Strategic approaches to restoring ecosystems can triple conservation gains and halve costs

Bernardo B. N. Strassburg[1,2,3], Hawthorne Beyer[4], Renato Crouzeilles[1,2,3], Alvaro Iribarrem[1,2], Felipe Barros[2], Marinez Ferreira de Siqueira[5], Andrea Sánchez-Tapia[5], Andrew Balmford[6], Jerônimo Boelsums Barreto Sansevero[7], Pedro Henrique Santin Brancalion[8], Eben North Broadbent[9], Robin Chazdon[2,10,11], Ary Oliveira Filho[12,] Toby Gardner[2,13], Ascelin Gordon[14], Agnieszka Latawiec[1,2,15,16], Rafael Loyola[17], Jean Paul Metzger[18], Morena Mills[19], Hugh P. Possingham[20,21], Ricardo Ribeiro Rodrigues[22], Carlos Alberto de Mattos Scaramuzza[23], Fabio Rubio Scarano[3,24], Leandro Tambosi[25], Maria Uriarte[26]

1 – Rio Conservation and Sustainability Science Centre, Department of Geography and the Environment, Pontifícia Universidade Católica, 22453900, Rio de Janeiro, Brazil

2 – International Institute for Sustainability, Estrada Dona Castorina 124, 22460-320, Rio de Janeiro, Brazil

3 – Programa de Pós Graduacão em Ecologia, Universidade Federal do Rio de Janeiro, 21941-590, Rio de Janeiro, Brazil

4 – ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences, University of Queensland, St. Lucia, 4072, Queensland, Australia

5 – Botanical Garden Research Institute of Rio de Janeiro, Rua Jardim Botânico 1008, 22470-180 Rio de Janeiro, Brazil

6 – Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2 3EJ, UK

7 – Department of Environmental Science, Instituto de Florestas, Federal Rural University of Rio de Janeiro, Rodovia BR 465, Km 07, s/n - Rural, Seropédica, 23890-000, Brazil

8 – Departamento de Ciências Florestais – Esalq/USP, Av. Pádua Dias 11, 13.418-900, Piracicaba, SP, Brazil

9 – Spatial Ecology and Conservation Lab, School of Forest Resources and Conservation, University of Florida, Gainesville, Florida, USA, 32611

10 – Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N. Eagleville Road, Unit 3043, Storrs, CT 06269-3043, U.S.A.

11 – World Resources Institute, Global Restoration Initiative, 10 G Street, NE Suite 800, Washington, D.C. 20002 - USA

12 – Department of Botanic, Federal University of Minas Gerais, Av. Antônio Carlos, 6627, 31270-901, Belo Horizonte, MG, Brazil

13 – Stockholm Environment Institute, Linnégatan 87D, 115 23 Stockholm, Sweden

14 – School of Global Urban and Social Studies, RMIT University, GPO Box 2476 Melbourne, Australia 3001

15 – Institute of Agricultural Engineering and Informatics, Faculty of Production and Power Engineering, University of Agriculture in Kraków, Balicka 116B, 30-149 Kraków, Poland

16 – School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom

17 – Laboratório de Biogeografia da Conservação, Departamento de Ecologia, Universidade Federal de Goiás, Goiânia, GO, Brazil

18 – Department of Ecology, Institute of Biosciences, University of São Paulo, Rua do Matão, 321, Travessa 14, 05508-900, São Paulo, SP, Brazil

19 – Faculty of Natural Sciences, Department of Life Sciences, Silwood Park, Imperial College London, London SW7 2AZ, UK

20 – The Nature Conservancy, 4245 Fairfax Drive, Arlington, VA 22203, USA

21 – The University of Queensland, St Lucia, QD, 4072, Australia

22 – Department of Biological Science, Escola Superior de Agricultura Luiz de Queiroz, University of São Paulo, Avenida Pádua Dias n. 11, Centro, 13418900 Piracicaba, SP, Brazil

23 – Department of Ecosystems Conservation, Brazilian Ministry of the Environment (MMA). Ed. Marie Prendi Cruz, SEPN 505 Norte, Bloco "B" 4 º andar sala 416, 70.730-542, Brasília, Brazil

24 – The Brazilian Foundation for Sustainable Development, R. Eng. Álvaro Niemeyer, 76 - São Conrado, Rio de Janeiro - RJ, 22610-180, Brazil

25 – Centro de Engenharia, Modelagem e Ciências Sociais Aplicadas, Federal University of ABC, Av. dos Estados, 5001, Bairro Santa Terezinha, Santo André, SP, Brazil

26 – Department of Ecology, Evolution and Environmental Biology, Columbia University, 116th St & Broadway, New York, NY 10027, USA

International commitments for ecosystem restoration add-up to one-quarter of the world´s arable land[1]. Fulfilling them would ease global challenges such as climate change[2] and biodiversity decline[3], but could displace food production[4] and impose financial costs on farmers[5]. Here we show a novel restoration prioritization approach capable of revealing these synergies and trade-offs, incorporating for the first time ecological and economic efficiencies of scale and modelling specific policy options. We show, for an actual large-scale restoration target of the Atlantic Forest hotspot, that our approach can deliver an eightfold increase in cost-effectiveness for biodiversity conservation compared to a baseline of non-systematic restoration. A compromise solution avoids 26% of the biome's current extinction debt of 2864 plant and animal species (an increase of 257% compared to the baseline), and sequesters 1 billion tonnes of CO_2Eq (a 105% increase) while reducing costs by US$ 28 billion (a 57% decrease). Seizing similar opportunities elsewhere would offer substantial contributions to some of humankind´s greatest challenges

Ecosystem restoration can provide multiple benefits to people and help to achieve multiple Sustainable Development Goals[6-8], including climate change mitigation and nature conservation. For these reasons, 47 countries have collectively committed to have 150 and 350 million hectares of degraded lands under restoration by 2020 and 2030, respectively, and have included major restoration targets in national pledges to the Paris Climate Agreement[1]. Restoration, however, has both direct costs – those required for implementation and maintenance – and indirect costs, including the loss of revenues from foregone agricultural production. Crucially, these restoration costs and benefits present trade-offs and synergies that vary greatly across space[9-11]. In the context of safeguarding existing habitats there has been considerable progress in understanding some of these trade-offs[3], with the field of Systematic Conservation Planning (SCP) providing methods for spatial prioritisation that maximize benefits while minimizing costs[12]. Despite some recent efforts[9-10,13], applications of comprehensive SCP approaches to complex large-scale restoration problems with multiple objectives remain sparse.

