

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

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60 **International commitments for ecosystem restoration add-up to one-quarter of the world's**
61 **arable land¹. Fulfilling them would ease global challenges such as climate change² and**
62 **biodiversity decline³, but could displace food production⁴ and impose financial costs on**
63 **farmers⁵. Here we show a novel restoration prioritization approach capable of revealing**
64 **these synergies and trade-offs, incorporating for the first time ecological and economic**
65 **efficiencies of scale and modelling specific policy options. We show, for an actual large-**
66 **scale restoration target of the Atlantic Forest hotspot, that our approach can deliver an**
67 **eightfold increase in cost-effectiveness for biodiversity conservation compared to a baseline**
68 **of non-systematic restoration. A compromise solution avoids 26% of the biome's current**
69 **extinction debt of 2864 plant and animal species (an increase of 257% compared to the**
70 **baseline), and sequesters 1 billion tonnes of CO₂Eq (a 105% increase) while reducing costs**
71 **by US\$ 28 billion (a 57% decrease). Seizing similar opportunities elsewhere would offer**
72 **substantial contributions to some of humankind's greatest challenges**

73 Ecosystem restoration can provide multiple benefits to people and help to achieve multiple
74 Sustainable Development Goals⁶⁻⁸, including climate change mitigation and nature conservation.
75 For these reasons, 47 countries have collectively committed to have 150 and 350 million hectares
76 of degraded lands under restoration by 2020 and 2030, respectively, and have included major
77 restoration targets in national pledges to the Paris Climate Agreement¹. Restoration, however,
78 has both direct costs – those required for implementation and maintenance – and indirect costs,
79 including the loss of revenues from foregone agricultural production. Crucially, these restoration
80 costs and benefits present trade-offs and synergies that vary greatly across space⁹⁻¹¹. In the
81 context of safeguarding existing habitats there has been considerable progress in understanding
82 some of these trade-offs³, with the field of Systematic Conservation Planning (SCP) providing

83 methods for spatial prioritisation that maximize benefits while minimizing costs¹². Despite some
84 recent efforts^{9-10,13}, applications of comprehensive SCP approaches to complex large-scale
85 restoration problems with multiple objectives remain sparse.

86 Here we present a novel restoration prioritization approach based on Linear Programming (LP)
87 to solve customized complex restoration problems at large scales. We apply this approach to
88 solve a problem of global significance that will inform restoration policy and practice at a
89 national scale in the Brazilian Atlantic Forest hotspot¹⁴⁻¹⁵, a highly deforested and fragmented
90 region poised to undergo one of the biggest large-scale restoration efforts¹⁶. We identify exact
91 cost-effective solutions that consider multiple benefits, costs and policy scenarios and
92 investigate: i) trade-offs in benefits and costs across different scenarios, and ii) the impacts of
93 increasing the size of restoration projects. LP can find exact solutions that can perform at least
94 30% better than mainstream SCP software¹⁷. It can also be more fully customized, allowing the
95 incorporation of complex aspects of restoration relevant to particular socioecological contexts. In
96 this application, we aimed at maximising restoration benefits for biodiversity conservation and
97 climate change mitigation while reducing restoration and opportunity costs.

98 We divided the biome into 1.3 million planning units of 1 km². For biodiversity conservation,
99 benefit was measured as the reduction in projected extinctions owing to habitat restoration¹⁸. We
100 gathered and analysed species occurrence data in the Atlantic Forest and, following data
101 cleaning, identification of endemism by specialists and model selection (Methods), generated
102 potential species occurrence models for 785 species of plants, birds and amphibians endemic to
103 the Atlantic Forest, representing the best set of biodiversity data currently available for this
104 biome. We then calculated the marginal contribution of each hectare restored to reducing each
105 species' extinction probability, based on a function^{11,19} derived from the species-area

106 relationship. The benefit of habitat restoration to each species is dynamic in that the value of
107 restoring additional habitat for that species diminishes as the total area of habitat increases. Our
108 approach explicitly accounts for this effect, though for visualisation purposes we can aggregate
109 the restoration value of each planning unit across all species, thereby generating a biodiversity
110 conservation benefits surface (Extended Data Fig. 1). Our species data confirmed the severity of
111 the biodiversity crisis underway in the Atlantic Rainforest, with an estimated 27-32% of the
112 biome's endemic species currently committed to extinction (2,621-3,107 plants and animals, see
113 Methods). For climate change mitigation, benefit was measured as the potential aboveground
114 carbon sequestration in the first 20 years following habitat restoration²⁰. We produced the
115 climate change mitigation surface (Extended Data Fig. 2a) by applying and extending a recently
116 published empirical model of the carbon sequestration potential of restoration²⁰ to the whole of
117 the Atlantic Rainforest. Restoration implementation costs, including maintenance and
118 monitoring, were estimated based on a survey with restoration companies active in the Atlantic
119 Rainforest, spatially adjusted by a proxy for natural regeneration potential based on a recently
120 published model for ecological uncertainty of tropical forest restoration success²¹ (Methods).
121 Opportunity costs, a measure of potential conflict with agricultural production, were estimated
122 based on land acquisition costs and spatial distributions of agriculture and pasturelands²². A
123 restoration costs surface (Extended Data Fig. 2b) was built based on these two costs (hereafter
124 referred to as total cost).

125 We also introduced advances regarding the impacts that the scale of a restoration project has on
126 its costs and benefits. Costs per unit area restored reduce with increasing area of the restoration
127 project, so we modelled these economies of scale using field evidence on how unitary costs fall
128 as projects grow (Methods and Extended Data Fig. 3). The size of the restoration project also

129 affects ecological outcomes, an effect which we term “ecologies of scale”, such as biomass
130 accumulation through edge effects. We also incorporated this into the prioritization using
131 empirically derived edge-effects estimate for Atlantic Forest remnants²³.

