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

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International commitments for ecosystem restoration add up to one-quarter of the world's arable land. Fulfilling them would ease global challenges such as climate change and biodiversity decline but could displace food production and impose financial costs on farmers. Here, we present a restoration prioritization approach capable of revealing these synergies and trade-offs, incorporating ecological and economic efficiencies of scale and modelling specific policy options. Using an actual large-scale restoration target of the Atlantic Forest hotspot, we show that our approach can deliver an eightfold increase in cost-effectiveness for biodiversity conservation compared with a baseline of non-systematic restoration. A compromise solution avoids 26% of the biome's current extinction debt of 2,864 plant and animal species (an increase of 257% compared with the baseline). Moreover, this solution sequesters 1 billion tonnes of CO_2-equivalent (a 105% increase) while reducing costs by US$28 billion (a 57% decrease). Seizing similar opportunities elsewhere would offer substantial contributions to some of the greatest challenges for humankind.

Ecosystem restoration can provide multiple benefits to people and help to achieve multiple Sustainable Development Goals[1–3], including climate change mitigation[4] and nature conservation[5]. Thus, 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[6]. Restoration, however, has both direct costs (those required for implementation and maintenance) and indirect costs, including the potential loss of revenues from foregone agricultural production[7]. These restoration costs and benefits present trade-offs and synergies that vary across space[8–10] and have been progressively better studied[5]. Indeed, the field of systematic conservation planning (SCP) provides methods for spatial prioritization that maximizes benefits while minimizing costs[11]. Despite recent efforts[8,9,12], applications of comprehensive SCP approaches to complex large-scale restoration problems with multiple objectives remain sparse.

Here, we present a restoration prioritization approach based on linear programming 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[13,14]. This area is highly deforested and fragmented and is poised to undergo one of the biggest large-scale restoration efforts[15]. We identify exact cost-effective solutions that consider multiple benefits, costs and policy scenarios. We also investigate trade-offs in benefits and costs

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across different scenarios, and impacts of increasing the size of restoration projects. Linear programming can find exact solutions that can perform at least 30% better than mainstream SCP software[16]. It can also be better customized, allowing the incorporation of restoration aspects relevant to particular socioecological contexts. In this application, we aim to maximize 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[17]. We gathered and analysed species occurrence data in the Atlantic Forest and then performed data cleaning, identification of endemism by specialists and model selection (Methods). Next, we 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 utilized a function[10,18] derived from the species–area relationship to calculate the marginal contribution of each hectare restored towards reducing the extinction probability for each species. 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 accounts for this effect, although for visualization purposes, we aggregate the restoration value of each planning unit across all species, thereby generating a biodiversity conservation benefits surface (Supplementary Fig. 1). Our species data confirmed the severity of the biodiversity crisis in the Atlantic Rainforest, with an estimated 27–32% of the endemic species of the biome currently committed to extinction (Methods). For climate change mitigation, benefit was measured as the potential aboveground carbon sequestration in the first 20 years following habitat restoration[4]. We produced the climate change mitigation surface (Supplementary Fig. 2a) by applying and extending a recently published empirical model of the carbon sequestration potential of restoration[4] to the whole Atlantic Rainforest. Restoration implementation costs, including maintenance and monitoring, were estimated based on a survey with restoration companies active in the area. Costs were spatially adjusted via a proxy for the natural regeneration potential based on a model of ecological uncertainty of tropical forest restoration success[19] (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[20]. A restoration costs surface (Supplementary Fig. 2b) was built based on these two costs (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 project, so we modelled these economies of scale using field evidence on how unitary costs fall as projects grow (Methods and Supplementary Fig. 3). The size of the project also affects ecological outcomes, an effect that 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[21].

The Brazilian Native Vegetation Protection Law[22] requires Atlantic Forest farmers to keep at least 20% of their farms under native vegetation. Farmers currently below this threshold must comply either by implementing 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[22], 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 also guide restoration projects with smaller targets (Methods and Supplementary Fig. 4). In our 'Baseline' scenario, farmers restore this target inside their own farms until this minimum threshold is met. In a set of alternative scenarios, we simulate different ways of prioritizing benefits and costs of restoration, considering variations in the size of projects. These 362 alternative scenarios focused on combinations of maximizing the benefits for biodiversity conservation and climate change mitigation while minimizing costs (Methods and Supplementary Fig. 5). We also investigated the impacts of limiting offsets to the farmer's own state (a policy option currently pursued by some Brazilian states).

Results

The Baseline scenario has the worst performance for biodiversity conservation, the fourth worst for carbon sequestration and the highest costs across all 363 scenarios analysed (Baseline, in Fig. 1). For a total cost of US$50.2 billion, this allocation would avoid 7.2% of the projected extinctions for the central estimate (which is 6.8% for the lower and 7.7% for the upper). Moreover, it would sequester 0.5 billion tonnes of CO_2-equivalent (CO_{2e}) for the central estimate (which is 0.4 for the lower and 0.6 for the upper; further lower and upper estimates are presented in Supplementary Tables 1 and 2). This 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 interests of farmers.

