amazon 11; Cerrado 3) provided by 2 consultants, 2 NGOs, and 7 private companies.

We calculated the average cost per hectare of each restoration method, activity and input for each biome, separating ecosystem types in Cerrado. Restoration activity costs were provided by interviewees on a per hectare basis. Total input costs per hectare were calculated by multiplying the average amount of input used per hectare (first survey, Table S1) by the average cost of the input provided in the second round of the survey (Table S3) and budget worksheets (Table S4). In cases where surveys for restoration activities or inputs in a given biome/ecosystem were ≤ 3 , we used the average cost of all replies, regardless of biogeographical context, for cost estimation. Total restoration implementation and maintenance costs were calculated by summing up all inputs and activities described for each method in each biome/ecosystem. We used the date of project implementation (Table S1; 1988–2016) and responses on input costs (Tables S3 and S4; throughout 2015) to standardize prices, using the General Price Index - Internal Availability (IGP-DI) of the Fundação Getúlio Vargas, and express costs in their December 2018 value in US\$.hectare⁻¹ (US\$1.00 = R\$3.87).

2.3. Estimating the costs for implementing Brazil's plan for native vegetation recovery

PLANAVEG was launched in 2017 by the federal government and aims to support the implementation of restoration activities in 12 million hectares by 2030, consistent with the restoration areas designated by the 2012 Native Vegetation Protection Law (21 million hectares; Soares et al., 2014), Brazil's Nationally Determined Contribution to the

Table 1

Description of the average per hectare and total cost associated with implementing four restoration scenarios, determined by the proportion of the total area to be restored through different methods (high to low proportion of tree planting), of Brazil's Plan for Native Vegetation Recovery (numbers after means represent the standard deviation).

Methods surveyed in this work	Mean cost (US\$. ha ⁻¹)	Methods described in PLANAVEG	Mean cost (US\$. ha ⁻¹)	Scenarios			
				High	Moderate	Low	Very low
Seedling planting	\$ 2328.06 ± \$ 465	Total planting	\$ 2041.27 ± \$ 728	0.50	0.40	0.30	0.20
Direct seeding	\$ 1754.48 ± \$ 991	Enrichment planting at low and high seedling density	\$ 788.52 ± \$ 478	0.30	0.30	0.30	0.30
Enrichment planting	\$ 788.52 ± \$ 478						
Assisted natural regeneration	\$ 344.07 ± \$ 156	Natural regeneration with fences	\$ 344.07 ± \$ 156	0.10	0.15	0.20	0.25
Natural regeneration	\$ 48.87 ± \$ 0.7	Natural regeneration without fences	\$ 48.87 ± \$ 0.7	0.10	0.15	0.20	0.25
Per hectare cost (US\$. ha⁻¹)				\$ 1296.49	\$ 1112.01	\$ 927.53	\$ 760.25
Total cost (12 Mha; billion US \$)				\$ 15.56	\$ 13.34	\$ 11.13	\$ 9.12

Paris Climate Agreement (12 million hectares; Brazil, 2017), the Aichi Target 15 of the Convention on Biological Diversity that aims to restore 15% of all degraded ecosystems by 2020 (43 million hectares), and national pledges to the Bonn Challenge (12 million hectares; bonnchallenge.com).

To estimate the total restoration implementation cost of PLANAVEG at the national level, we first calculated the mean cost of each restoration method per hectare of each biome/ecosystem individually and then summarized them (Table S5). Since PLANAVEG did not define how much area should be restored in each biome, and restoration costs were similar for each method in the different biomes/ecosystems, we calculated the mean cost of each restoration method regardless of the biome/ecosystem (Table S5), and we matched the restoration methods surveyed in this research with the restoration methods described in PLANAVEG (Table 1). PLANAVEG presents four restoration scenarios, with different proportions of restoration methods, from higher to lower dependence on active restoration (e.g. 50, 40, 30 and 20% of seedling planting and 10, 15, 20 and 25% of natural regeneration, in the same order; see Table 1 for a complete description of all scenarios). We weighted the cost of each restoration method by its percentage of use in each scenario (Table 1) and multiplied this per hectare cost by the total restoration area (12 Mha) to obtain the total restoration implementation cost estimate for each scenario.

3. Results

Most surveys (60–90%) reported using the costly methods of planting seedlings or sowing seeds throughout the site to restore terrestrial Brazilian ecosystems, regardless of the biome; direct seeding was used frequently in Cerrado savannas (43%) and occasionally in the Amazon (23%; Fig. 1A). In contrast, the less expensive natural regeneration and assisted regeneration approaches were used in < 15% of projects (Fig. 1A). Maintenance activities lasted for a few years regardless of the biome with nearly 80% of projects ending maintenance within 30 months (Fig. 1B). The relative frequency of using different restoration activities (e. g., protection, weed control, planting), was similar across biomes both in the implementation (Fig. 1C) and the maintenance (Fig. 1D) phases. Site preparation was the most frequent implementation activity (~60% of projects; Fig. 1C), and protection against disturbances (e.g. fences, firebreaks) and weed control were the most common maintenance activities (nearly 30% each; Fig. 1D).

The cost of different restoration methods did not differ markedly across biomes, with the exceptions of higher seedling planting costs in Cerrado savanna and lower direct seeding costs in the Amazon (Fig. 2A). The vast majority of costs were incurred during the implementation phase for all methods, except for assisted regeneration, in which total restoration costs were divided evenly between implementation and maintenance (Fig. 2A). Direct seeding and seedling planting cost approximately ten times more (~US\$2000. ha⁻¹) than

less intensive restoration approaches (natural and assisted regeneration, and enrichment planting; ~US\$200. ha⁻¹), mostly due to the higher input costs (Fig. 2B). The activity comprising the majority of the costs of each restoration method varied; site protection against disturbances was the only expense for natural regeneration, weed control was the predominant cost of assisted regeneration, and direct seeding and/or seedling planting were the major costs for the three methods involving active reintroduction of native plants in the restoration site (Fig. 2C).

Our calculations suggest that implementing the 12 million ha of restoration proposed by Brazil's Plan for Native Vegetation Recovery would cost between US\$8.9 billion to US\$15.6 billion depending on the proportion of the area to be restored by active restoration (Table 1). This implies a cost of approximately US\$0.7 to US\$1.2 billion per year in 2018 dollars to achieve the commitments by the 2030.

4. Discussion

Our results from the most systematic nationwide assessment of terrestrial restoration costs to date show that intensive restoration approaches, such as direct seeding and planting cost an order of magnitude more than less intensive restoration approaches such as assisted natural regeneration and enrichment or cluster planting, consistent with reports from prior studies (Zahawi and Holl, 2009; Hansson and Dargusch, 2017; Shoo et al., 2017). Restoration plantings costs in Brazil (~US\$2000) were within the range of those from mostly single project studies in other Latin American, African, and Asian countries (most range from \$1000-\$3000 per hectare; Zahawi and Holl, 2009; Ding et al., 2017; Hansson and Dargusch, 2017). These cost estimates vary substantially depending on labor pay rates in a given region, the duration of maintenance, and the extent of land degradation, as establishing native ecosystems on low resilience sites requires extensive labor and inputs (Holl and Aide, 2011). Inputs for active restoration comprised > 50% of the total restoration costs in our study, suggesting an opportunity to develop cost-saving innovations. Planting and seeding methods in Brazil mostly have been adapted from intensive forestry and agriculture and rely on the heavy use of machinery, fertilizers, and herbicides, all of which are costly. The cost of higher inputs may be compensated by greater yields in forestry and agriculture, but this is rarely the case for ecological restoration.

The short maintenance period of most projects (> 80% of projects for < 30 months) reflects the contracts established with restoration companies, which are usually hired to plant the trees and maintain them until the trees provide sufficient canopy cover to shade out invasive grasses. A well-established restoration plantation may reach this stage in approximately three years, but many restoration projects have problems with soil degradation, leaf-cutter ants, and competition with grasses that prevent trees from achieving a size to shade out grasses before the maintenance is over (Brancalion et al., 2016b). The

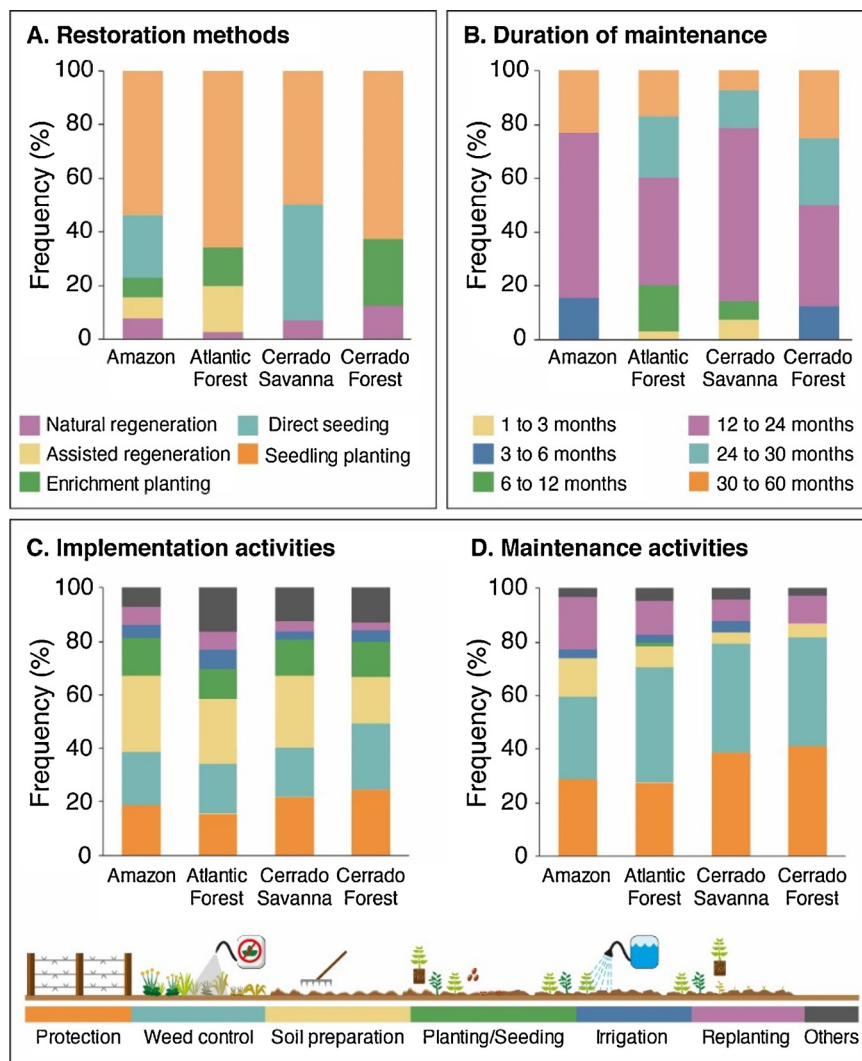


Fig. 1. Characterization of restoration methods and activities employed in Brazilian biomes: (a) main restoration methods, (b) duration of the maintenance phase, and (c) frequency of restoration activities included in the implementation and (d) maintenance phases of restoration projects (number of restoration projects per biome/ecosystem: Amazon = 7; Atlantic Forest = 32; Cerrado Savanna = 12; Cerrado Forest = 7). In figures “a” and “b”, each respondent selected a single main method/maintenance period per project, so the percentage values represent the proportion of projects per biome. In figures “c” and “d”, each respondent could select more than one activity per project, so the percentage values represent the number of times that a given activity was mentioned relative to the total number of activities mentioned.

mismatch between the typical 1 to 3-year duration of restoration funding, maintenance, and monitoring, and the decades to centuries it takes for ecosystems to recover, is a chronic problem in restoration (Holl and Cairns, 2002; Chaves et al., 2015; Bayraktarov et al., 2016). Our cost estimates are thus only for the initial stage of establishing early successional native vegetation structure and do not reflect the true cost of restoration, which would include complementary interventions to support long-term recovery and persistence of the ecosystems, which is a major concern since most regenerating forests are re-cleared within few decades (Reid et al., 2018).

Brazil is unique among Latin American countries in having established and enforced restoration laws over the past few decades, which favor the more intensive and costly restoration methods reported in our surveys (Brancalion et al., 2016b). The legal requirements are a primary reason the restoration methods, activities, and costs were quite similar across ecosystem types, despite the enormous ecological and social differences characteristic of a large country like Brazil and the fact that a one-size-fits-all approach in restoration is unlikely to result in widespread success (Aronson et al., 2011). Many restoration projects were implemented by private landholders who are mandated to restore native vegetation along rivers, streams, and other environmentally sensitive areas to comply with the 1965 Forest Code and more recently with the 2012 Native Vegetation Protection Law (Rodrigues et al., 2011; Brancalion et al., 2016a). Mandatory restoration projects tend to use more predictable, less risky restoration approaches, such as large-scale tree planting, in order to achieve minimum restoration standards

within the short time-frame for showing legal compliance (Holl, 2002; Brancalion et al., 2016b). Intensive restoration methods are certainly necessary for some highly degraded areas, but taking the approach of waiting a few years to assess natural regeneration first and then determining if and how to intervene most effectively to accelerate recovery is the most cost-effective approach to restore the largest area with limited restoration funds (Holl et al., 2018).

Many studies show that natural regeneration has been the main driver of tree cover increase globally (Yackulic et al., 2011; Aide et al., 2013; Sloan et al., 2016), except for a few government-centred programs focused on large-scale monoculture tree plantations (Temperton et al., 2014; Hua et al., 2016). As a consequence of the demonstrated potential to recover native ecosystems at large scales with lower costs, natural regeneration should comprise a major approach for upscaling restoration and achieving ambitious restoration commitments (Chazdon and Guariguata, 2016; Crouzeilles et al., 2017; Meli et al., 2017). In contrast, seedling planting and direct seeding were by far the most common restoration methods reported in our survey. These apparently-conflicting results do not mean that natural regeneration has had negligible importance in the recovery of Brazilian ecosystems, despite the lack systematic quantification. Rather, the low reporting of natural regeneration as a restoration approach likely reflects what the practitioners in our survey, and likely more broadly, perceive as restoration. Natural regeneration often occurs on lands where landowners cease agricultural uses for economic reasons rather than to intentionally promote forest recovery. We surveyed practitioners who mostly were

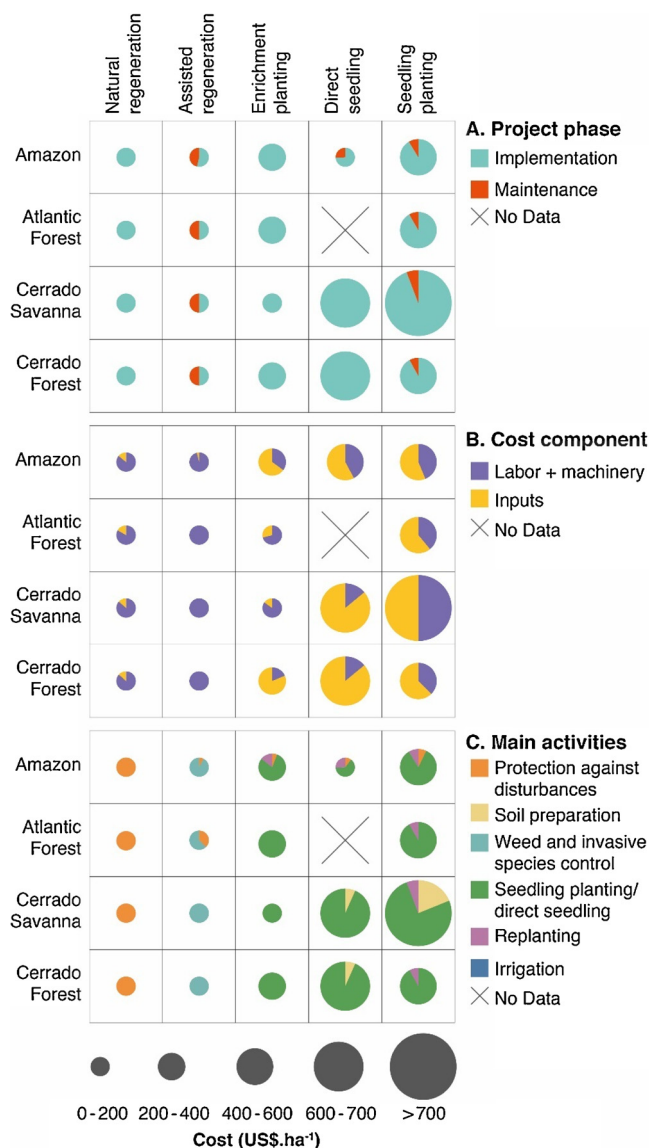


Fig. 2. Composition of costs for restoring Brazilian biomes as a function of (a) project phase, (b) component, and (c) main activities. Number of restoration projects assessed per biome/ecosystem: Amazon = 7; Atlantic Forest = 32; Cerrado Savanna = 12; Cerrado Forest = 7.

legally mandated and/or paid to restore forest, so they were much more likely to report intensive restoration methods.

The survey results and our personal experience suggest that in terrestrial systems in Brazil and probably other countries, the term “restoration” is often equated with intensive planting and seeding techniques, rather than recognizing the potential for natural and assisted regeneration approaches, which are much less costly. In fact, other recent observations suggest that natural regeneration in Brazil may far exceed those established by restoration plantings (de Rezende et al., 2015; Nanni et al., 2019). For instance, the Atlantic Forest Restoration Pact in Brazil, a multi-stakeholder coalition that aims to restore 15 million hectares of native forest in the biome by 2050, has registered 60,000 ha of restoration projects in its database from 2009 to 2018 (E. Santiami, personal communication). However, native forest has naturally regenerated on an area 20 times larger (1,206,000 ha) in this biome during the same period (Crouzeilles et al., 2019). Since the Atlantic Forest region has the longest history and spatial extent of agricultural use and other land degradation in Brazil, we expect that the potential for rapid natural regeneration will be much higher in other

biomes and regions, especially those located at the new deforestation frontiers, such as the south border of the Amazon and Cerrado, where native vegetation cover and resilience are often higher.

This underestimation of recovering forest area is problematic for a couple of reasons. First, these lands are rarely the focus of practitioners and land managers and hence may not be protected from subsequent re-clearing despite their conservation value (Reid et al., 2018). Second, if people perceive that intensive restoration methods like tree planting and direct seeding are the only restoration options, then it results in an overestimate of the cost of large-scale restoration, which may have been the case for our estimates for Brazil’s Plan for Native Vegetation Recovery. This result highlights the importance of clearly defining what ecosystem restoration approaches are considered in national and international commitments (Chazdon et al., 2016) and including natural and assisted regeneration among those approaches.

We estimate that implementing the 12 million ha target of Brazil’s restoration plan will be quite high (US\$8.9–15.6 billion total; US\$0.7–1.2 billion per year; 2017–2030), without considering potential cost increases over time or the potential reduction of costs resulting from restoration innovations and economies of scale. Moreover, our estimates do not include land opportunity costs (which may not apply to areas where restoration is mandatory) and price increases over time, and certainly underestimate the actual costs of the ongoing maintenance necessary to ensure restoration success. To put PLANAVEG cost estimates in context, Brazil spent ~US\$1.5 billion in subsidies for agriculture in 2017, which is one of the most important economic activities, with agribusiness producing 23.5% of the country GDP; the per hectare cost of tree planting (~US\$2000. ha⁻¹) is ~19 and 5 times higher than the annual revenue from extensive cattle ranching and crop production (Molin et al., 2018), the first and second most common agricultural land uses in Brazil (Lapola et al., 2014; Molin et al., 2018), and 8.3 times higher than the minimum salary in Brazil. Even the lowest cost scenario, which includes relying more on naturally regenerating forests, is very expensive. It is important to recognize, however, that the job and income generation from a massive investment in restoration could counterbalance these high costs (De Groot et al., 2013). Ecological restoration has been estimated to support an additional 95,000 jobs and \$15 billion in economic output in the United States through indirect linkages and increased household spending (BenDor et al., 2015). Moreover, the remission of environmental fines levied on farmers by the revision of the Forest Code (farmers do not have to pay the fines resulting from illegal deforestation and degradation that occurred before 2008 if they successfully implement a restoration program in the area), estimated at US\$3.29 billion, could help pay the bill. Further, innovation in restoration could also reduce implementation costs (Brancalion and van Melis, 2017).

Our survey can serve as starting point for restoration cost assessments in other regions, but we recommend future studies address additional critical questions that were outside the scope of our work. First, it is important to assess the costs and outcomes of a diversity of approaches to facilitating ecosystem recovery ranging from natural regeneration to various intermediate intervention, such as assisted regeneration and enrichment planting, to intensive planting. This would lead to reduced overall costs compared to our study which was biased towards resource intensive restoration methods. Second, more information is needed on whether an economy of scale could reduce restoration costs. We were unable to evaluate these questions as most of the projects in our survey were small, and past studies show mixed results on whether larger projects are less costly on a per area basis (Bayraktarov et al., 2016; Strassburg et al., 2019).

Our study advances the implementation of conservation science and management by moving ambitious ecosystem restoration programs beyond the simplistic definition of a target area. Our results allow Brazilian policymakers to estimate the cost of restoration commitments and plan their implementation under a more realistic context, in which resources are limited and fundraising is critical. Our detailed cost

estimates used in combination with analyses of spatial variation in land opportunity costs and local site resilience (e.g. Shoo et al., 2017; Toomey et al., 2017; Brancalion et al., 2019; Strassburg et al., 2019), enable investors, policy makers, restoration professionals, and local communities to work together to prioritize restoration locations and tailor methods to site conditions to most cost-effectively implement large-scale restoration programs (Table S6). Our approach, along with efforts to provide financial restoration incentives and generate income from restoration (Table S6), will help to surmount the major financial barriers for upscaling restoration.

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 associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2019.108274>.

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