132 The Brazilian Native Vegetation Protection Law (popularly known as the “the New Forest
133 Code”²⁴) requires Atlantic Forest farmers to keep at least 20% of their farms under native
134 vegetation. Farmers currently below this threshold must meet it either by restoration in their own
135 farms, or by financing conservation or restoration offsets elsewhere within the biome. If
136 enforced, it could lead to up to 5.17 million hectares of restoration²⁴, which is the restoration
137 target area we used in all scenarios. This represents approximately 4% of the original area of the
138 biome, which has lost 73-84% of its native vegetation cover. This target was chosen so that the
139 maps produced could guide restoration efforts even if all farmers decided to compensate their
140 debts by financing restoration efforts outside their farms. Our dynamic approach allocates this
141 target area in 20 steps, so our restoration priority maps can guide restoration projects with
142 smaller targets as well (Methods and Extended Data Fig. 4). In our “baseline scenario”, farmers
143 restore this target inside their own farms until this minimum threshold is met. In a large set of
144 alternative scenarios we simulate different ways of prioritizing benefits and costs of restoration,
145 considering variation in the size of restoration projects. These 362 alternative scenarios focus on
146 combinations of maximizing the benefits for biodiversity conservation and climate change
147 mitigation, while minimizing costs (Methods and Extended Data Fig. 5). We also investigate the
148 impacts of limiting offsets to the farmer’s own state (a policy option currently being pursued by a
149 few Brazilian states).

150

151 **Results**

152 The baseline scenario has the worst performance for biodiversity conservation, the fourth worst
153 for carbon sequestration and had the highest costs across all 363 scenarios analysed (“Baseline”,
154 in Fig. 1). This allocation would avoid 7.2% of the projected extinctions (for the central
155 estimate, or 6.8% for the lower and 7.7% for the upper estimate) and sequester 0.5 billion tonnes
156 of CO₂Eq (for the central estimate, or 0.4 for the lower and 0.6 for the upper estimate; further
157 lower and upper estimates are presented in extended Data Tables 1 and 2) at a total cost of US\$
158 50.2 billion. This poor outcome suggests that pursuing alternative spatial allocations for
159 restoration would deliver greater benefits at lower costs, therefore aligning species conservation
160 and climate mitigation targets with the farmer’s interests.

161 One of the advantages of compensation outside farms is the potential to increase the size of
162 individual restoration projects – and this has a very strong positive impact on cost-effectiveness,
163 due to both economic and ecological efficiencies of scale (Fig. 2). First, economies of scale
164 result in a substantial reduction in unitary restoration costs, with a 57% drop when projects grow
165 from 1 to 100 hectares (Fig. 2a). Second, ecologies of scale lead to improved efficiencies in
166 climate mitigation outcomes for larger projects (Fig. 2b), with 100-hectare projects sequestering
167 58% more than the same area of 1-hectare ones. The combination of both economic and
168 ecological efficiencies of scale results in synergistic and marked increases in cost-effectiveness
169 for larger restoration projects (Fig. 2c), with carbon prices needed to cover restoration costs
170 dropping 73% when increasing projects from 1 to 100 hectares – a 268% improvement in cost-
171 effectiveness. These scale impacts occur across all scenarios and are independent of the relative
172 weights of the benefits. Although we did not model the impacts of restoration projects’ size on

173 biodiversity conservation, we expect the same to apply to biodiversity outcomes given the
174 importance of edge-effects on populations in small forest fragments²⁵.

175 The other advantage of compensation outside farms is implementing restoration in areas that
176 would maximise benefits, thus improving the likelihood of long-term socio-ecological success.
177 Allocations based on maximising a single benefit reveal the maximum outcomes that restoration
178 prioritisation can achieve for each benefit. For biodiversity conservation, results are striking:
179 29.7% of the species committed to extinctions could be saved (“Maximum Biodiversity”, in Figs.
180 1a and 1b), an improvement of 311% in relation to the baseline scenario. Likewise, a focus on
181 climate change mitigation could sequester up to 1.3 GtCO₂Eq (“Maximum Climate”, in Figs. 1a
182 and 1c), a 174% increase from the baseline scenario. Focusing on costs would reduce them to
183 US\$ 15.2 billion (“Minimum Costs”, in Figs. 1a and 1d), a 69% saving on the baseline scenario.
184 But despite the marked improvements in relation to baseline, these single-focus allocations have
185 mixed and varied outcomes when all benefits and costs are considered. For instance, aiming
186 solely for biodiversity conservation benefit yields a much larger fraction of the greatest possible
187 climate change mitigation benefit (75% of those under “Maximum Climate”) than the reverse,
188 with only 51% of the “Maximum Biodiversity” benefit being captured by the climate-focused
189 allocation (Fig. 1). The latter metric is much higher for birds (72%), with plants benefiting the
190 least (45%) from the climate-focused solution (extended Data Figure 6). The biodiversity-
191 focused solution would cost US\$ 35 billion (delivering 44% of the potential costs savings and
192 resulting in benefit-costs ratios of US\$ 9 million per species saved and US\$ 35 per tonne of
193 CO₂Eq) whereas the climate-focused solution would cost US\$ 29 billion (59% of the cost-
194 savings achieved by “Minimum Costs” and benefit-costs ratios US\$ 15 million per species saved
195 and US\$ 23 per tonne of CO₂Eq).