One of the advantages of compensation outside farms is the potential to increase the size of individual projects, which has a 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 (57% drop when projects grow from 1 to 100 ha; Fig. 2a). Second, ecologies of scale lead to improved efficiencies in climate mitigation outcomes for larger projects (Fig. 2b), with 100-ha projects sequestering 58% more than the same area of 1-ha 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). Indeed, the carbon prices required to cover restoration costs drop 73% when increasing projects from 1 to 100 ha, 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 the size of the restoration projects on biodiversity conservation, we expect the same to apply to biodiversity outcomes given the importance of edge-effects on populations in small forest fragments[23].

Another advantage of compensation outside farms is implementing restoration in areas that would maximize benefits, thus improving the likelihood of long-term socioecological success. Allocations based on maximizing a single benefit reveal the maximum outcomes that restoration prioritization can achieve for each benefit. For biodiversity conservation, 29.7% of the species committed to extinctions could be saved ("Maximum Biodiversity" in Fig. 1a,b), an improvement of 311% in relation to the Baseline scenario. Likewise, a focus on climate change mitigation could sequester up to 1.3 $GtCO_{2e}$ ("Maximum Climate" in Fig. 1a,c), a 174% increase from the Baseline scenario. Focusing on costs would reduce them to US$15.2 billion ("Minimum Costs" in Fig. 1a,d), a 69% saving on the Baseline scenario. But despite the marked improvements in relation to Baseline, single-focus allocations have mixed and varied outcomes when all benefits and costs are considered. For instance, considering solely 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

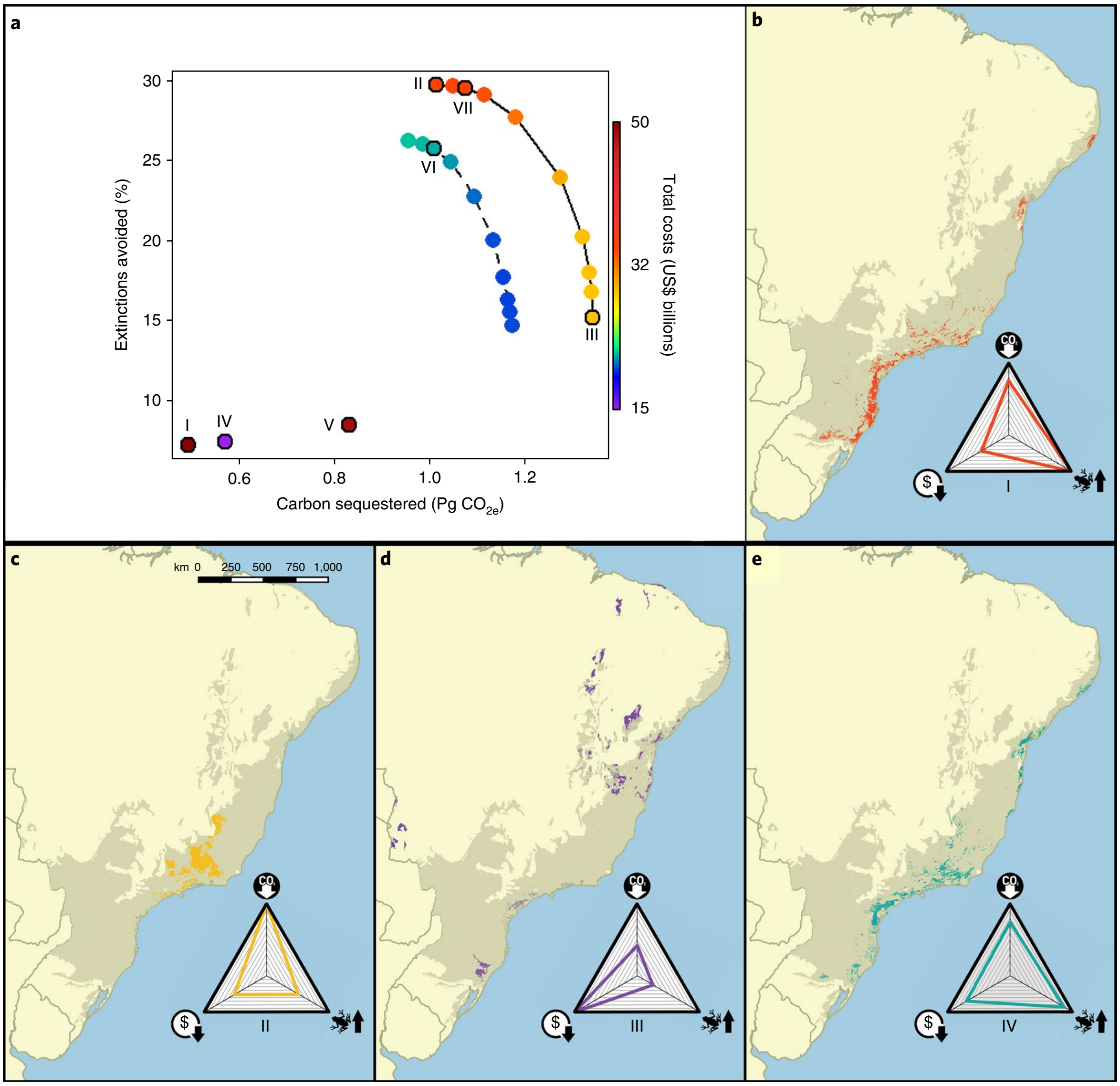

Fig. 1 | Spatial configurations and outcomes for climate change mitigation, avoided extinctions and total costs of selected scenarios. a, The following scenarios are considered: I, Baseline without offsets; II, Maximum Biodiversity; III, Maximum Climate; IV, Minimum Costs; V, Random; VI,Compromise; and VII, Environment Only. The unbroken (outer) line connects points in the efficiency frontier of environmental benefits when excluding costs from the prioritization algorithm. The broken (inner) line connects allocations for the cost-effective frontier. **b**–**e**, Spatial configurations and radar diagrams of outcomes for the Maximum Biodiversity (**b**), Maximum Climate (**c**), Minimum Costs (**d**) and Compromise (**e**) scenarios. Colours are related to the cost scale presented in **a**.