Here we present a novel restoration prioritization approach based on Linear Programming (LP) to solve customized complex restoration problems at large scales. We apply this approach to solve a problem of global significance that will inform restoration policy and practice at a national scale in the Brazilian Atlantic Forest hotspot[14-15], a highly deforested and fragmented region poised to undergo one of the biggest large-scale restoration efforts[16]. We identify exact cost-effective solutions that consider multiple benefits, costs and policy scenarios and investigate: i) trade-offs in benefits and costs across different scenarios, and ii) the impacts of increasing the size of restoration projects. LP can find exact solutions that can perform at least 30% better than mainstream SCP software[17]. It can also be more fully customized, allowing the incorporation of complex aspects of restoration relevant to particular socioecological contexts. In this application, we aimed at maximising restoration benefits for biodiversity conservation and climate change mitigation while reducing restoration and opportunity costs.

We divided the biome into 1.3 million planning units of 1 km^2. For biodiversity conservation, benefit was measured as the reduction in projected extinctions owing to habitat restoration[18]. We gathered and analysed species occurrence data in the Atlantic Forest and, following data cleaning, identification of endemism by specialists and model selection (Methods), generated potential species occurrence models for 785 species of plants, birds and amphibians endemic to the Atlantic Forest, representing the best set of biodiversity data currently available for this biome. We then calculated the marginal contribution of each hectare restored to reducing each species' extinction probability, based on a function[11,19] derived from the species-area relationship. The benefit of habitat restoration to each species is dynamic in that the value of restoring additional habitat for that species diminishes as the total area of habitat increases. Our approach explicitly accounts for this effect, though for visualisation purposes we can aggregate the restoration value of each planning unit across all species, thereby generating a biodiversity conservation benefits surface (Extended Data Fig. 1). Our species data confirmed the severity of the biodiversity crisis underway in the Atlantic Rainforest, with an estimated 27-32% of the biome's endemic species currently committed to extinction (2,621-3,107 plants and animals, see Methods). For climate change mitigation, benefit was measured as the potential aboveground carbon sequestration in the first 20 years following habitat restoration[20]. We produced the climate change mitigation surface (Extended Data Fig. 2a) by applying and extending a recently published empirical model of the carbon sequestration potential of restoration[20] to the whole of the Atlantic Rainforest. Restoration implementation costs, including maintenance and monitoring, were estimated based on a survey with restoration companies active in the Atlantic Rainforest, spatially adjusted by a proxy for natural regeneration potential based on a recently published model for ecological uncertainty of tropical forest restoration success[21] (Methods). Opportunity costs, a measure of potential conflict with agricultural production, were estimated based on land acquisition costs and spatial distributions of agriculture and pasturelands[22]. A restoration costs surface (Extended Data Fig. 2b) was built based on these two costs (hereafter referred to as total cost).

We also introduced advances regarding the impacts that the scale of a restoration project has on its costs and benefits. Costs per unit area restored reduce with increasing area of the restoration project, so we modelled these economies of scale using field evidence on how unitary costs fall as projects grow (Methods and Extended Data Fig. 3). The size of the restoration project also affects ecological outcomes, an effect which we term “ecologies of scale”, such as biomass accumulation through edge effects. We also incorporated this into the prioritization using empirically derived edge-effects estimate for Atlantic Forest remnants[23].

The Brazilian Native Vegetation Protection Law (popularly known as the “the New Forest Code”[24]) requires Atlantic Forest farmers to keep at least 20% of their farms under native vegetation. Farmers currently below this threshold must meet it either by restoration in their own farms, or by financing conservation or restoration offsets elsewhere within the biome. If enforced, it could lead to up to 5.17 million hectares of restoration[24], which is the restoration target area we used in all scenarios. This represents approximately 4% of the original area of the biome, which has lost 73-84% of its native vegetation cover. This target was chosen so that the maps produced could guide restoration efforts even if all farmers decided to compensate their debts by financing restoration efforts outside their farms. Our dynamic approach allocates this target area in 20 steps, so our restoration priority maps can guide restoration projects with smaller targets as well (Methods and Extended Data Fig. 4). In our “baseline scenario”, farmers restore this target inside their own farms until this minimum threshold is met. In a large set of alternative scenarios we simulate different ways of prioritizing benefits and costs of restoration, considering variation in the size of restoration projects. These 362 alternative scenarios focus on combinations of maximizing the benefits for biodiversity conservation and climate change mitigation, while minimizing costs (Methods and Extended Data Fig. 5). We also investigate the impacts of limiting offsets to the farmer’s own state (a policy option currently being pursued by a few Brazilian states).

Results

The baseline scenario has the worst performance for biodiversity conservation, the fourth worst for carbon sequestration and had the highest costs across all 363 scenarios analysed (“Baseline”, in Fig. 1). This allocation would avoid 7.2% of the projected extinctions (for the central estimate, or 6.8% for the lower and 7.7% for the upper estimate) and sequester 0.5 billion tonnes of CO_2Eq (for the central estimate, or 0.4 for the lower and 0.6 for the upper estimate; further lower and upper estimates are presented in extended Data Tables 1 and 2) at a total cost of US$ 50.2 billion. This poor outcome suggests that pursuing alternative spatial allocations for restoration would deliver greater benefits at lower costs, therefore aligning species conservation and climate mitigation targets with the farmer’s interests.

One of the advantages of compensation outside farms is the potential to increase the size of individual restoration projects – and this has a very strong positive impact on cost-effectiveness, due to both economic and ecological efficiencies of scale (Fig. 2). First, economies of scale result in a substantial reduction in unitary restoration costs, with a 57% drop when projects grow from 1 to 100 hectares (Fig. 2a). Second, ecologies of scale lead to improved efficiencies in climate mitigation outcomes for larger projects (Fig. 2b), with 100-hectare projects sequestering 58% more than the same area of 1-hectare ones. The combination of both economic and ecological efficiencies of scale results in synergistic and marked increases in cost-effectiveness for larger restoration projects (Fig. 2c), with carbon prices needed to cover restoration costs dropping 73% when increasing projects from 1 to 100 hectares – a 268% improvement in cost-effectiveness. These scale impacts occur across all scenarios and are independent of the relative weights of the benefits. Although we did not model the impacts of restoration projects’ size on biodiversity conservation, we expect the same to apply to biodiversity outcomes given the importance of edge-effects on populations in small forest fragments[25].