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

202 Compromise solutions can simultaneously deliver a substantial fraction of the maximum
203 outcome for each benefit. Our approach allowed us to combine the efficiencies of scale with
204 multicriteria spatial prioritisation to systematically generate and evaluate solutions that combine
205 different weights for benefits and costs, generating efficiency frontiers (Fig 1). The outer frontier
206 is generated by eliminating the costs component from the algorithm, whereas the “Cost-effective
207 frontier” is produced by maximising cost-effective benefits for biodiversity and climate change
208 mitigation. One of the solutions on the cost-effective efficiency frontier (“Compromise” in Figs.
209 1a and 1e) increases biodiversity benefits by 257% (equivalent to 94% of those achieved under
210 “Maximum Biodiversity”), improves by 105% the climate change mitigation benefit (79% of
211 “Maximum Climate”), and reduces costs by 57% (83% of the reduction achieved by “Minimum
212 Costs”), when compared to the baseline scenario. This translates into an eightfold increase in
213 cost-effectiveness for biodiversity conservation.

214 These compromise solutions arise from the concave shape of the efficiency frontier curves (Fig.
215 1a), which indicate that when departing from single-focus solutions, large gains for one benefit
216 can be achieved at relative modest cost to others. Indeed, moving from “Maximum Climate” to
217 “Compromise” results in a loss of 20% in climate change mitigation but a gain of 95% in
218 avoided extinctions. In absolute terms, sequestering 0.27 GtCO₂Eq less would save 411 animal

219 and plants from extinction, when applying the relative reduction in extinctions to the overall
220 extinction debt of plants and animals in the biome (Extended Data Table 1), a trade-off ratio of 1
221 animal or plant extinction avoided for every 0.7 million tonnes of CO₂Eq not sequestered. Given
222 biodiversity's key role in driving the productivity of ecosystems²⁶, such compromise might result
223 in climate mitigation gains in the long term. Climate change adaptation might also benefit from
224 improved ecosystem-based adaptation²⁷ due to more resilient ecosystems. Furthermore, it can be
225 argued that species extinctions are irreversible losses whereas reductions in carbon sequestration
226 are reversible and can be compensated for, suggesting that greater importance should be given to
227 the former. Revealing trade-offs in units that people can relate to helps to inform the stark
228 decisions that need to be made in a context of scarcity.

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

240 Spreading restoration across wider areas by considering that not all deforested lands in priority
241 landscapes would be restored might be more feasible in practice and would not have overly large

242 impacts on the benefits. Indeed, restricting the maximum restoration allowed in each planning
243 unit has moderate impacts for biodiversity outcomes and small ones for carbon. When restricting
244 the proportion of the planning unit that can be reforested to 65% and 35%, biodiversity outcomes
245 fall by 6% and 17% respectively (Extended Data Figure 9). For climate mitigation, the same
246 restrictions result in reductions of 2% and 6% respectively (Extended Data Figure 9). These
247 decreased outcomes arise from selecting areas that have comparatively lower priority for those
248 benefits, as these caps lead to restoration being allocated beyond the very highest priority
249 planning units.

250 Our results also provide important insights for considering how to share the costs of achieving
251 the restoration targets between farmers and the wider society. Benefits from restoration are
252 shared between farmers and the wider society (in Brazil and elsewhere), whereas the opportunity
253 and restoration costs would be borne by the farmers, as the target being analysed here arises from
254 past deforestation beyond legal limits. On the one hand, the overall cheapest solution for farmers
255 (“Minimum Costs”) would be US\$ 19 billion cheaper than a solution that combines large
256 benefits for biodiversity and climate change mitigation without considering costs (“Environment
257 Only”), so it could be argued that the collective benefits would justify that society pay for this
258 difference if the latter solution is to be achieved. Payments for Ecosystem Services (PES)
259 schemes are a way to incentive farmers to pursue options more beneficial to the wider society.
260 Carbon-based incentives of US\$ 38/t CO₂Eq, species-based incentives of US\$ 30
261 million/extinction avoided or a combination of both would be enough to pay for the difference in
262 costs. On the other hand, the “Environment Only” solution is US\$ 14 billion cheaper than the
263 baseline scenario, which would have to be paid individually by farmers. Therefore, it could be
264 argued that farmers could choose intermediate solutions, since this reduction in costs is made

265 possible by the Brazilian society decision in 2012 to allow compensation outside their farms. The
266 intermediate “Compromise” solution still delivers reasonable environmental outcomes and, being
267 US\$ 7 billion more expensive than the cheapest possible but US\$ 29 billion cheaper than the
268 baseline scenario, could be seen as a reasonable compromise for farmers to invest in.
269 Alternatively or complementarily, carbon incentives of US\$ 15/t CO₂Eq, species-based
270 incentives of US\$ 9 million/extinction avoided or a combination of both would be enough to
271 cover the difference from the cheapest solution. It is important to highlight that restoration
272 projects can lead to positive financial returns based on revenues from sustainable management of
273 timber or non-timber forest products, potentially complemented by PES schemes⁵.

274 Introducing broad scale spatial restrictions on restoration – such as allowing off-farm
275 compensation but only within state borders – generates more nuanced outcomes. On the one
276 hand, constraining restoration by state borders leads to worse outcomes when compared to the
277 unconstrained version of each goal, whether assessed for biodiversity conservation (10% lower),
278 climate change mitigation (14% lower) or cost minimization (17% more expensive) (Extended
279 Data Table 1). On the other hand, a state-constrained cost-minimization scenario would yield
280 103% and 44% higher returns for biodiversity and climate respectively, compared with an
281 entirely unconstrained “Minimum Costs” scenario (Extended Data Table 1). So if the alternative
282 is that farmers offset in the cheapest areas of the biome, constraining their choices to the
283 cheapest areas in their home states would bring substantially higher environmental benefits at
284 modest additional cost.