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 (Supplementary Fig. 6). The biodiversity-focused solution would cost US$35 billion, delivering 44% of the potential costs savings and resulting in benefit–cost ratios of US$9 million per species saved and US$35 per tonne of CO_{2e}. By contrast, the climate-focused solution would cost US$29 billion, delivering 59% of the cost-savings achieved by Minimum Costs and resulting in benefit–cost ratios of US$15 million per species saved and US$23 per tonne of CO_{2e}.

In turn, restoration plans designed solely to minimize costs have a 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 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" in Fig. 1).

Compromise solutions can simultaneously deliver a substantial fraction of the maximum outcome for each benefit. Our approach allowed us to combine efficiencies of scale with multicriteria spatial prioritization 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 maximizing cost-effective benefits for biodiversity and climate change mitigation. Compared to the Baseline scenario, one of the solutions for the Cost-effective efficiency frontier ('Compromise' in Fig. 1a,e) increases biodiversity benefits by 257% (equivalent to 94% of those achieved under Maximum Biodiversity). Moreover, the climate change mitigation

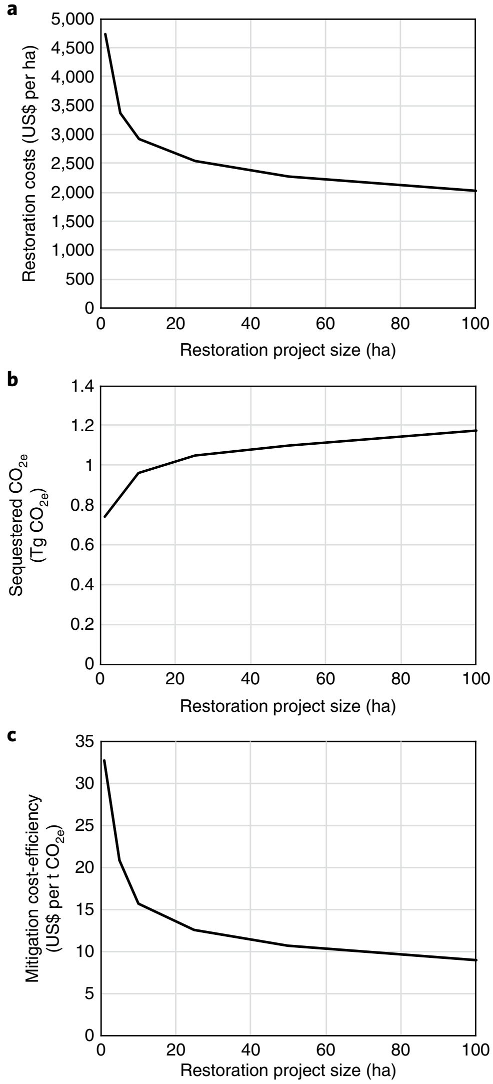

Fig. 2 | Impacts of economic and ecological efficiencies of scale on cost-effectiveness. a, The relation between increasing restoration project sizes and the restoration costs per unit area. **b**, The relation between increasing project size and the total CO_{2e} sequestered in the Maximum Climate scenario. **c**, The combined effect of these two relations on mitigation cost-effectiveness as project sizes grow. All data presented are results from the Maximum Climate scenario.

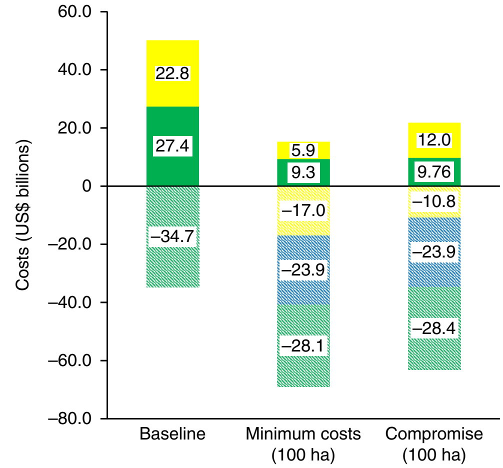

Fig. 3 | Impacts of economies of scale and of spatial prioritization for reducing opportunity and restoration costs across different scenarios. Filled rectangles are actual restoration (green) and opportunity (yellow) costs incurred in each scenario. Diagonally striped rectangles represent reductions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