The other advantage of compensation outside farms is implementing restoration in areas that would maximise benefits, thus improving the likelihood of long-term socio-ecological success. Allocations based on maximising a single benefit reveal the maximum outcomes that restoration prioritisation can achieve for each benefit. For biodiversity conservation, results are striking: 29.7% of the species committed to extinctions could be saved ("Maximum Biodiversity", in Figs. 1a and 1b), an improvement of 311% in relation to the baseline scenario. Likewise, a focus on climate change mitigation could sequester up to 1.3 GtCO_2Eq ("Maximum Climate", in Figs. 1a and 1c), a 174% increase from the baseline scenario. Focusing on costs would reduce them to US$ 15.2 billion ("Minimum Costs", in Figs. 1a and 1d), a 69% saving on the baseline scenario. But despite the marked improvements in relation to baseline, these single-focus allocations have mixed and varied outcomes when all benefits and costs are considered. For instance, aiming solely for biodiversity conservation benefit yields a much larger fraction of the greatest possible climate change mitigation benefit (75% of those under "Maximum Climate") than the reverse, with only 51% of the "Maximum Biodiversity" benefit being captured by the climate-focused allocation (Fig. 1). The latter metric is much higher for birds (72%), with plants benefiting the least (45%) from the climate-focused solution (extended Data Figure 6). The biodiversity-focused solution would cost US$ 35 billion (delivering 44% of the potential costs savings and resulting in benefit-costs ratios of US$ 9 million per species saved and US$ 35 per tonne of CO_2Eq) whereas the climate-focused solution would cost US$ 29 billion (59% of the cost-savings achieved by "Minimum Costs" and benefit-costs ratios US$ 15 million per species saved and US$ 23 per tonne of CO_2Eq).

In turn, restoration plans designed solely to minimize costs have a very poor environmental performance. The "Minimum Costs" scenario underperforms substantially for climate mitigation and biodiversity conservation. It would yield only 25% and 42% of the potential biodiversity and climate mitigation benefits, respectively. These outcomes are even worse than those under a random allocation of restoration efforts, which would on average achieve 29% and 62% of the potential biodiversity and climate mitigation benefits, respectively ("Random", Fig 1).

Compromise solutions can simultaneously deliver a substantial fraction of the maximum outcome for each benefit. Our approach allowed us to combine the efficiencies of scale with multicriteria spatial prioritisation to systematically generate and evaluate solutions that combine different weights for benefits and costs, generating efficiency frontiers (Fig 1). The outer frontier is generated by eliminating the costs component from the algorithm, whereas the "Cost-effective frontier" is produced by maximising cost-effective benefits for biodiversity and climate change mitigation. One of the solutions on the cost-effective efficiency frontier ("Compromise" in Figs. 1a and 1e) increases biodiversity benefits by 257% (equivalent to 94% of those achieved under "Maximum Biodiversity"), improves by 105% the climate change mitigation benefit (79% of "Maximum Climate"), and reduces costs by 57% (83% of the reduction achieved by "Minimum Costs"), when compared to the baseline scenario. This translates into an eightfold increase in cost-effectiveness for biodiversity conservation.

These compromise solutions arise from the concave shape of the efficiency frontier curves (Fig. 1a), which indicate that when departing from single-focus solutions, large gains for one benefit can be achieved at relative modest cost to others. Indeed, moving from "Maximum Climate" to "Compromise" results in a loss of 20% in climate change mitigation but a gain of 95% in avoided extinctions. In absolute terms, sequestering 0.27 $GtCO_2Eq$ less would save 411 animal and plants from extinction, when applying the relative reduction in extinctions to the overall extinction debt of plants and animals in the biome (Extended Data Table 1), a trade-off ratio of 1 animal or plant extinction avoided for every 0.7 million tonnes of CO_2Eq not sequestered. Given biodiversity's key role in driving the productivity of ecosystems[26], such compromise might result in climate mitigation gains in the long term. Climate change adaptation might also benefit from improved ecosystem-based adaptation[27] due to more resilient ecosystems. Furthermore, it can be argued that species extinctions are irreversible losses whereas reductions in carbon sequestration are reversible and can be compensated for, suggesting that greater importance should be given to the former. Revealing trade-offs in units that people can relate to helps to inform the stark decisions that need to be made in a context of scarcity.

The substantial reductions in total costs arise from the combination of efficiencies of scale and the ability to prioritise areas with lower opportunity costs and higher potential for natural regeneration. The relative contribution of each of these factors varies across scenarios (Fig. 4). In comparison with the baseline scenario, assumed to comprise 1-hectare projects, economies of scale reduce costs by US$ 23.9 billion when moving to 100-hectare projects. Identifying areas with lower opportunity costs reduces these by between US$ 10.8 billion ("Compromise") and US$ 17.0 billion ("Minimum Costs"), demonstrating great scope for avoiding restoration conflicts with agricultural production. The strong impact of natural regeneration to reduce restoration costs is felt across all scenarios, reducing restoration costs by 56% (or US$ 35 billion) in the baseline scenario, 76% (or US$ 29 billion) in the "Minimum costs" and 74% (or US$ 28 billion) in the "Compromise" scenario.

Spreading restoration across wider areas by considering that not all deforested lands in priority landscapes would be restored might be more feasible in practice and would not have overly large impacts on the benefits. Indeed, restricting the maximum restoration allowed in each planning unit has moderate impacts for biodiversity outcomes and small ones for carbon. When restricting the proportion of the planning unit that can be reforested to 65% and 35%, biodiversity outcomes fall by 6% and 17% respectively (Extended Data Figure 9). For climate mitigation, the same restrictions result in reductions of 2% and 6% respectively (Extended Data Figure 9). These decreased outcomes arise from selecting areas that have comparatively lower priority for those benefits, as these caps lead to restoration being allocated beyond the very highest priority planning units.

Our results also provide important insights for considering how to share the costs of achieving the restoration targets between farmers and the wider society. Benefits from restoration are shared between farmers and the wider society (in Brazil and elsewhere), whereas the opportunity and restoration costs would be borne by the farmers, as the target being analysed here arises from past deforestation beyond legal limits. On the one hand, the overall cheapest solution for farmers ("Minimum Costs") would be US$ 19 billion cheaper than a solution that combines large benefits for biodiversity and climate change mitigation without considering costs ("Environment Only"), so it could be argued that the collective benefits would justify that society pay for this difference if the latter solution is to be achieved. Payments for Ecosystem Services (PES) schemes are a way to incentive farmers to pursue options more beneficial to the wider society. Carbon-based incentives of US$ 38/t CO_2Eq, species-based incentives of US$ 30 million/extinction avoided or a combination of both would be enough to pay for the difference in costs. On the other hand, the "Environment Only" solution is US$ 14 billion cheaper than the baseline scenario, which would have to be paid individually by farmers. Therefore, it could be argued that farmers could choose intermediate solutions, since this reduction in costs is made possible by the Brazilian society decision in 2012 to allow compensation outside their farms. The intermediate “Compromise” solution still delivers reasonable environmental outcomes and, being US$ 7 billion more expensive than the cheapest possible but US$ 29 billion cheaper than the baseline scenario, could be seen as a reasonable compromise for farmers to invest in. Alternatively or complementarily, carbon incentives of US$ 15/t CO_2Eq, species-based incentives of US$ 9 million/extinction avoided or a combination of both would be enough to cover the difference from the cheapest solution. It is important to highlight that restoration projects can lead to positive financial returns based on revenues from sustainable management of timber or non-timber forest products, potentially complemented by PES schemes[5].

Introducing broad scale spatial restrictions on restoration – such as allowing off-farm compensation but only within state borders – generates more nuanced outcomes. On the one hand, constraining restoration by state borders leads to worse outcomes when compared to the unconstrained version of each goal, whether assessed for biodiversity conservation (10% lower), climate change mitigation (14% lower) or cost minimization (17% more expensive) (Extended Data Table 1). On the other hand, a state-constrained cost-minimization scenario would yield 103% and 44% higher returns for biodiversity and climate respectively, compared with an entirely unconstrained “Minimum Costs” scenario (Extended Data Table 1). So if the alternative is that farmers offset in the cheapest areas of the biome, constraining their choices to the cheapest areas in their home states would bring substantially higher environmental benefits at modest additional cost.

Discussion

It is important to highlight that while the baseline scenario performs very poorly in terms of all three outcomes analysed in this study, having smaller patches of restoration dispersed across the entire biome would have other benefits. For instance, the provision of local ecosystem services such as soil retention, improved water quality and pollination tends to be more widely distributed across the landscapes with small and dispersed restored sites[28], while the ecological equivalence between remnants , the representation of different ecological communities and community integrity across the biome[29] can be higher. Crucially, the Law of Native Vegetation Protection also mandates that mountaintops and riparian areas should be preserved, a requirement estimated to lead to another 5.2 million hectares of restoration. As these are fixed in space (so not subject to spatial prioritisation) and dispersed throughout all watersheds of the biome, the combination of restoring legal reserves in priority areas and riparian and mountaintop areas throughout the biome could deliver increased local, regional and global benefits at lower costs.

Although we strived to apply recognised best practices in all stages of our analyses, some limitations should be highlighted (see methods for further discussions). Some species distribution models relied on a relative small number of occurrences and all present the usual limitations associated to correlative models. The approach to estimate extinction risk is an imperfect approximation and our climate benefits did not include belowground biomass or soil carbon. Also importantly, shifts in species distribution as a result of climate change were not taken into account.

The technical advances and high degree of customisation to context-specific policies and goals led the Brazilian Ministry of Environment to decide to use the decision supporting tool and the maps introduced here as the key prioritization information for restoring the Atlantic Rainforest, and to commission the replication of our approach to the other five Brazilian biomes as part of the National Plan for Native Vegetation Recovery - PLANAVEG[30]. The potential of this approach for easily exploring large numbers of scenarios will be of particularly importance for two PLANAVEG strategies, the Spatial Planning & Monitoring and Finance. These ongoing biome-specific initiatives are tapping into our approach's ability to include customised sets of benefits and costs, such as water (Atlantic Forest); farmers income (originated from ecosystem services and forest products in all biogeographical regions); pollination (Amazon), firewood production (Caatinga) and ecotourism-related species (Pantanal). Furthermore, the time-efficiency of the linear programming approach permits assessment of thousands of variations of factor weightings in a few hours (for applications of the size and complexity presented here), allowing stakeholders to select the most desirable allocations based on final outcomes, avoiding the often-contentious task of selecting relative weights a priori.

To fulfil its promise as a substantial contributor to overcoming major global and local sustainable development challenges, large-scale restoration needs to carefully balance its multiple costs and benefits with diverse stakeholders' interests. Our results show that substantial benefits for biodiversity conservation and climate change mitigation can be achieved in the Atlantic Forest alongside marked reduction in total costs. They illustrate that multicriteria spatial planning can be an important tool to reveal and manage the trade-offs and synergies involved in and, consequently, increase the impact and feasibility of large-scale restoration.

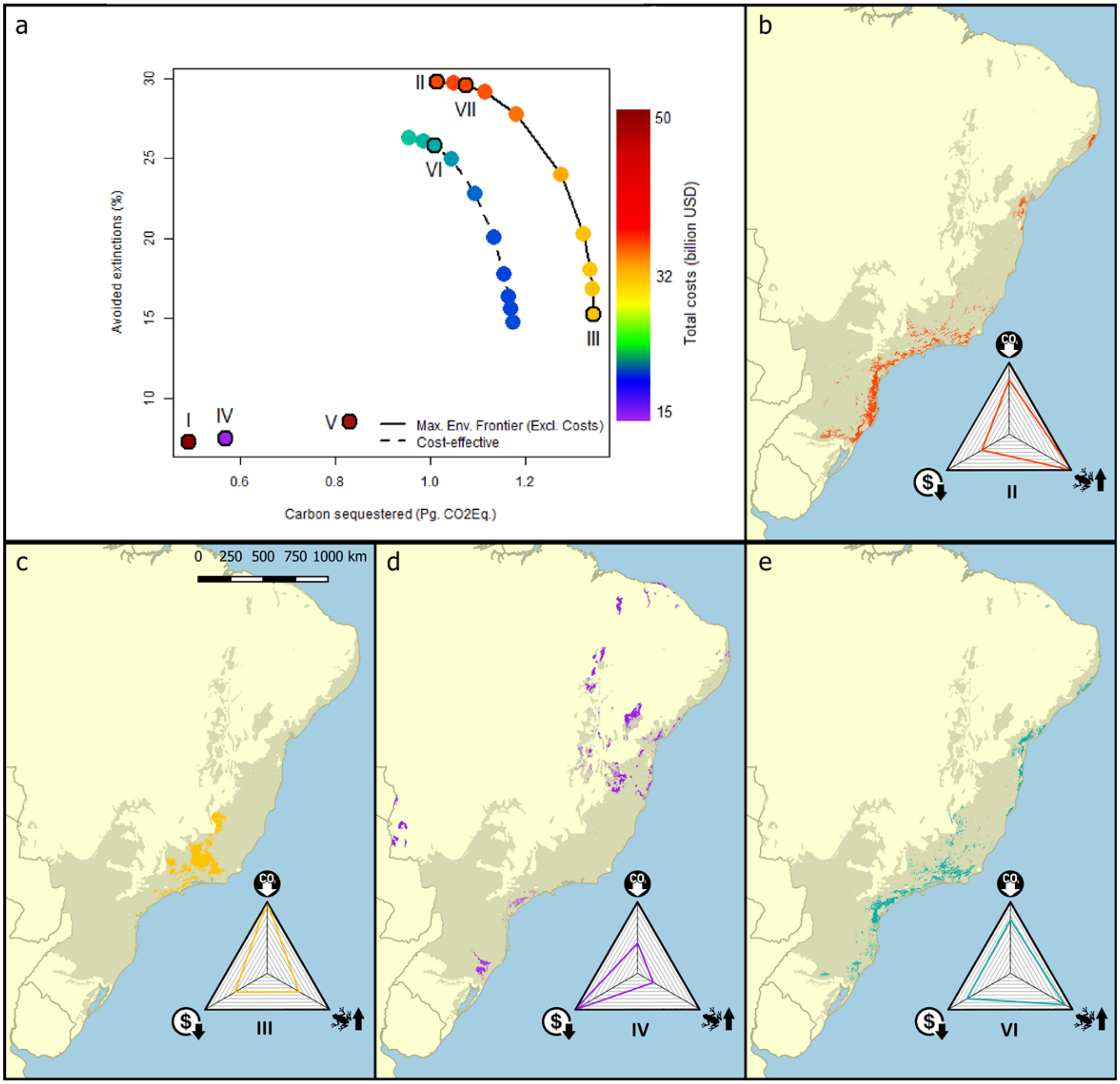

Figure 1 - Spatial configurations and outcomes for climate change mitigation, avoided extinctions and total costs of selected scenarios. In panel **a,** point "I" corresponds to the baseline scenario without offsets, "II" is the "Maximum Biodiversity" scenario, "III" is "Maximum Climate; "IV" is "Minimum Costs", "V" is "Random", "VI" corresponds to the "Compromise" scenario and "VII" to a "Environment Only" scenario. The full (outer) line connects points in the efficiency frontier of environmental benefits, when excluding costs from

the prioritisation algorithm. The dashed (inner) line connects allocations for the cost-effective frontier. Panels **b-e** present the spatial configurations and radar diagrams of outcomes for the “Maximum Biodiversity”, “Maximum Climate, “Minimum Costs” and “Compromise” scenarios, respectively. Colours are related to the cost scale presented in panel **a**.

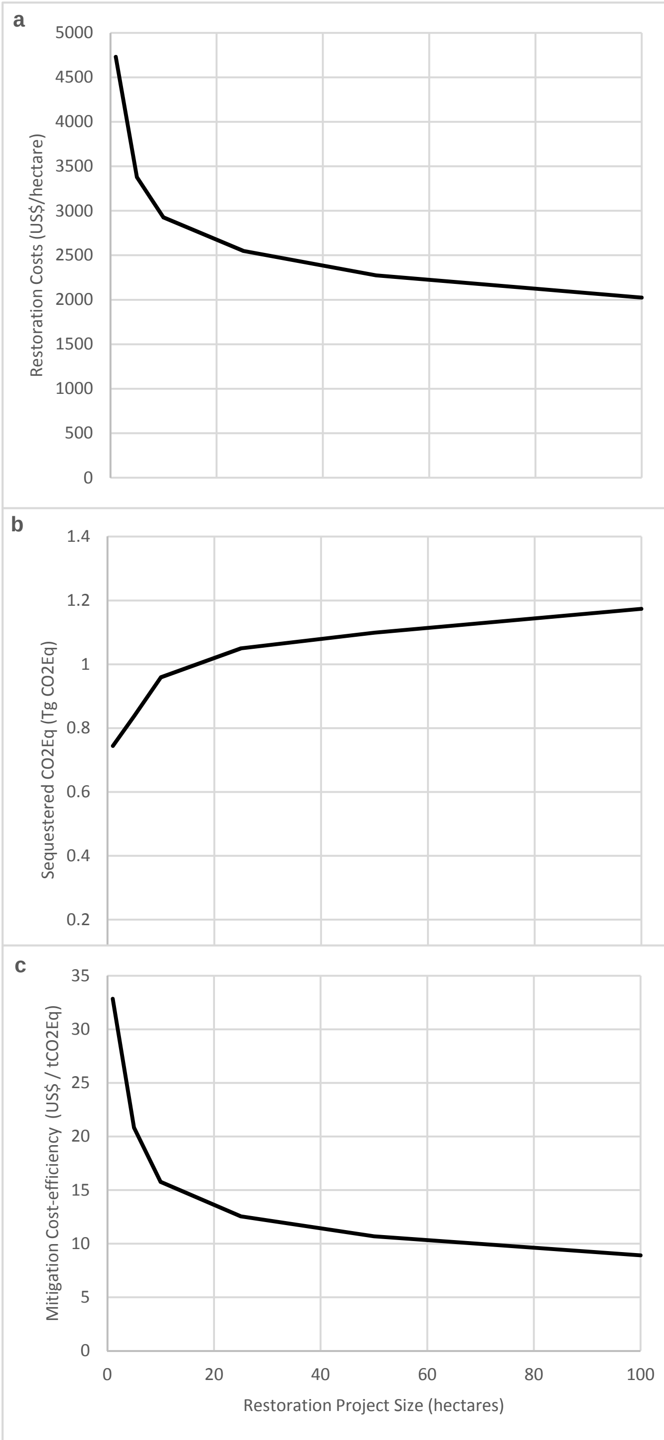

Figure 2 - Impacts of economic and ecological efficiencies of scale on cost-effectiveness. a. shows the relation between increasing restoration project sizes and the restoration costs per unit area; **b.** shows the relation between increasing project size and the total CO_2Eq sequestered in the "Maximum Climate" scenario; **c.** shows their combined effect on mitigation cost-effectiveness as project sizes grow. All data presented are results from the "Maximum Climate" scenario.

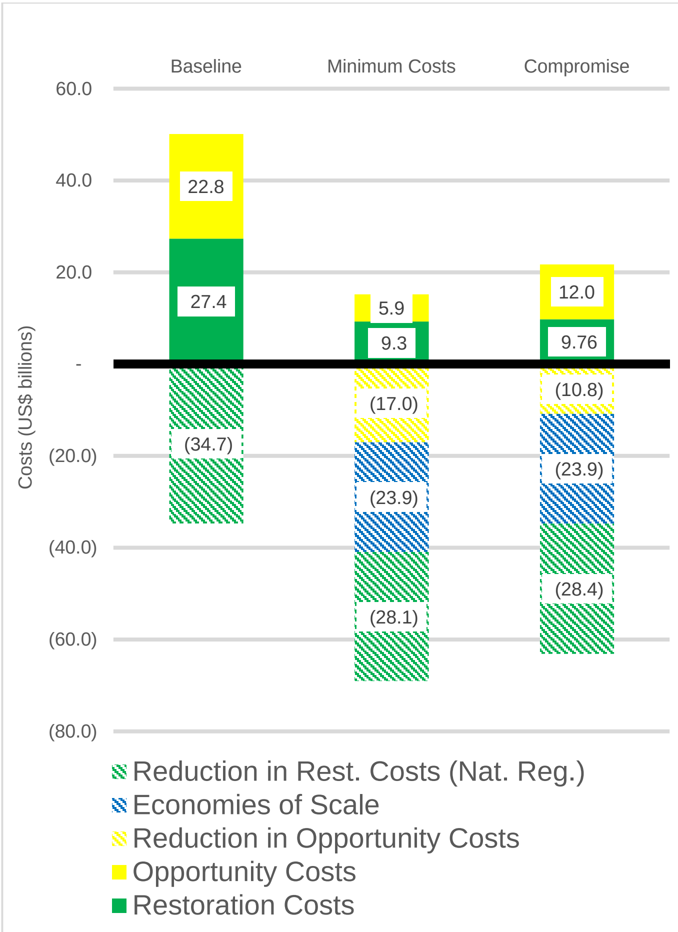

Figure 3 – Impacts of economies of scale and of spatial prioritization for reducing opportunity and restoration costs across different scenarios. Filled rectangles are actual restoration (green) and opportunity (yellow) costs incurred in each scenario. Diagonally stripped rectangles represent reductions in costs due to natural regeneration (green stripes), reduction in opportunity costs (yellow stripes) and economies of scale (blue stripes).

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Author Contributions

BBNS conceived the study, coordinated the development of the multicriteria approach and wrote the first version of the paper. HB, BBNS, RC and AI led the optimisation modelling, MFS, FB, AST developed the environmental niche modelling; BBNS, HB, RC, AI, MM, HPP, FB, MFS, AB, JB, PHSB, RC, AG, AL, JPM, RRR, CAMS, FRS, LT, TG and MU developed the multicriteria prioritisation approach; RL, JPM and AOF contributed biodiversity data, RC and ENB developed the climate mitigation surface, CAMS coordinated the interface with policy applications; all authors analysed the results and provided input into subsequent versions of the manuscript.

Author Information

Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Correspondence and requests for materials should be addressed to B.B.N.S. (b.strassburg@iis-rio.org).

Methods

In this study, we developed a multi-criteria spatial restoration prioritization approach for the Brazilian Atlantic Forest hotspot to investigate alternative restoration scenarios. We simulated the restoration of approximately 5.17 Million hectares (estimated deficit of Legal Reserve in the Atlantic Forest[24]) to: 1) quantify variation in costs and benefits of restoration among a range of possible scenarios governing where restoration occurs; 2) quantify trade-offs among costs and benefits in order to identify good compromise solutions; 3) quantify the effects of economies of scale and analogous ecologies of scale impacts on carbon sequestration by using restoration block sizes of 1, 5, 10, 25, 50 or 100 ha; and 4) quantify the effects of restricting the maximum proportion of land that can be restored within each planning unit (up to 35, 65 and 100%).

Our multi-criteria spatial restoration prioritization approach was based on five main steps: 1) conduct consultations with representatives of the Ministry of Environment and other stakeholders of the Atlantic Forest biogeographical region to identify critical variables to be included in our modelling and to develop restoration scenarios that reflect the policy objectives and multi-stakeholder preferences; 2) gather and model variables to be used as inputs; 3) develop a novel multi-criteria spatial restoration prioritization framework implemented as an Integer Linear Programming problem (hereafter ILP); 4) simulate restoration scenarios; and 5) analyse and interpret the solutions and their trade-offs.

We developed spatial surfaces for the three benefits of biodiversity – conservation, climate change mitigation and costs reduction. We detail each of these below, followed by explanations of the scenarios analysed and the optimisation model itself.

Biodiversity conservation benefits

Benefits to biodiversity conservation are quantified using species extinction functions reflecting diminishing returns associated with increasing areas of habitat for each species (Extended Data Figure 1). This function is based on a re-working of the Species-area relationship and operates at the level of individual species[18]. This approach is imperfect, as it ignores the possibility of negative density-dependence at very low population sizes, and says nothing about the time scale of resulting extinctions, which will vary with species' life history and ecology. However unlike simpler formulations, it takes account of the non-linearity of the response of persistence to changes in population size, and has been used in several similar studies[11,18,19]. If existing habitat area is small there is a large benefit to increasing that area, but as the area of habitat increases there is a diminishing benefit for the addition of more habitat area. Following reference #11, the change in extinction risk (*r*) for each individual species as a function of habitat area was modelled as

$$r = 1 - (x/\mathrm{A}_0)^z \qquad (1)$$

where A_0 is the current habitat area, x is additional habitat area that would arise from habitat restoration, and the power z describes the rate of diminishing returns in value of additional area at reducing extinction risk. We used $z = 0.25$ for the central estimates presented in the main text (following references #11, 18 and 19) and z=0.15 and z=0.35 for sensitivity analyses presented in the Extended Data. To implement these curves in an ILP framework we quantify benefit as the tangent to these curves at a given current area of species habitat and update these benefit values after solving each of the 20 increments of total restoration area target.

Ecological niche models

In order to identify areas that, if restored, would be suitable habitat for each species, we developed ecological niche models for endemic amphibians, birds and woody plants in the

Brazilian Atlantic Forest. We used the potential species distribution instead of the current species distribution because restoration would expand available habitat area for the species. This is a different approach than usual in conservation prioritization where the aim is to conserve current habitats by using species' distribution that falls within native vegetation.

Species occurrence data

We collated all freely available occurrence data on endemic amphibians, birds and woody plants in the Brazilian Atlantic Forest. Data on amphibian occurrence was obtained from[31], with updates from the authors, and comprised 114 endemic species (3,786 occurrences). Data on bird occurrence was obtained from the Global Biodiversity Information Facility database[32], and comprised 223 endemic species (12,085 occurrences). Data on plants occurrence was obtained from NeoTropTree and SpeciesLink[33] , and comprised 846 endemic species and 44, 024 records. The original plant names were based on the NeoTropTree database[34] and updated according to the List of Species of the Brazilian Flora[35], using R package 'flora' [36], which is based on the List's Integrated Publishing Toolkit database[37].

We cleaned the data for each species by deleting: i) records that fell out of the environmental layers, ii) duplicated records, iii) non-duplicated records that fell in the same planning unit (1 km-pixel). The species' endemism status was assessed by consulting amphibian experts, following reference #38 for birds, and the Brazilian Flora 2020 for woody plants.

Environmental data

The initial environmental dataset was composed of 28 variables –the 19 bioclimatic variables from Worldclim[39], four CGIAR CSI geohydrologic variables (actual evapotranspiration, aridity index, soil water balance and potential evapotranspiration[40]) and five USGS topographic variables (elevation, slope, aspect and topographic index[40]). All variables had a spatial resolution of 1 km². Since aspect is a circular variable, its sine and cosine were calculated to be used as two different variables instead.

We summarized these variables into ten orthogonal variables, calculated through a PCA of the whole raster set. These account for 95% of the overall environmental variation in the BAF. The PCA variables were used to reduce errors in the modelling process, caused by the spatial autocorrelation of presence data or the multi-collinearity of the environmental predictors[41-42].

Ecological niche modelling methods

Preliminary ecological niche models were produced to define the best algorithms to run the final models. The tested algorithms were Bioclim, Domain, Generalized Linear Models, MaxEnt, RandomForest, and Support Vector Machines. Their performance was tested by calculating the True Skill Statistics (TSS)[43]. During the preliminary round of models only MaxEnt, Random Forest and SVM showed average high TSS scores (>0.7) and low variance (Extended Data Figure 7). The final models were thus run using these three algorithms. TSS values for each algorithm used in the Environmental Niche Modelling varied little across the three biodiversity groups (Extended Data Figure 8).

For each species, random pseudo-absence points were sorted within a maximum distance buffer (i.e. the radius of the buffer is the maximal geographic distance between the occurrence points). This procedure reduces the modelling background area, assuring better estimates, once pseudoabsences were sampled only in areas where species could disperse[44-46] at the same time controlling the low prevalence associated with generating pseudoabsences inside large range areas.

Species were modelled using a three-fold cross-validation procedure, to guarantee a minimum number of presence records in the test set due to the small number of samples for some species. For each partition and algorithm, a model was fitted and its performance was tested by calculating TSS. Only models with TSS > 0.7 were retained. As a consequence, at the end of this modelling phase 51 amphibian species, 122 bird species, and 612 woody plant species endemic to the Brazilian Atlantic Forest composed the final potential richness maps. Retained models were cut by the threshold that maximizes their TSS and ensemble models were built by the majority consensus rule (i.e. area where at least half of the algorithms predict a potential presence of the species[47]), resulting in a binary map of species potential distribution. The steps described above were taken in order to reduce some of the limitations of the species distribution models, such as the fact that they are merely correlative, and not mechanistic models, and to control overfitting and inflated evaluation statistics when species are very restricted compared to the total geographic area..

The modelling was performed using ModelR[48], a set of R scripts for species distribution model fitting and assessment based on packages, XML[49], dismo[50], raster[50], rgdal[51], maps[52], rgeos[53], randomForest[54], and e1071[55].

Climate mitigation Benefits

We built a potential above ground biomass recovery map for the Brazilian Atlantic Forest, which is a proxy for above ground potential carbon sequestration in degraded areas (Extended Data Figure 2). The map has a resolution of 1 km^2 and followed the methods of reference #[20]. That study included three biomes: 1) tropical and subtropical moist broadleaf forests, 2) tropical and subtropical dry broadleaf forests, and 3) tropical and subtropical coniferous forests[20]. These biomes were defined based on a map of world ecoregions obtained from the Nature Conservancy[56]. Total annual precipitation was calculated by summing the individual monthly totals provided by WorldClim[57]. Data for mean annual rainfall (defined as the average of 1950–2000) and rainfall seasonality were obtained at a 30” resolution (approx. 1 km × 1 km) from WorldClim[57], and Climatic Water Deficit (CWD) was obtained from reference #[58].

We calculated the total potential above ground biomass recovery (AGB) accumulation over 20 years of secondary forest growth (assuming that the initial year 0 condition was a fully cleared area), based on annual rainfall, rainfall seasonality, and CWD. The regression equation obtained by reference #[20] estimates AGB after 20 years based on best-fit models that incorporate climatic variables as follow:

$$AGB\_20y = 135.17 - 103{,}950 \times 1/\text{rainfall} + 1.521983 \times \text{rainfall seasonality} + 0.1148 \times CWD \quad (2)$$

where estimated AGB_20y indicates the absolute biomass recovery potential over 20 years based on chronosequence models[20]. Realized local rates of biomass recovery may vary because of differences in local soil conditions, land use history, the surrounding matrix, and availability of seed sources.

In order to insert uncertainty measures into this analysis, the raw data from reference #[20] was obtained and used to generate similar equations for the lower bound and upper bound of the 95% confidence interval. These estimates were incorporated into the optimisation and the corresponding results are presented in Extended Data Table 1.

We did not include changes in carbon stocks in the soils, as very few studies investigate the carbon accumulation or loss in soils following restoration in the Atlantic Rainforest[59]. We believe this is a conservative assumption. A recent global study showing the impact of land-use change on soil organic carbon[60]shows significant losses following deforestation in the Atlantic Rainforest. Further research would enable future studies to overcome this limitation.

Costs

The cost of land restoration for each area within the Brazilian Atlantic Forest was based on the opportunity cost for restoration of the land and the cost associated to restoring it, actively or passively. Opportunity cost is the potential loss of revenue from agriculture or livestock from areas being restored. We used the land acquisition cost as a proxy for opportunity cost, which is based on an established economic assumption that higher acquisition costs are due to land generating greater economic gains[22], as land acquisition cost should reflect the discounted future revenues from that land. We combined spatial data on the distribution of pasturelands and croplands (MMA unpublished data) with county level data on the land acquisition costs for these two categories[61].

The restoration costs vary widely according to the methods applied, ranging from lower-cost approaches for natural regeneration (passive or assisted) to higher-cost approaches for active restoration (e.g., tree plantings using nursery stock)[62-63]. Natural regeneration is the spontaneous recovery of native tree species that colonize and establish in abandoned fields, while active restoration requires planting of nursery-grown seedlings, direct seeding, and/or the manipulation of disturbance regimes (e.g. thinning and burning)[63].

The likelihood of an area requiring active or passive restoration is determined by socio-economic factors that determine the likelihood of an area been abandoned to regrowth and on ecological factors that determine the resilience of the ecosystem to disturbance. As this information is not available for the Atlantic Forest, we used the ecological uncertainty of forest restoration success for plant biodiversity[21] as a proxy for it. The recent global meta-analysis of reference #21 revealed a clear pattern of increasing the success of forest restoration (by comparing plant biodiversity in reference and restored/degraded systems) and decreasing uncertainty as the amount of forest cover increases. We built our map on the ecological uncertainty of forest restoration success by calculating the amount of forest cover surrounding each non-forested pixel within a buffer size of 5 km (the strongest scale of effect). We subsequently applied the negative non-linear equation of reference #[21] over the map. Finally, we standardized the values within each pixel (dividing its value by the highest value found across all pixels) to provide an index that varies from 0 (low uncertainty) to 1 (high uncertainty). Our restoration costs map therefore identifies areas where natural regeneration and/or active restoration methods are most likely to foster plant biodiversity recovery to similar levels found in reference systems (i.e. old-growth or less-disturbed forests).

Restoration cost (r) was calculated as

$$r = u \times c + f \qquad (3)$$

where u is the ecological uncertainty of forest restoration success, c is the cost of the full planting, and f is the cost of the fencing. Areas with lower ecological uncertainty of forest restoration success will be less expensive for restoration, i.e. will require less human intervention. The cost of full planting method (the most expensive method for active restoration) was obtained from[30]. Thus, our total costs map (Extended Data Figure 3) was produced by adding, for each panning unit, the values of the opportunity costs map with the values from the restoration costs map.

We also incorporated cost reductions based on economies of scale for restoration projects of different sizes for the first time. To understand how per-unit costs reduce with scale, we gathered information from five active forest planting companies in the Atlantic Forest. We obtained cost estimates for restoration projects of the following sizes: 1, 5, 10, 25, 50 and 100 ha. We then analysed how the average costs per project scaled with project size and fitted linear functions to this data (Extended Data Figure 4). In each of the size-related scenarios (corresponding to the six project sizes listed above), restoration was constrained to happen up to that size.

Other variables

Forest cover data was obtained from the map produced by[64], derived from TM/Landsat 5, ETM+/Landsat 7 or CCD/CBERS-2 images, available at a scale of 1:50,000 in vector format, and delimiting remnants ≥ 3 ha. This data was used to calculate the: i) proportion of existing forest (*f*) within a planning unit, ii) environmental deficits according to the Native Vegetation Protection Law, and iii) amount of area that could be restored within each planning unit. Our analysis was focused on areas where the native vegetation was forest, therefore excluding areas such as natural grasslands or mangroves. In addition to the forest cover, we also masked areas that could not be restored (e.g. urban areas, roads, lakes, etc) within each planning unit. All geographic information system data were converted to Albers projection to assure accurate area and distance calculations.

Prioritization model

Our objective function determines how much forest to restore in each planning unit in order to maximize ecosystem services benefits (biodiversity conservation and/or carbon sequestration) and/or minimizes total cost (opportunity and restoration costs). Specifically:

$$\begin{aligned} \max \quad & w_1 \sum_{i=1}^{N} \sum_{j=1}^{M} \frac{b_{ij}}{c_i + e_i} x_i + w_2 \sum_{i=1}^{N} \frac{s_i}{c_i + e_i} x_i \\ \text{s.t.} \quad & 0 \leq x_i \leq f_i, i \in N \\ & \sum_{i=1}^{N} x_i \leq A \end{aligned}$$

(4)

where x is the decision variable representing the proportion of forest to restore within each planning unit i. The two components of the objective function represent the returns (benefit/cost) of forest restoration to biodiversity conservation ($b/(c + e)$; benefit US$$^{-1}$ km^{-2}) for each species j and carbon sequestration ($s/(c + e)$; tonnes US$$^{-1}$ km^{-2}), where the total cost of forest restoration is the sum of the opportunity cost (c; US$$^{-1}$ km^{-2}) and the restoration cost (e; US$$^{-1}$ km^{-2}). N is the total number of planning units and M is the total number of species. The first constraint ensures that the proportion of forest restored ranges from 0 to a maximum value (f), which accounts for the proportion of the planning unit that is already forested or represents a land use that cannot be restored. In scenarios that limited the maximum proportion of forest in each planning unit to 35% or 65%, the functions $min(0.35, f)$ or $min(0.65, f)$ were used to define the upper limit of x. The second constraint limits the total area of forest to be restored (A; km^2), where A = 5,179,088 ha. The user-defined parameters w_1 and w_2 weight the relative contribution of the biodiversity and carbon sequestration components of the objective function. They are required because the equivalence of objectives with different units is a subjective decision that must be made by decision makers. The objective function can be solved over a range of relative weights in order to understand how these components trade-off. The model was solved iteratively in 20 increments of the target area A in order to approximate the non-linear function describing biodiversity conservation values, that is, the target was not prioritized at once only. We tested the influence that running even greater intervals (up to 1000), and found very marginal gains after 10 runs (biodiversity benefits varied by -1,20E-06 between the 10 and 1000 runs simulations). Alternative scenarios involved removal of components of this model, such as the removal of the total cost denominators ($c + e$) in order to maximise benefits regardless of cost, or the addition of further constraints for the scenarios that limited the area of restoration within each state. Exact solutions to this ILP problem were found using the software Gurobi (version 6.5.1).

Scenarios

We evaluated 382 restoration scenarios. These included 360 that combined 10 different weights to the objectives of maximising biodiversity conservation, maximising carbon sequestration and minimising total cost with variations in the maximum area of the planning unit allowed to be restored (35, 65 and 100%)(Extended Data Figure 9), and six restoration project sizes (1,5,10,25. 50 and 100 ha).

Another 20 scenarios repeated some of the above combinations but restricted restoration to within state borders by allocating the Legal Reserves deficit of each state only within state borders. We repeated this last exercise allowing restoration within state borders or outside the state in priority areas for biodiversity conservation. Finally, we also ran a scenario where the restoration target was uniformly distributed to farms below the 20% threshold of Legal Reserve in the Atlantic Forest (our Baseline scenario). These scenarios reflect a range of possible implementations of the Native Vegetation Protection Law.

We contrasted these restoration scenarios in terms of both cost-effectiveness, i.e. benefits per unit of cost, and trade-off curves between biodiversity conservation and carbon sequestration.

Code Availability

The R package with the workflow for species distribution modelling is available and can be installed from https://github.com/Model-R/Model-R. A repository with example data can be found at https://github.com/Model-R/Back-end/releases/tag/coordenador-IIS

Data availability

The datasets generated during the current study are available from the corresponding author on reasonable request. A free online platform for integrated land-use planning including these datasets will be available at www.iis-rio.org/ilup from 2019.

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