285 **Discussion**

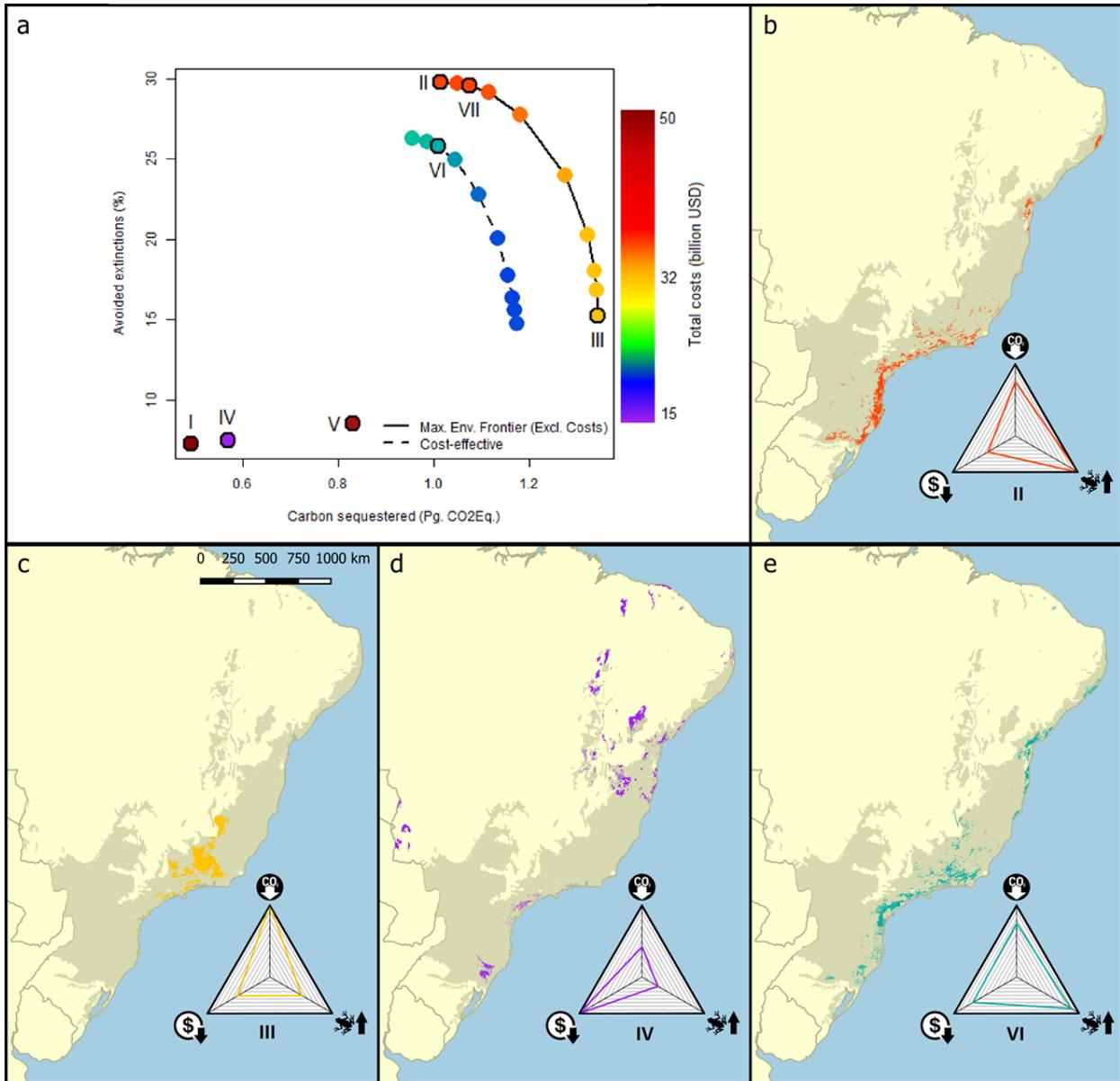
286 It is important to highlight that while the baseline scenario performs very poorly in terms of all
287 three outcomes analysed in this study, having smaller patches of restoration dispersed across the
288 entire biome would have other benefits. For instance, the provision of local ecosystem services
289 such as soil retention, improved water quality and pollination tends to be more widely distributed
290 across the landscapes with small and dispersed restored sites²⁸, while the ecological equivalence
291 between remnants, the representation of different ecological communities and community
292 integrity across the biome²⁹ can be higher. Crucially, the Law of Native Vegetation Protection
293 also mandates that mountaintops and riparian areas should be preserved, a requirement estimated
294 to lead to another 5.2 million hectares of restoration. As these are fixed in space (so not subject
295 to spatial prioritisation) and dispersed throughout all watersheds of the biome, the combination
296 of restoring legal reserves in priority areas and riparian and mountaintop areas throughout the
297 biome could deliver increased local, regional and global benefits at lower costs.

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

305 The technical advances and high degree of customisation to context-specific policies and goals
306 led the Brazilian Ministry of Environment to decide to use the decision supporting tool and the
307 maps introduced here as the key prioritization information for restoring the Atlantic Rainforest,
308 and to commission the replication of our approach to the other five Brazilian biomes as part of

309 the National Plan for Native Vegetation Recovery - PLANAVEG³⁰. The potential of this
310 approach for easily exploring large numbers of scenarios will be of particularly importance for
311 two PLANAVEG strategies, the Spatial Planning & Monitoring and Finance. These ongoing
312 biome-specific initiatives are tapping into our approach's ability to include customised sets of
313 benefits and costs, such as water (Atlantic Forest); farmers income (originated from ecosystem
314 services and forest products in all biogeographical regions); pollination (Amazon), firewood
315 production (Caatinga) and ecotourism-related species (Pantanal). Furthermore, the time-
316 efficiency of the linear programming approach permits assessment of thousands of variations of
317 factor weightings in a few hours (for applications of the size and complexity presented here),
318 allowing stakeholders to select the most desirable allocations based on final outcomes, avoiding
319 the often-contentious task of selecting relative weights a priori.