benefit increases by 105% (79% of Maximum Climate), and reduces costs by 57% (83% of the reduction achieved by Minimum Costs). 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 relatively 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. Therefore, sequestering 0.27 $GtCO_{2e}$ less would save 411 animals and plants from extinction when applying the relative reduction in extinctions to the overall extinction debt of plants and animals in the biome (Supplementary Table 1). This results in a trade-off ratio of 1 animal or plant extinction avoided for every 0.7 million tonnes of CO_{2e} not sequestered. Given the key role that biodiversity has in driving the productivity of ecosystems[24], such a compromise might result in climate mitigation gains in the long term. Climate change adaptation might also benefit from improved ecosystem-based adaptation[25] 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 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 prioritize areas with lower opportunity costs and higher potential for natural regeneration. The relative contribution of each of these factors varies across scenarios (Fig. 3). In comparison with the Baseline scenario, assumed to comprise 1-ha projects, economies of scale reduce costs by US$23.9 billion when moving to 100-ha projects. Identifying areas with lower opportunity costs reduces these by between US$10.8 billion (Compromise) and US$17.0 billion (Minimum Costs), demonstrating that there is great scope for avoiding restoration conflicts with agricultural production. The strong impact of natural regeneration on reducing restoration costs is felt across all scenarios, reducing it by 56% (or US$35 billion) in the Baseline scenario, by 76% (or US$29 billion) in the Minimum costs scenario and by 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 on 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 (Supplementary Fig. 7). For climate mitigation, the same restrictions result in reductions of 2% and 6%, respectively (Supplementary Fig. 7). 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 into considering how the costs of achieving restoration targets can be shared between farmers and the wider society. Benefits from restoration are shared between farmers and the wider society (in Brazil and elsewhere), whereas opportunity and restoration costs would be borne by the farmers, as the target analysed here arises from past deforestation beyond legal limits. Although 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"), 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 schemes are a way to motivate farmers to pursue options that are more beneficial to the wider society. Carbon-based incentives of US$38 per tonne of CO_{2e}, species-based incentives of US$30 million per extinction avoided or a combination of both would be enough to pay for the difference in costs. Although the Environment Only solution is US$14 billion cheaper than the Baseline scenario, which would have to be paid individually by farmers, it could be argued that farmers could choose intermediate solutions, since this reduction in costs is made possible by the decision in 2012 by Brazilian society 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 per tonne of CO_{2e}, species-based incentives of US$9 million per 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 payments for ecosystem services schemes[26].

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 with the unconstrained version of each goal. The outcomes are irrespective of whether assessed for biodiversity conservation (10% lower), climate change mitigation (14% lower) or cost minimization (17% more expensive). 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. 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[27]. By contrast, the ecological equivalence between remnants, the representation of different ecological communities and community integrity across the biome[28] 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 prioritization) 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 recognized best practices to all stages of our analyses, some limitations should be highlighted (see Methods for further discussions). Some species distribution models relied on a relatively small number of occurrences, and all present the usual limitations associated with correlative models. The approach used 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 customization to context-specific policies and goals led to 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. Moreover, our results led to the commission of the replication of our approach to the other five Brazilian biomes as part of the National Plan for Native Vegetation Recovery—PLANAVEG[29]. The potential of this approach for easily exploring large numbers of scenarios will be of particular importance for two PLANAVEG strategies: Spatial Planning and Monitoring and Finance. These ongoing biome-specific initiatives are tapping into the ability of our approach to include customized sets of benefits and costs, such as the following: 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 the diverse interests of stakeholders. 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.

Methods

In this study, we developed a multicriteria 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 the Legal Reserve in the Atlantic Forest[22]) to achieve the following: (1) quantify the variation in costs and benefits of restoration among a range of possible scenarios governing where restoration occurs; (2) quantify the trade-offs among costs and benefits 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 multicriteria spatial restoration prioritization approach was based on the following 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 multistakeholder preferences; (2) gather and model variables to be used as inputs; (3) develop a multicriteria spatial restoration prioritization framework implemented as an integer linear programming problem; (4) simulate restoration scenarios; and (5) analyse and interpret the solutions and their trade-offs.

We developed spatial surfaces for the following 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 optimization model itself.

Biodiversity conservation benefits. Benefits to biodiversity conservation were quantified using species extinction functions reflecting diminishing returns associated with increasing areas of habitat for each species (Supplementary Fig. 1). This function is based on a re-working of the species–area relationship and operates at the level of individual species[17]. This approach is imperfect, as it ignores the possibility of negative density-dependence at very low population sizes, and does not consider the time scale of resulting extinctions, which will vary with the life history and ecology of a species. However, unlike simpler formulations, it takes into account the non-linearity of the response of persistence to changes in population size, and has been used in several similar studies[10,17,18]. If the 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. On the basis of a previous study[10], the change in extinction risk (r) for each individual species as a function of habitat area was modelled as follows:

$$r = 1 - (x / A_0)^z \quad (1)$$

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 previous studies[10,17,18]), and $z = 0.15$ and $z = 0.35$ for sensitivity analyses presented in Supplementary Fig. 8 and Supplementary Table 2. To implement these curves in an linear programming problem 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. To identify areas that, if restored, would be a 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 the available habitat area for the species. This is a different approach to the usual used in conservation prioritization, where the aim is to conserve current habitats by using the distribution of species 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 were obtained from a previous study[30], with updates from the authors, and comprised 114 endemic species (3,786 occurrences). Data on bird occurrence were obtained from the Global Biodiversity Information Facility database[31] and comprised 223 endemic species (12,085 occurrences). Data on plant occurrence were obtained from NeoTropTree and SpeciesLink[32], and comprised 846 endemic species and 44,024 records. The original plant names were based on the NeoTropTree database[33] and updated according to the List of Species of the Brazilian Flora[34] using R package 'flora'[35], which is based on the List's Integrated Publishing Toolkit database[36].

We cleaned the data for each species by deleting the following: records that fell out of the environmental layers; duplicated records; and non-duplicated records that fell in the same planning unit (1 km-pixel). The endemism status of species was assessed by consulting amphibian experts and by following a previously described method[37] for birds and the Brazilian Flora 2020 for woody plants.

Environmental data. The initial environmental dataset was composed of the following 28 variables: the 19 bioclimatic variables from Worldclim[38]; 4 CGIAR CSI geohydrological variables (actual evapotranspiration, aridity index, soil water balance and potential evapotranspiration[39]); and 5 USGS topographical variables (elevation, slope, aspect and topographic index[39]). Since aspect is a circular variable, its sine and cosine were calculated to be used as two different variables. All variables had a spatial resolution of 1 km².

We summarized these variables into ten orthogonal variables, calculated through a principal component analysis of the whole raster set. These account for 95% of the overall environmental variation in the Brazilian Atlantic Forest. The principal component analysis variables were used to reduce errors in the modelling process, which are caused by the spatial autocorrelation of presence data or the multicollinearity of the environmental predictors[40,41].

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, random forest and support vector machines. Their performance was tested by calculating the true skill statistics (TSS)[42]. During the preliminary round of models only MaxEnt, random forest and support vector machines showed average high TSS scores (>0.7) and low variance (Supplementary Fig. 9). The final models were therefore run using these three algorithms. TSS values for each algorithm used in the Environmental Niche Modelling varied little across the three biodiversity groups (Supplementary Fig. 10).

For each species, random pseudoabsence points were sorted within a maximum distance buffer (that is, the radius of the buffer is the maximal geographical distance between the occurrence points). This procedure reduces the modelling background area, ensuring better estimates, once pseudoabsences were sampled only in areas where species could disperse[43–45] while controlling for the low prevalence associated with generating pseudoabsences inside large range areas.

Species were modelled using a threefold 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 values of >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 constituted 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 (that is, the area in which at least half of the algorithms predict a potential presence of the species[46]), resulting in a binary map of the potential distribution of species. The steps described above were taken 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 geographical area.

The modelling was performed using ModelR[47], a set of R scripts for species distribution model fitting and assessment based on packages XML[48], dismo[49], raster[49], rgdal[50], maps[51], rgeos[52], random forest[53] and e1071[54].

Climate mitigation benefits. We built a potential aboveground biomass recovery map for the Brazilian Atlantic Forest, which is a proxy for aboveground potential carbon sequestration in degraded areas (Supplementary Fig. 2). The map has a resolution of 1 km² and followed the methods of of a previous study[55]. That study included the following three biomes: tropical and subtropical moist broadleaf forests; tropical and subtropical dry broadleaf forests; and tropical and subtropical coniferous forest[55]. 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 (approximately 1 km × 1 km) from WorldClim[57], and the climatic water deficit (CWD) was obtained from a previous study[58].

We calculated the total potential aboveground 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 from a previous study[55] estimates AGB after 20 years based on best-fit models that incorporate climatic variables as follows:

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

where estimated AGB_20y indicates the absolute biomass recovery potential over 20 years based on chronosequence models[55]. 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.

To insert uncertainty measures into this analysis, the raw data from a previous study[55]were 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 optimization process, and the corresponding results are presented in Supplementary 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 in 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[20], as land acquisition cost should reflect the discounted future revenues from that land. We combined spatial data on the distribution of pasturelands and croplands[61] with county-level data on the land acquisition costs for these two categories[62].

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 (for example, tree plantings using nursery stock)[63,64]. 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 (for example, thinning and burning)[64].

The likelihood of an area requiring active or passive restoration is determined by socioeconomic factors that in turn determine the likelihood of an area being abandoned to regrow 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[20] as a proxy. A recent global meta-analysis[20] revealed a clear pattern of increasing the success of forest restoration (by comparing plant biodiversity in reference and restored and 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 from a previous study[20] 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 (that is, old-growth or less-disturbed forests).

Restoration cost (r) was calculated as follows:

$$r = u \times c + f \tag{3}$$

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; that is, it will require less human intervention. The cost of a full planting method (the most expensive method for active restoration) was obtained from a previous study[29]. Thus, our total costs map (Supplementary Fig. 3) was produced by adding, for each planning 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. 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 dataset (Supplementary Fig. 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 were obtained from a map produced in a previous study[65], which were 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 dataset was used to calculate the following: (1) the proportion of existing forest (f) within a planning unit; (2) environmental deficits according to the Native Vegetation Protection Law; and (3) the 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 (for example, urban areas, roads and lakes) within each planning unit. All geographical information system data were converted to Albers projection to ensure accurate area and distance calculations.