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



327

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

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

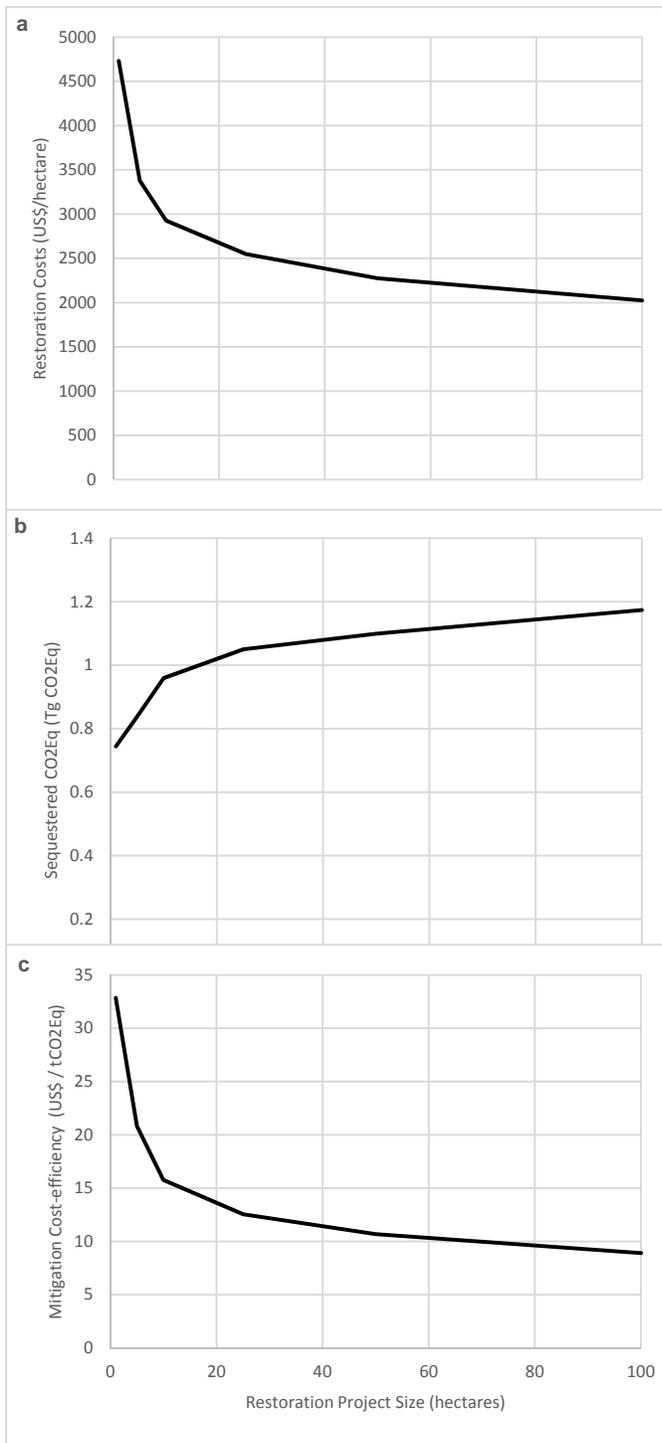
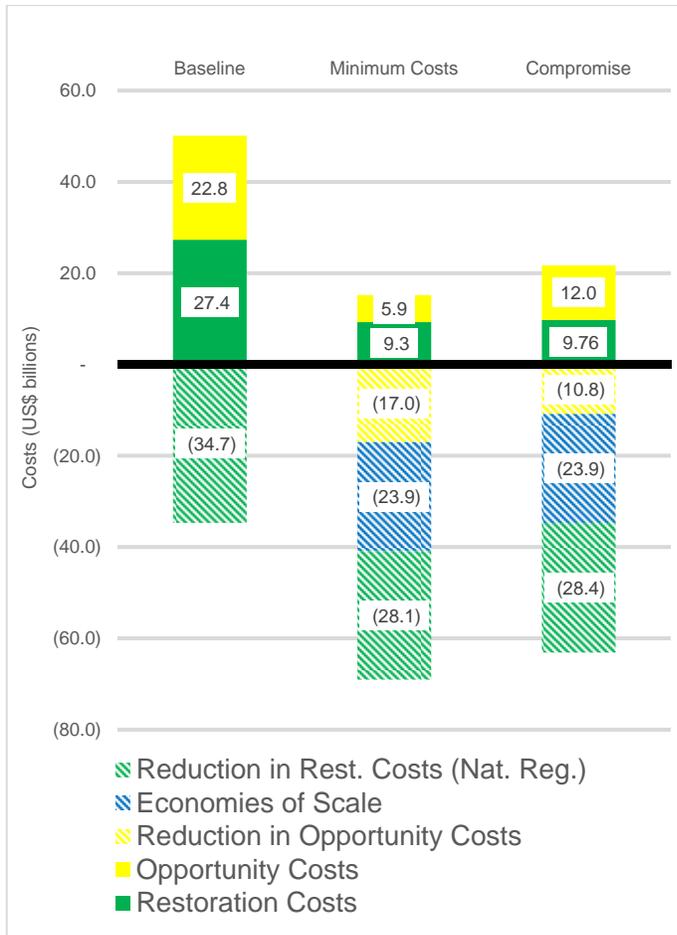


Figure 2 - Impacts of economic and ecological efficiencies of scale on cost-effectiveness. **a.** shows the relation between increasing restoration project sizes and the restoration costs per unit area; **b.** shows the relation between increasing project size and the total CO₂Eq sequestered in the “Maximum 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.