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

$$\begin{aligned} &\max\ \omega_1 \sum_{i=1}^{N}\sum_{j=1}^{M} \frac{b_{i,j}}{c_i+e_i}x_i + \omega_2 \sum_{i=1}^{N} \frac{s_i}{c_i+e_i}x_i \\ &\text{s.t. } 0 \le x_i \le f_i, i \in N \\ &\sum_{i=1}^{N} x_i \le A \end{aligned} \tag{4}$$

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 and 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, respectively, 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 to understand how these components trade-off. The model was solved iteratively in 20 increments of the target area A to approximate the non-linear function describing biodiversity conservation values; that is, the target was not prioritized at once only. We tested the influence of running even greater intervals (up to 1,000) and found very marginal gains after 10 runs (biodiversity benefits varied by -1.20×10^{-06} between the 10 and 1,000 runs simulations). Alternative scenarios involved the removal of components of this model, such as the removal of the total cost denominators ($c + e$) to maximize 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 linear programming problem were found using the software Gurobi (v.6.5.1).

Scenarios. We evaluated 382 restoration scenarios. These included 360 that combined 10 different weights to the objectives of maximizing biodiversity conservation, maximizing carbon sequestration and minimizing total cost with variations in the maximum area of the planning unit allowed to be restored (35, 65 and 100%) (Supplementary Fig. 7), 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 whereby 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 (that is, benefits per unit of cost) and trade-off curves between biodiversity conservation and carbon sequestration.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

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 upon 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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References

1. *United Nations Sustainable Development Goals* (United Nations, accessed 17 November 2017); http://www.un.org/sustainabledevelopment/sustainable-development-goals/
2. Griggs, D. et al. Sustainable development goals for people and planet. *Nature* **495**, 305–307 (2013).
3. Chazdon, R. L. et al. A policy-driven knowledge agenda for global forest and landscape restoration. *Conserv. Lett.* **10**, 125–132 (2017).
4. Chazdon, R. L. et al. Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Sci. Adv.* **2**, e1501639 (2016).
5. Crouzeilles, R. Ecological restoration success is higher for natural regeneration than for active restoration in tropical forests. *Sci. Adv.* **3**, e1701345 (2017).
6. Verdone, M. & Seidl, A. Time, space, place, and the Bonn Challenge global forest restoration target. *Rest. Ecol.* **25**, 903–911 (2017).
7. Smith, P. et al. How much land-based greenhouse gas mitigation can be achieved without compromising food security and environmental goals? *Glob. Change Biol.* **19**(8), 2285–2302 (2013).
8. Gourevitch, J. D. et al. Optimizing investments in national-scale forest landscape restoration in Uganda to maximize multiple benefits. *Environ. Res. Lett.* **11**, 114027 (2016).
9. Zwiener, V. P. et al. Planning for conservation and restoration under climate and land use change in the Brazilian Atlantic Forest. *Divers. Distrib.* **23**, 955–966 (2017).
10. Strassburg, B. B. N. et al. Moment of truth for the Cerrado hotspot. *Nat. Ecol. Evol.* **1**, 0099 (2017).
11. Pouzols, F. M. et al. Global protected area expansion is compromised by projected land-use and parochialism. *Nature* **516**, 383–386 (2014).
12. Possingham, H. P., Bode, M. & Klein, C. J. Optimal conservation outcomes require both restoration and protection. *PLoS Biol.* **13**, 1–15 (2015).

13. Laurance, W. F. Conserving the hottest of the hotspots. *Biol. Conserv.* **142**, 1137 (2009).
14. Mittermeier, R. A. et al. *Hotspots Revisited: Earth's Biologically Richest and Most Endangered Terrestrial Ecoregions* (Conservation International, 2004).
15. Latawiec et al. Creating space for large-scale restoration in tropical agricultural landscapes. *Front. Ecol. Env.* **13**, 211–218 (2015).
16. Beyer, H. L., Dujardin, Y., Watts, M. E. & Possingham, H. P. Solving conservation planning problems with integer linear programming. *Ecol. Model.* **328**, 14–22 (2016).
17. Thomas, C. D. et al. Extinction risk from climate change. *Nature* **427**, 145–148 (2004).
18. Strassburg et al. Impacts of incentives to reduce emissions from deforestation on global species extinctions. *Nat. Clim. Change* **2**, 350–355 (2012).
19. Crouzeilles, R. & Curran, M. Which landscape size best predicts the influence of forest cover on restoration success? A global meta-analysis on the scale of effect. *J. Appl. Ecol.* **53**, 440–448 (2016).
20. Crouzeilles, R., Beyer, H. L., Mills, M., Grelle, C. E. V. & Possingham, H. P. Incorporating habitat availability into systematic planning for restoration: a species-specific approach for Atlantic Forest mammals. *Divers. Distrib.* **21**, 1027–1037 (2015).
21. Groeneveld, J. et al. The impact of fragmentation and density regulation on forest succession in the Atlantic rain forest. *Ecol. Model.* **220**, 2450–2459 (2009).
22. Soares-Filho, B. et al. Cracking Brazil's forest code. *Science* **344**, 363–364 (2014).
23. Kennedy, C. M. et al. Bigger is better: improved nature conservation and economic returns from landscape-level mitigation. *Sci. Adv.* **2**, e1501021 (2016).
24. Duffy, J. E., Godwin, C. M. & Cardinale, B. J. Biodiversity effects in the wild are common and as strong as key drivers of productivity. *Nature* **549**, 261–264 (2017).
25. Scarano, F. R. Ecosystem-based adaptation to climate change: concept, scalability and a role for conservation science. *Perspect. Ecol. Conserv.* **15**, 65–73 (2017).
26. Brancalion, P. H. S., Viani, R. A. G., Strassburg, B. B. N. & Rodrigues, R. R. Finding the money for tropical forest restoration. *Unasylva* **63**, 239 (2012).
27. Mitchell, M. G. E. et al. Reframing landscape fragmentation's effects on ecosystem services. *Trends Ecol. Evol.* **30**, 190–198 (2015).
28. Banks-Leite, C. et al. Using ecological thresholds to evaluate the costs and benefits of set-asides in a biodiversity hotspot. *Science* **345**, 1041–1045 (2014).
29. *PLANAVEG: The National Vegetation Recovery Plan* Federal Decree No. 8.972/2017 (Brazilian Ministry of Environment, 2017).
30. Lemes, P., Melo, A. S. & Loyola, R. D. Climate change threatens protected areas of the Atlantic Forest. *Biodivers. Conserv.* **23**, 357–368 (2014).
31. *Global Biodiversity Information Facility Database* (GBIF, accessed 15 March 2017); www.gbif.org
32. *SpeciesLink* (SpeciesLink, accessd 15 March 2017); http://splink.cria.org.br/
33. Oliveira-Filho, A. T. *NeoTropTree, Flora Arbórea da Região Neotropical: Um Banco de Dados Envolvendo Biogeografia, Diversidade e Conservação* (Universidade Federal de Minas Gerais, 2017); http://www.neotroptree.info/
34. *Flora do Brasil 2020 Under Construction* (Jardim Botânico do Rio de Janeiro, accessed 20 March 2017); http://floradobrasil.jbrj.gov.br/
35. Carvalho, G. *Package 'flora' 2016: Tools for Interacting with the Brazilian Flora 2020* R Package Version 0.3.0 (R Foundation for Statistical Computing, 2017); https://cran.r-project.org/web/packages/flora/flora.pdf
36. Robertson, T. et al. The GBIF integrated publishing toolkit: facilitating the efficient publishing of biodiversity data on the internet. *PLoS ONE* **9**, 102623 (2014).
37. Stotz, D. F., Fitzpatrick, J. W., Parker, T. A. III. & Moskovits, D. K. *Neotropical Birds: Ecology and Conservation*. (Univ. Chicago Press, Chicago, 1996).
38. Hijmans, R. J., Cameron, S. E., Parra, J. L., Jones, P. G. & Jarvis, A. Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
39. Jones, P. G. & Thornton, P. K. Generating downscaled weather data from a suite of climate models for agricultural modelling applications. *Agric. Syst.* **114**, 1–5 (2013).
40. Dormann, C. F. et al. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* **36**, 27–46 (2013).
41. Cruz-Cárdenas, G., López-Mata, L., Villaseñor, J. L. & Ortiz, E. Potential species distribution modelling and the use of principal component analysis as predictor variables. *Rev. Mex. Biodivers.* **85**, 189–199 (2014).
42. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). *J. Appl. Ecol.* **43**, 1223–1232 (2006).
43. Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods Ecol. Evol.* **3**, 327–338 (2012).
44. Barve, N. et al. The crucial role of the accessible area in ecological niche modelling and species distribution modelling. *Ecol. Model.* **222**, 1810–1819 (2011).
45. Stokland, J. N., Halvorsen, R. & Støa, B. Species distribution modelling-effect of design and sample size of pseudo-absence observations. *Ecol. Model.* **222**, 1800–1809 (2011).
46. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
47. Sánchez-Tapia, A. et al. Model-R: a framework for scalable and reproducible ecological niche modeling. In High Performance Computing Fourth Latin American Conference, CARLA 2017. *Comm. Comp. Inform. Sci.* **796**, 218–232 (2017).
48. Lang, D. T. et al. *XML: Tools for Parsing and Generating XML within R and S-Plus* R Package Version 3.98-1.1 (R Foundation for Statistical Computing, 2013); https://rdrr.io/cran/XML/
49. Hijmans, R. J., Phillips, S., Leathwick, J. & Elith, J. *dismo: Species Distribution Modeling* R Package Version 1.1-4 (R Foundation for Statistical Computing, 2016); https://cran.r-project.org/web/packages/dismo/index.html
50. Bivand, R., Keitt, T. & Rowlingson, B. *rgdal: Bindings for the Geospatial Data Abstraction Library* R Package Version 0.8-16 (R Foundation for Statistical Computing, 2014); https://cran.r-project.org/web/packages/rgdal/index.html
51. Becker, R., Wilks, A., Brownrigg, R., Minka, T. & Deckmyn, A. *maps: Draw Geographical Maps* R Package Version 3.1. 0 (R Foundation for Statistical Computing, 2016); https://cran.r-project.org/web/packages/maps/index.html
52. Bivand, R. & Rundel, C. *rgeos: Interface to Geometry Engine-Open Source (GEOS)* R Package Version 0.3-8 (R Foundation for Statistical Computing, 2014); https://cran.r-project.org/web/packages/rgeos/index.html
53. Liaw, A. & Wiener, M. Classification and regression by randomforest. *R News* **2**, 18–22 (2002).
54. Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A. & Leisch F. *e1071: Misc Functions of the Department of Statistics (e1071)* R Package Version 1–6 (R Foundation for Statistical Computing, 2014); https://rdrr.io/rforge/e1071/
55. Poorter, L., Bongers, F. & Rozendall, D. M. A. Biomass resilience of Neotropical secondary forests. *Nature* **530**, 211–214 (2016).
56. *TNC Maps* (The Nature Conservancy, accessed 21 October 2016); http://maps.tnc.org/gis_data.html
57. *WorldClim - Global Climate Data* (WorldClim, accessed 27 October 2016); http://www.worldclim.org/current
58. Chave, L. et al. Improved allometric models to estimate the above ground biomass of tropical trees. *Glob. Change Biol.* **20**, 3177–3190 (2014).
59. Mendes, M. S. et al. Look down—there is a gap—the need to include soil data in Atlantic Forest restoration. *Restor. Ecol.* https://doi.org/10.1111/rec.12875 (2018).
60. Sanderman, J., Tomislav, H. & Gregory, J. F. Soil carbon debt of 12,000 years of human land use. *Proc. Natl Acad. Sci. USA* **114**, 9575–9580 (2017).
61. Ministério do Meio Ambiente *Potencial de Regeneração Natural da Vegetação no Brasil* (World Resources Institute: Brasil, Brasília, 2017).
62. *Anuário da Agricultura Brasileira: Agrianual 2015* (Informa Economics FNP, São Paulo, 2014).
63. Chazdon, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* **320**, 1458–1460 (2008).
64. Holl, H. D. & Aide, T. M. When and where to actively restore ecosystems? *Forest Ecol. Manag.* **261**, 1558–1563 (2011).
65. SOS Mata Atlântica & INPE *Atlas dos Remanescentes Florestais da Mata Atlântica - Período de 2011* (Fundação SOS Mata Atlântica, São Paulo, 2012); mapas.sosma.org.br