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Figure 3 – Impacts of economies of scale and of spatial prioritization for reducing

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opportunity and restoration costs across different scenarios. Filled rectangles are actual

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restoration (green) and opportunity (yellow) costs incurred in each scenario. Diagonally striped

356

rectangles represent reductions in costs due to natural regeneration (green stripes), reduction in

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opportunity costs (yellow stripes) and economies of scale (blue stripes).

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425

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434

435 **Author Contributions**

436 BBNS conceived the study, coordinated the development of the multicriteria approach and wrote
437 the first version of the paper. HB, BBNS, RC and AI led the optimisation modelling, MFS, FB,

438 AST developed the environmental niche modelling; BBNS, HB, RC, AI, MM, HPP, FB, MFS,
439 AB, JB, PHSB, RC, AG, AL, JPM, RRR, CAMS, FRS, LT, TG and MU developed the
440 multicriteria prioritisation approach; RL, JPM and AOF contributed biodiversity data, RC and
441 ENB developed the climate mitigation surface, CAMS coordinated the interface with policy
442 applications; all authors analysed the results and provided input into subsequent versions of the
443 manuscript.

444

445 **Author Information**

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447 declare no competing financial interests. Correspondence and requests for materials should be
448 addressed to B.B.N.S. (b.strassburg@iis-rio.org).

449 **Methods**

450 In this study, we developed a multi-criteria spatial restoration prioritization approach for the
451 Brazilian Atlantic Forest hotspot to investigate alternative restoration scenarios. We simulated
452 the restoration of approximately 5.17 Million hectares (estimated deficit of Legal Reserve in the
453 Atlantic Forest²⁴) to: 1) quantify variation in costs and benefits of restoration among a range of
454 possible scenarios governing where restoration occurs; 2) quantify trade-offs among costs and
455 benefits in order to identify good compromise solutions; 3) quantify the effects of economies of
456 scale and analogous ecologies of scale impacts on carbon sequestration by using restoration
457 block sizes of 1, 5, 10, 25, 50 or 100 ha; and 4) quantify the effects of restricting the maximum
458 proportion of land that can be restored within each planning unit (up to 35, 65 and 100%).
459 Our multi-criteria spatial restoration prioritization approach was based on five main steps: 1)
460 conduct consultations with representatives of the Ministry of Environment and other
461 stakeholders of the Atlantic Forest biogeographical region to identify critical variables to be
462 included in our modelling and to develop restoration scenarios that reflect the policy objectives
463 and multi-stakeholder preferences; 2) gather and model variables to be used as inputs; 3) develop
464 a novel multi-criteria spatial restoration prioritization framework implemented as an Integer
465 Linear Programming problem (hereafter ILP); 4) simulate restoration scenarios; and 5) analyse
466 and interpret the solutions and their trade-offs.
467 We developed spatial surfaces for the three benefits of biodiversity – conservation, climate
468 change mitigation and costs reduction. We detail each of these below, followed by explanations
469 of the scenarios analysed and the optimisation model itself.

470 **Biodiversity conservation benefits**

471 Benefits to biodiversity conservation are quantified using species extinction functions reflecting
472 diminishing returns associated with increasing areas of habitat for each species (Extended Data
473 Figure 1). This function is based on a re-working of the Species-area relationship and operates at
474 the level of individual species¹⁸. This approach is imperfect, as it ignores the possibility of
475 negative density-dependence at very low population sizes, and says nothing about the time scale
476 of resulting extinctions, which will vary with species' life history and ecology. However unlike
477 simpler formulations, it takes account of the non-linearity of the response of persistence to
478 changes in population size, and has been used in several similar studies^{11,18,19}. If existing habitat
479 area is small there is a large benefit to increasing that area, but as the area of habitat increases
480 there is a diminishing benefit for the addition of more habitat area. Following reference #11, the
481 change in extinction risk (r) for each individual species as a function of habitat area was
482 modelled as

$$483 \quad r = 1 - (x/A_0)^z \quad (1)$$

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

491 **Ecological niche models**

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

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

498 *Species occurrence data*

499 We collated all freely available occurrence data on endemic amphibians, birds and woody plants
500 in the Brazilian Atlantic Forest. Data on amphibian occurrence was obtained from³¹, with
501 updates from the authors, and comprised 114 endemic species (3,786 occurrences). Data on bird
502 occurrence was obtained from the Global Biodiversity Information Facility database³², and
503 comprised 223 endemic species (12,085 occurrences). Data on plants occurrence was obtained
504 from NeoTropTree and SpeciesLink³³, and comprised 846 endemic species and 44, 024 records.
505 The original plant names were based on the NeoTropTree database³⁴ and updated according to
506 the List of Species of the Brazilian Flora³⁵, using R package 'flora'³⁶, which is based on the
507 List's Integrated Publishing Toolkit database³⁷.

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

512

513 *Environmental data*

514 The initial environmental dataset was composed of 28 variables –the 19 bioclimatic variables
515 from Worldclim³⁹, four CGIAR CSI geohydrologic variables (actual evapotranspiration, aridity
516 index, soil water balance and potential evapotranspiration⁴⁰) and five USGS topographic

517 variables (elevation, slope, aspect and topographic index⁴⁰). All variables had a spatial resolution
518 of 1 km². Since aspect is a circular variable, its sine and cosine were calculated to be used as two
519 different variables instead.

520 We summarized these variables into ten orthogonal variables, calculated through a PCA of the
521 whole raster set. These account for 95% of the overall environmental variation in the BAF. The
522 PCA variables were used to reduce errors in the modelling process, caused by the spatial
523 autocorrelation of presence data or the multi-collinearity of the environmental predictors⁴¹⁻⁴².

524 *Ecological niche modelling methods*

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

533 For each species, random pseudo-absence points were sorted within a maximum distance buffer
534 (i.e. the radius of the buffer is the maximal geographic distance between the occurrence points).
535 This procedure reduces the modelling background area, assuring better estimates, once
536 pseudoabsences were sampled only in areas where species could disperse⁴⁴⁻⁴⁶ at the same time
537 controlling the low prevalence associated with generating pseudoabsences inside large range
538 areas.

539 Species were modelled using a three-fold cross-validation procedure, to guarantee a minimum
540 number of presence records in the test set due to the small number of samples for some species.
541 For each partition and algorithm, a model was fitted and its performance was tested by
542 calculating TSS. Only models with TSS > 0.7 were retained. As a consequence, at the end of this
543 modelling phase 51 amphibian species, 122 bird species, and 612 woody plant species endemic
544 to the Brazilian Atlantic Forest composed the final potential richness maps. Retained models
545 were cut by the threshold that maximizes their TSS and ensemble models were built by the
546 majority consensus rule (i.e. area where at least half of the algorithms predict a potential
547 presence of the species⁴⁷), resulting in a binary map of species potential distribution. The steps
548 described above were taken in order to reduce some of the limitations of the species distribution
549 models, such as the fact that they are merely correlative, and not mechanistic models, and to
550 control overfitting and inflated evaluation statistics when species are very restricted compared to
551 the total geographic area..

552

553 The modelling was performed using ModelR⁴⁸, a set of R scripts for species distribution model
554 fitting and assessment based on packages, XML⁴⁹, dismo⁵⁰, raster⁵⁰, rgdal⁵¹, maps⁵², rgeos⁵³,
555 randomForest⁵⁴, and e1071^[55].

556

557 **Climate mitigation Benefits**

558 We built a potential above ground biomass recovery map for the Brazilian Atlantic Forest, which
559 is a proxy for above ground potential carbon sequestration in degraded areas (Extended Data
560 Figure 2). The map has a resolution of 1 km² and followed the methods of reference #[20]. That
561 study included three biomes: 1) tropical and subtropical moist broadleaf forests, 2) tropical and

562 subtropical dry broadleaf forests, and 3) tropical and subtropical coniferous forests²⁰. These
563 biomes were defined based on a map of world ecoregions obtained from the Nature
564 Conservancy⁵⁶. Total annual precipitation was calculated by summing the individual monthly
565 totals provided by WorldClim⁵⁷. Data for mean annual rainfall (defined as the average of 1950–
566 2000) and rainfall seasonality were obtained at a 30” resolution (approx. 1 km × 1 km) from
567 WorldClim⁵⁷, and Climatic Water Deficit (CWD) was obtained from reference #[58].

568 We calculated the total potential above ground biomass recovery (AGB) accumulation over
569 20 years of secondary forest growth (assuming that the initial year 0 condition was a fully
570 cleared area), based on annual rainfall, rainfall seasonality, and CWD. The regression equation
571 obtained by reference #[20] estimates AGB after 20 years based on best-fit models that
572 incorporate climatic variables as follow:

$$573 \text{AGB}_{20y} = 135.17 - 103,950 \times 1/\text{rainfall} + 1.521983 \times \text{rainfall seasonality} + 0.1148 \times \text{CWD} \quad (2)$$

574 where estimated AGB_{20y} indicates the absolute biomass recovery potential over 20 years based
575 on chronosequence models²⁰. Realized local rates of biomass recovery may vary because of
576 differences in local soil conditions, land use history, the surrounding matrix, and availability of
577 seed sources.

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

582 We did not include changes in carbon stocks in the soils, as very few studies investigate the
583 carbon accumulation or loss in soils following restoration in the Atlantic Rainforest⁵⁹. We
584 believe this is a conservative assumption. A recent global study showing the impact of land-use

585 change on soil organic carbon⁶⁰ shows significant losses following deforestation in the Atlantic
586 Rainforest. Further research would enable future studies to overcome this limitation.

587

588 **Costs**

589 The cost of land restoration for each area within the Brazilian Atlantic Forest was based on the
590 opportunity cost for restoration of the land and the cost associated to restoring it, actively or
591 passively. Opportunity cost is the potential loss of revenue from agriculture or livestock from
592 areas being restored. We used the land acquisition cost as a proxy for opportunity cost, which is
593 based on an established economic assumption that higher acquisition costs are due to land
594 generating greater economic gains²², as land acquisition cost should reflect the discounted future
595 revenues from that land. We combined spatial data on the distribution of pasturelands and
596 croplands (MMA unpublished data) with county level data on the land acquisition costs for these
597 two categories⁶¹.

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

604 The likelihood of an area requiring active or passive restoration is determined by socio-economic
605 factors that determine the likelihood of an area been abandoned to regrowth and on ecological
606 factors that determine the resilience of the ecosystem to disturbance. As this information is not
607 available for the Atlantic Forest, we used the ecological uncertainty of forest restoration success

608 for plant biodiversity²¹ as a proxy for it. The recent global meta-analysis of reference #21
609 revealed a clear pattern of increasing the success of forest restoration (by comparing plant
610 biodiversity in reference and restored/degraded systems) and decreasing uncertainty as the
611 amount of forest cover increases. We built our map on the ecological uncertainty of forest
612 restoration success by calculating the amount of forest cover surrounding each non-forested pixel
613 within a buffer size of 5 km (the strongest scale of effect). We subsequently applied the negative
614 non-linear equation of reference #[21] over the map. Finally, we standardized the values within
615 each pixel (dividing its value by the highest value found across all pixels) to provide an index
616 that varies from 0 (low uncertainty) to 1 (high uncertainty). Our restoration costs map therefore
617 identifies areas where natural regeneration and/or active restoration methods are most likely to
618 foster plant biodiversity recovery to similar levels found in reference systems (i.e. old-growth or
619 less-disturbed forests).

620 Restoration cost (r) was calculated as

621
$$r = u \times c + f \quad (3)$$

622 where u is the ecological uncertainty of forest restoration success, c is the cost of the full
623 planting, and f is the cost of the fencing. Areas with lower ecological uncertainty of forest
624 restoration success will be less expensive for restoration, i.e. will require less human
625 intervention. The cost of full planting method (the most expensive method for active restoration)
626 was obtained from³⁰. Thus, our total costs map (Extended Data Figure 3) was produced by
627 adding, for each panning unit, the values of the opportunity costs map with the values from the
628 restoration costs map.

629 We also incorporated cost reductions based on economies of scale for restoration projects of
630 different sizes for the first time. To understand how per-unit costs reduce with scale, we gathered

631 information from five active forest planting companies in the Atlantic Forest. We obtained cost
 632 estimates for restoration projects of the following sizes: 1, 5, 10, 25, 50 and 100 ha. We then
 633 analysed how the average costs per project scaled with project size and fitted linear functions to
 634 this data (Extended Data Figure 4). In each of the size-related scenarios (corresponding to the six
 635 project sizes listed above), restoration was constrained to happen up to that size.

636 **Other variables**

637 Forest cover data was obtained from the map produced by⁶⁴, derived from TM/Landsat 5,
 638 ETM+/Landsat 7 or CCD/CBERS-2 images, available at a scale of 1:50,000 in vector format,
 639 and delimiting remnants ≥ 3 ha. This data was used to calculate the: i) proportion of existing
 640 forest (f) within a planning unit, ii) environmental deficits according to the Native Vegetation
 641 Protection Law, and iii) amount of area that could be restored within each planning unit. Our
 642 analysis was focused on areas where the native vegetation was forest, therefore excluding areas
 643 such as natural grasslands or mangroves. In addition to the forest cover, we also masked areas
 644 that could not be restored (e.g. urban areas, roads, lakes, etc) within each planning unit. All
 645 geographic information system data were converted to Albers projection to assure accurate area
 646 and distance calculations.

647 **Prioritization model**

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

651

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

654 (4)

655

656

657 where x is the decision variable representing the proportion of forest to restore within each
658 planning unit i . The two components of the objective function represent the returns (benefit/cost)
659 of forest restoration to biodiversity conservation ($b/(c + e)$; benefit $\text{US}\$^{-1} \text{km}^{-2}$) for each species j
660 and carbon sequestration ($s/(c + e)$; tonnes $\text{US}\$^{-1} \text{km}^{-2}$), where the total cost of forest restoration
661 is the sum of the opportunity cost (c ; $\text{US}\$^{-1} \text{km}^{-2}$) and the restoration cost (e ; $\text{US}\$^{-1} \text{km}^{-2}$). N is
662 the total number of planning units and M is the total number of species. The first constraint
663 ensures that the proportion of forest restored ranges from 0 to a maximum value (f), which
664 accounts for the proportion of the planning unit that is already forested or represents a land use
665 that cannot be restored. In scenarios that limited the maximum proportion of forest in each
666 planning unit to 35% or 65%, the functions $\min(0.35, f)$ or $\min(0.65, f)$ were used to define the
667 upper limit of x . The second constraint limits the total area of forest to be restored (A ; km^2),
668 where $A = 5,179,088$ ha. The user-defined parameters w_1 and w_2 weight the relative contribution
669 of the biodiversity and carbon sequestration components of the objective function. They are
670 required because the equivalence of objectives with different units is a subjective decision that
671 must be made by decision makers. The objective function can be solved over a range of relative
672 weights in order to understand how these components trade-off. The model was solved
673 iteratively in 20 increments of the target area A in order to approximate the non-linear function
674 describing biodiversity conservation values, that is, the target was not prioritized at once only.
675 We tested the influence that running even greater intervals (up to 1000), and found very marginal
676 gains after 10 runs (biodiversity benefits varied by $-1,20\text{E}-06$ between the 10 and 1000 runs

677 simulations). Alternative scenarios involved removal of components of this model, such as the
678 removal of the total cost denominators ($c + e$) in order to maximise benefits regardless of cost, or
679 the addition of further constraints for the scenarios that limited the area of restoration within each
680 state. Exact solutions to this ILP problem were found using the software Gurobi (version 6.5.1).

681 **Scenarios**

682 We evaluated 382 restoration scenarios. These included 360 that combined 10 different weights
683 to the objectives of maximising biodiversity conservation, maximising carbon sequestration and
684 minimising total cost with variations in the maximum area of the planning unit allowed to be
685 restored (35, 65 and 100%)(Extended Data Figure 9), and six restoration project sizes (1,5,10,25,
686 50 and 100 ha).

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

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

696 **Code Availability**

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

700 **Data availability**

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

704

705 **Methods References**

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