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Author contributions

B.B.N.S. conceived the study, coordinated the development of the multicriteria approach and wrote the first version of the paper. H.L.B., B.B.N.S., R.C. and A.I. led the optimization modelling, while M.F.S., F.B. and A.S.-T. developed the environmental niche modelling. B.B.N.S., H.L.B., R.C., A.I., M.M., H.P.P., F.B.,

M.F.S., A.B., J.B.B.S., P.H.S.B., R.L.C., A.G., A.L., J.P.M., R.R.R., C.A.M.S., F.R.S., L.T., T.A.G. and M.U. developed the multicriteria prioritization approach. R.L., J.P.M. and A.O.F. contributed biodiversity data, and R.L.C. and E.N.B. developed the climate mitigation surface. C.A.M.S. coordinated the interface with policy applications. All authors analysed the results and provided input into subsequent versions of the manuscript.

Competing interests
The authors declare no competing interests.

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Software and code

Policy information about availability of computer code

Data collection	The Methodology did not involve direct sampling, so data was acquired from other studies.
Data analysis	The following software were used in the study: R Studio QGIS Geographic Information System Gurobi The script to generate all the Environmental Niche Models used in this study is available at https://github.com/Model-R

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Study description	Our approach combines the most comprehensive multi-criteria database on large-scale restoration ever compiled for any region in the world with innovative breakthroughs in systematic conservation planning methods, including multicriteria linear programming (LP) and the first ever accounting for economic and ecological efficiencies of scale in systematic planning. Our approach is customizable to any specific socioecological context and set of objectives, allowing it to be readily adapted to any region of the world. Other key capabilities are precision (LP can deliver exact optimum solutions that are superior to the approximations of standard SCP software) and the ability to apply this approach to large areas at high resolution (our application had 1.3 million planning units) yet calculate solutions quickly. The latter leads to a crucial advantage of our method, the ability to map out a solution space consisting of hundreds of combinations of multiple objectives in a few hours and focus attention on the outcomes of these scenarios (as opposed to contentious and subjective a priori weighting common in multicriteria approaches).
Research sample	We applied and tested our approach in the global biodiversity hotspot of the Atlantic Rainforest which is poised to undergo a large-scale restoration effort of up to 5 million hectares as part of Brazil´s new National Restoration Plan.
Sampling strategy	The study was conducted in the Atlantic Forest due to its status as a biodiversity hotspot and because it is poised to undergo a large-scale restoration effort of up to 5 million hectares as part of Brazil´s new National Restoration Plan.
Data collection	Data on amphibian occurrence was obtained from Lemes et al. (2014), 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 and comprised 223 endemic species (12,085 occurrences). Data on plants occurrence was obtained from NeoTropTree and SpeciesLink, and comprised 846 endemic species and 44, 024 records. The original plant names were based on the NeoTropTree database and updated according to the List of Species of the Brazilian Flora, using R package 'flora', which is based on the List's Integrated Publishing Toolkit database.
Timing and spatial scale	We applied and tested our approach in the global biodiversity hotspot of the Atlantic Rainforest which is poised to undergo a large-scale restoration effort of up to 5 million hectares as part of Brazil´s new National Restoration Plan.
Data exclusions	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 Stotz et al. (1996) for birds, and the Brazilian Flora 2020 for woody plants.
Reproducibility	Methodology is fully described under the Methods section in a way that can be reproduced by other studies. Furthermore, 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.
Randomization	The Methodology did not involve direct sampling, so data was acquired from other studies. Therefore, "randomization" was not applicable.
Blinding	The Methodology did not involve direct sampling, so data was acquired from other studies. Therefore, "blinding" was not applicable.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study
☒	☐ Unique biological materials
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging