

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

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

9  
10 1 – Rio Conservation and Sustainability Science Centre, Department of Geography and the  
11 Environment, Pontifícia Universidade Católica, 22453900, Rio de Janeiro, Brazil

12 2 – International Institute for Sustainability, Estrada Dona Castorina 124, 22460-320, Rio de  
13 Janeiro, Brazil

14 3 – Programa de Pós Graduação em Ecologia, Universidade Federal do Rio de Janeiro, 21941-  
15 590, Rio de Janeiro, Brazil

16 4 – ARC Centre of Excellence for Environmental Decisions, School of Biological Sciences,  
17 University of Queensland, St. Lucia, 4072, Queensland, Australia

18 5 – Botanical Garden Research Institute of Rio de Janeiro, Rua Jardim Botânico 1008, 22470-  
19 180 Rio de Janeiro, Brazil

20 6 – Department of Zoology, University of Cambridge, Downing Street, Cambridge, CB2  
21 3EJ, UK

22 7 – Department of Environmental Science, Instituto de Florestas, Federal Rural University of Rio  
23 de Janeiro, Rodovia BR 465, Km 07, s/n - Rural, Seropédica, 23890-000, Brazil

24 8 – Departamento de Ciências Florestais – Esalq/USP, Av. Pádua Dias 11, 13.418-900,  
25 Piracicaba, SP, Brazil

26 9 – Spatial Ecology and Conservation Lab, School of Forest Resources and Conservation,  
27 University of Florida, Gainesville, Florida, USA, 32611

28 10 – Department of Ecology and Evolutionary Biology, University of Connecticut, 75 N.  
29 Eagleville Road, Unit 3043, Storrs, CT 06269-3043, U.S.A.

30 11 – World Resources Institute, Global Restoration Initiative, 10 G Street, NE Suite 800,  
31 Washington, D.C. 20002 - USA

32 12 – Department of Botanic, Federal University of Minas Gerais, Av. Antônio Carlos, 6627,  
33 31270-901, Belo Horizonte, MG, Brazil

- 34 13 – Stockholm Environment Institute, Linnégatan 87D, 115 23 Stockholm, Sweden
- 35 14 – School of Global Urban and Social Studies, RMIT University, GPO Box 2476 Melbourne,  
36 Australia 3001
- 37 15 – Institute of Agricultural Engineering and Informatics, Faculty of Production and Power  
38 Engineering, University of Agriculture in Kraków, Balicka 116B, 30-149 Kraków, Poland
- 39 16 – School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United  
40 Kingdom
- 41 17 – Laboratório de Biogeografia da Conservação, Departamento de Ecologia, Universidade  
42 Federal de Goiás, Goiânia, GO, Brazil
- 43 18 – Department of Ecology, Institute of Biosciences, University of São Paulo, Rua do Matão,  
44 321, Travessa 14, 05508-900, São Paulo, SP, Brazil
- 45 19 – Faculty of Natural Sciences, Department of Life Sciences, Silwood Park, Imperial College  
46 London, London SW7 2AZ, UK
- 47 20 – The Nature Conservancy, 4245 Fairfax Drive, Arlington, VA 22203, USA
- 48 21 – The University of Queensland, St Lucia, QD, 4072, Australia
- 49 22 – Department of Biological Science, Escola Superior de Agricultura Luiz de Queiroz,  
50 University of São Paulo, Avenida Pádua Dias n. 11, Centro, 13418900 Piracicaba, SP, Brazil
- 51 23 – Department of Ecosystems Conservation, Brazilian Ministry of the Environment (MMA).  
52 Ed. Marie Prendi Cruz, SEPN 505 Norte, Bloco "B" 4 ° andar sala 416, 70.730-542, Brasília,  
53 Brazil
- 54 24 – The Brazilian Foundation for Sustainable Development, R. Eng. Álvaro Niemeyer, 76 - São  
55 Conrado, Rio de Janeiro - RJ, 22610-180, Brazil
- 56 25 – Centro de Engenharia, Modelagem e Ciências Sociais Aplicadas, Federal University of  
57 ABC, Av. dos Estados, 5001, Bairro Santa Terezinha, Santo André, SP, Brazil
- 58 26 – Department of Ecology, Evolution and Environmental Biology, Columbia University, 116th  
59 St & Broadway, New York, NY 10027, USA

60 **International commitments for ecosystem restoration add-up to one-quarter of the world's**  
61 **arable land<sup>1</sup>. Fulfilling them would ease global challenges such as climate change<sup>2</sup> and**  
62 **biodiversity decline<sup>3</sup>, but could displace food production<sup>4</sup> and impose financial costs on**  
63 **farmers<sup>5</sup>. 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 CO<sub>2</sub>Eq (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 Goals<sup>6-8</sup>, 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 Agreement<sup>1</sup>. 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 space<sup>9-11</sup>. In the  
81 context of safeguarding existing habitats there has been considerable progress in understanding  
82 some of these trade-offs<sup>3</sup>, with the field of Systematic Conservation Planning (SCP) providing

83 methods for spatial prioritisation that maximize benefits while minimizing costs<sup>12</sup>. Despite some  
84 recent efforts<sup>9-10,13</sup>, 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 hotspot<sup>14-15</sup>, a highly deforested and fragmented  
90 region poised to undergo one of the biggest large-scale restoration efforts<sup>16</sup>. 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 software<sup>17</sup>. 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 km<sup>2</sup>. For biodiversity conservation,  
99 benefit was measured as the reduction in projected extinctions owing to habitat restoration<sup>18</sup>. 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<sup>11,19</sup> 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 restoration<sup>20</sup>. 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 restoration<sup>20</sup> 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 success<sup>21</sup> (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 pasturelands<sup>22</sup>. 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 remnants<sup>23</sup>.

132 The Brazilian Native Vegetation Protection Law (popularly known as the “the New Forest  
133 Code”<sup>24</sup>) 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 restoration<sup>24</sup>, 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 CO<sub>2</sub>Eq (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 fragments<sup>25</sup>.

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 GtCO<sub>2</sub>Eq (“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 CO<sub>2</sub>Eq) 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 CO<sub>2</sub>Eq).



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 GtCO<sub>2</sub>Eq 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 CO<sub>2</sub>Eq not sequestered. Given  
222 biodiversity's key role in driving the productivity of ecosystems<sup>26</sup>, such compromise might result  
223 in climate mitigation gains in the long term. Climate change adaptation might also benefit from  
224 improved ecosystem-based adaptation<sup>27</sup> 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 CO<sub>2</sub>Eq, 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 CO<sub>2</sub>Eq, 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 schemes<sup>5</sup>.

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**

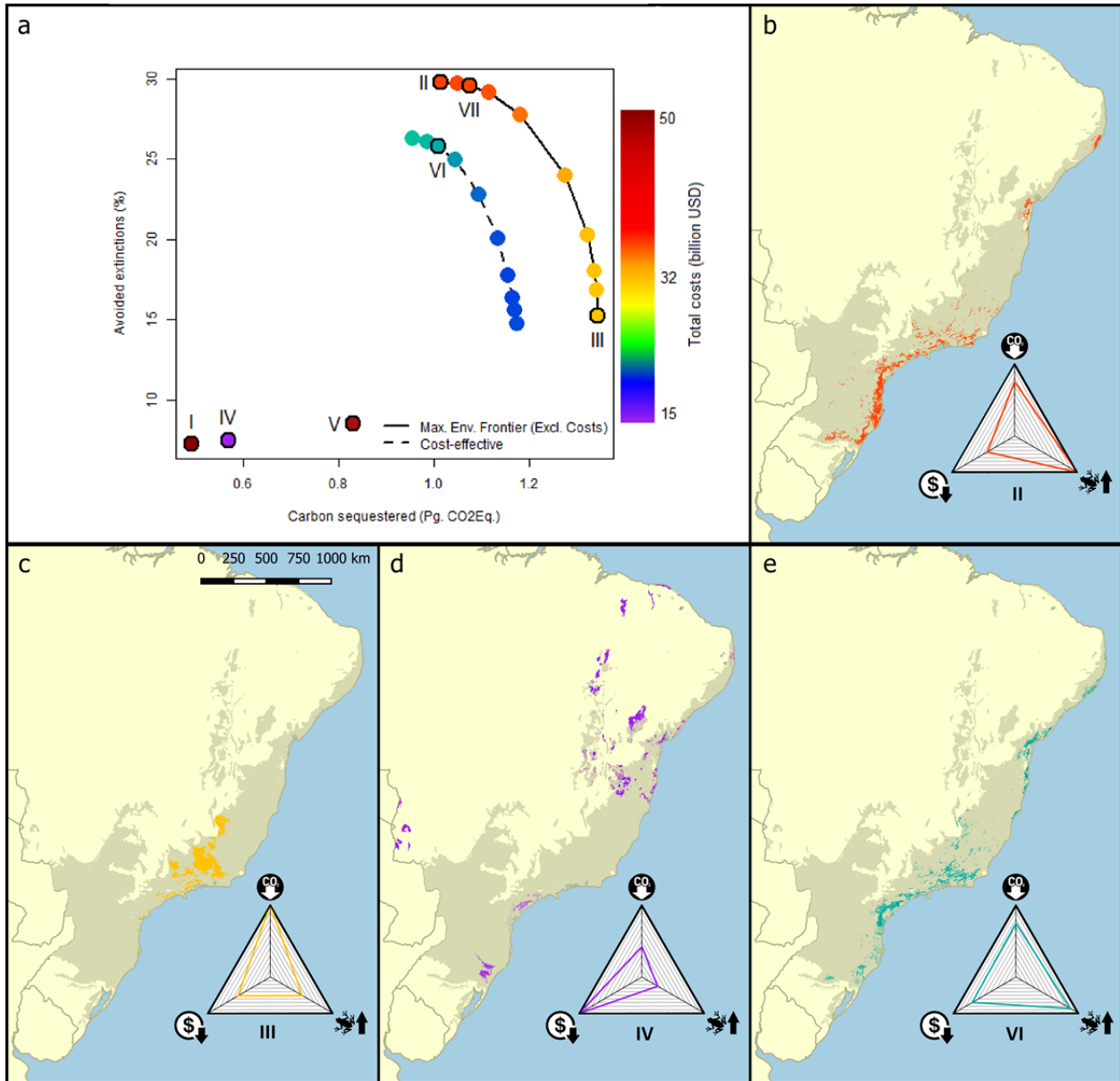
286 It is important to highlight that while the baseline scenario performs very poorly in terms of all  
287 three outcomes analysed in this study, having smaller patches of restoration dispersed across the  
288 entire biome would have other benefits. For instance, the provision of local ecosystem services  
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 sites<sup>28</sup>, while the ecological equivalence  
291 between remnants, the representation of different ecological communities and community  
292 integrity across the biome<sup>29</sup> 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 - PLANAVEG<sup>30</sup>. 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.

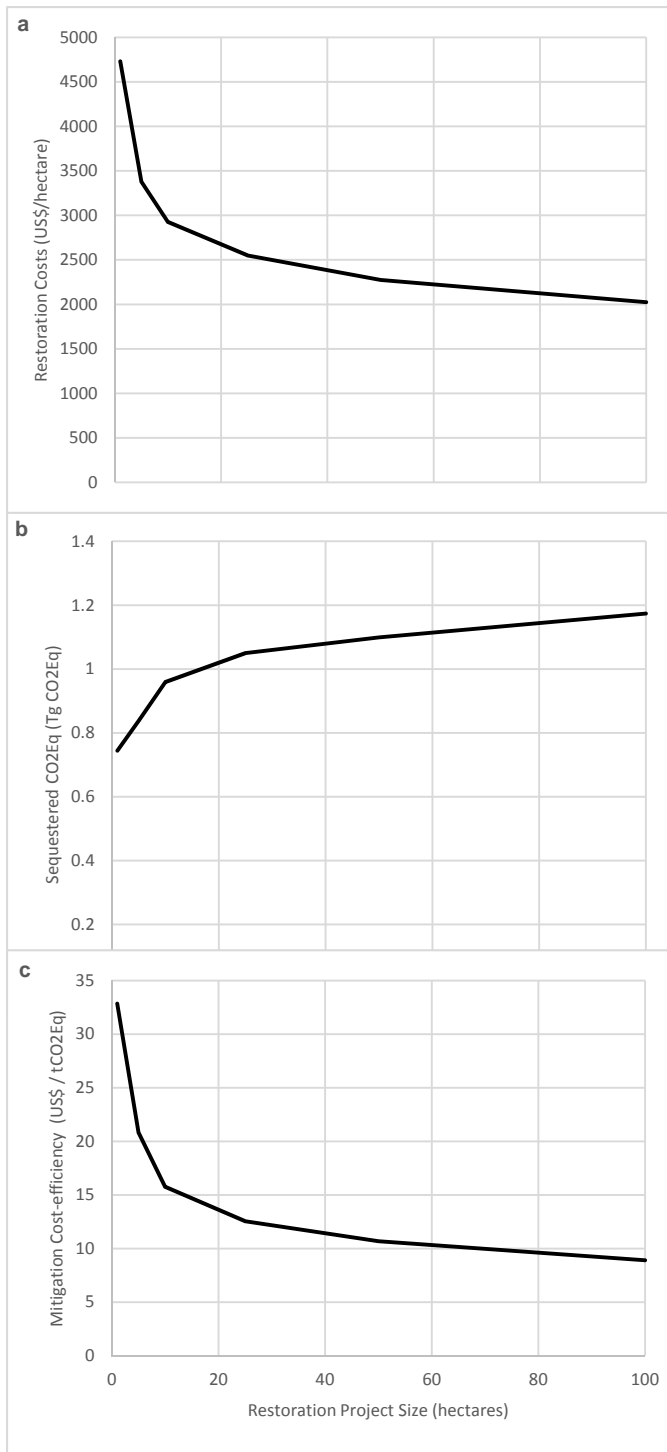


327

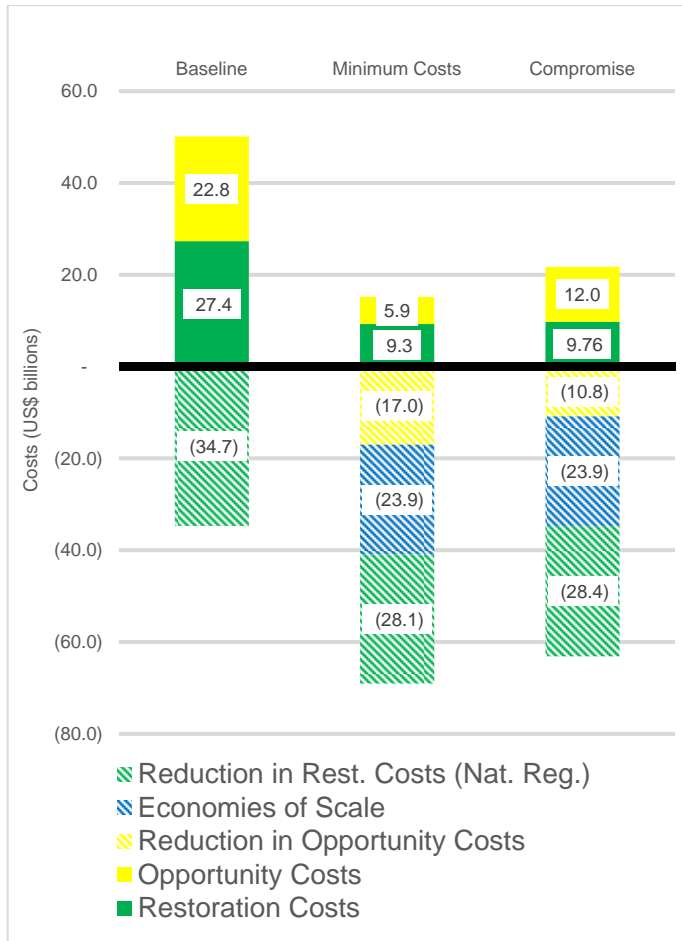
328 **Figure 1 - Spatial configurations and outcomes for climate change mitigation, avoided**  
 329 **extinctions and total costs of selected scenarios.** In panel a, point “I” corresponds to the  
 330 baseline scenario without offsets, “II” is the “Maximum Biodiversity” scenario, “III” is  
 331 “Maximum 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 CO<sub>2</sub>Eq 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.



351  
352

353

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

354

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

355

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

356

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

357

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

358 **References**

- 359 1. Verdone, M. & Seidl, A. Time, space, place, and the Bonn Challenge global forest  
360 restoration target. *Rest Ecol* **25**, 903-911 (2017).
- 361 2. Chazdon, R.L. *et al.* Carbon sequestration potential of second-growth forest  
362 regeneration in the Latin American tropics. *Science Advances* **2**, e1501639 (2016).
- 363 3. Crouzeilles, R. Ecological restoration success is higher for natural regeneration than  
364 for active restoration in tropical forests. *Science Advances* **3**, e1701345 (2017).
- 365 4. Smith, P. *et al.* How much land-based greenhouse gas mitigation can be achieved  
366 without compromising food security and environmental goals? *Global Change Biology*  
367 **19**, 2285-2302 (2013).
- 368 5. Brancalion, P.H.S., Viani, R.A.G., Strassburg, B.B.N. & Rodrigues, R.R. Finding the  
369 money for tropical forest restoration. *Unasylva* **63**, 239 (2012).
- 370 96. United Nations Sustainable Development Goals, available on  
371 <http://www.un.org/sustainabledevelopment/sustainable-development-goals/>, accessed on  
372 17 November 2017.
- 373 7. Griggs *et al.* Policy: Sustainable development goals for people and planet. *Nature* **495**,  
374 305 - 307 (2013)
- 375 8. Chazdon, R. L. *et al.* A policy-driven knowledge agenda for global forest and  
376 landscape restoration. *Conservation Letters* **10**, 125-132 (2017).

- 377 9. Gourevitch, J. D. *et al.* Optimizing investments in national-scale forest landscape  
378 restoration in Uganda to maximize multiple benefits. *Environmental Research Letters* **11**,  
379 114027 (2016).
- 380 10. Zwiener, V. P. *et al.* Planning for conservation and restoration under climate and land  
381 use change in the Brazilian Atlantic Forest. *Divers. Distrib.* **23**, 955–966 (2017).
- 382 11. Strassburg B. B. N. *et al.* Moment of truth for the Cerrado hotspot, *Nature Ecology*  
383 *and Evolution* **1**, 0099 (2017).
- 384 12. Pouzols, F. M., et al., Global protected area expansion is compromised by projected  
385 land-use and parochialism, *Nature* **516**, 383–386 (2014).
- 386 13. Possingham, H.P., Bode, M. & Klein, C.J. Optimal Conservation Outcomes Require  
387 Both Restoration and Protection. *PLoS Biol* **13**, 1-15 (2015)
- 388 14. Laurance, W.F. Conserving the hottest of the hotspots. *Biol Conserv* **142**, 1137  
389 (2009).
- 390 15. Mittermeier, R. A. *et al.* *Hotspots Revisited: Earth's Biologically Richest and Most*  
391 *Endangered Terrestrial Ecoregions.* (CEMEX, 2004).
- 392 16. Latawiec *et al.* Creating space for large-scale restoration in tropical agricultural  
393 landscapes. *Front Ecol Env* **13**, 211-218 (2015).
- 394 17. Beyer, H.L., Dujardin, Y., Watts, M.E. & Possingham, H.P. Solving conservation  
395 planning problems with integer linear programming. *Ecological Modelling* **328**, 14-22  
396 (2016).

- 397 18. Thomas, C.D et al. Extinction risk from climate change. *Nature* **427**, 145-148 (2004).
- 398 19. Strassburg *et al.* Impacts of incentives to reduce emissions from deforestation on  
399 global species extinctions. *Nature Climate Change* **2**, 350-355 (2012).
- 400 20. Poorter, L. Bongers, F. & Rozendall, D.M.A. Biomass resilience of Neotropical  
401 secondary forests. *Nature* **530**, 211-214 (2016).
- 402 21. Crouzeilles, R. & Curran, M. Which landscape size best predicts the influence of  
403 forest cover on restoration success? A global meta-analysis on the scale of effect. *J. Appl.*  
404 *Ecol.* **53**, 440–448 (2016).
- 405 22. Crouzeilles, R. Beyer, H.L., Mills M., Grelle, C.E.V. & Possingham H.P.  
406 Incorporating habitat availability into systematic planning for restoration: a species-  
407 specific approach for Atlantic Forest mammals. *Diversity and Distributions* **21**, 1027-  
408 1037 (2015).
- 409 23. Groeneveld, J. *et al.* The impact of fragmentation and density regulation on forest  
410 succession in the Atlantic rain forest. *Ecological Modelling*, **220(19)**, 2450-2459 (2009).
- 411 24. Soares-Filho, B. *et al.* Cracking Brazil's Forest Code. *Science* **344**, 363-364 (2014).
- 412 25. Kennedy, C. M. *et al.* Bigger is better: Improved nature conservation and economic  
413 returns from landscape-level mitigation. *Science Advances* **2**, e1501021 (2016).
- 414 26. Duffy, J.E., Godwin, C.M. & Cardinale, B.J. Biodiversity effects in the wild are  
415 common and as strong as key drivers of productivity. *Nature* **549**, 261–264 (2017).

- 416 27. Scarano, F.R. Ecosystem-based adaptation to climate change: concept, scalability and  
417 a role for conservation science. *Perspectives in Ecology and Conservation* **15**, 65-73  
418 (2017)
- 419 28. Mitchell, M.G.E. et al. Reframing landscape fragmentation's effects on ecosystem  
420 services. *Trends in Ecology and Evolution*, **30** (4), pp. 190-198 (2015)
- 421 29. Banks-Leite, C. et al. Using ecological thresholds to evaluate the costs and benefits of  
422 set-asides in a biodiversity hotspot. *Science* **345**, 1041-1045 (2014).
- 423 30. PLANAVEG: The National Vegetation Recovery Plan Federal decree no. 8.972/2017  
424 (Brazilian Ministry of Environment) (2017).

425

#### 426 **Acknowledgements**

427 We acknowledge the support and inputs from the Brazilian Ministry of the Environment, the  
428 Secretariat of the Convention of Biological Diversity and experts from the Intergovernmental  
429 Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). BBNS acknowledges  
430 that this work was supported by the Serrapilheira Institute (grant number Serra-1709-19329).  
431 BBNS , RC, AI and AL acknowledge the support of the German Ministry of the Environment's  
432 International Climate Initiative. RL thanks to CNPq (grant 308532/2014-7) and O Boticário  
433 Group Foundation for Nature Protection (grant PROG\_0008\_2013).

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**

446 Reprints and permissions information is available at [www.nature.com/reprints](http://www.nature.com/reprints). The authors  
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](mailto: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 Forest<sup>24</sup>) 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 species<sup>18</sup>. 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<sup>11,18,19</sup>. 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 from<sup>31</sup>, 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 database<sup>32</sup>, and  
503 comprised 223 endemic species (12,085 occurrences). Data on plants occurrence was obtained  
504 from NeoTropTree and SpeciesLink<sup>33</sup>, and comprised 846 endemic species and 44, 024 records.  
505 The original plant names were based on the NeoTropTree database<sup>34</sup> and updated according to  
506 the List of Species of the Brazilian Flora<sup>35</sup>, using R package 'flora'<sup>36</sup>, which is based on the  
507 List's Integrated Publishing Toolkit database<sup>37</sup>.

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 Worldclim<sup>39</sup>, four CGIAR CSI geohydrologic variables (actual evapotranspiration, aridity  
516 index, soil water balance and potential evapotranspiration<sup>40</sup>) and five USGS topographic

517 variables (elevation, slope, aspect and topographic index<sup>40</sup>). All variables had a spatial resolution  
518 of 1 km<sup>2</sup>. 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 predictors<sup>41-42</sup>.

#### 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)<sup>43</sup>. 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 disperse<sup>44-46</sup> 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 species<sup>47</sup>), 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 ModelR<sup>48</sup>, a set of R scripts for species distribution model  
554 fitting and assessment based on packages, XML<sup>49</sup>, dismo<sup>50</sup>, raster<sup>50</sup>, rgdal<sup>51</sup>, maps<sup>52</sup>, rgeos<sup>53</sup>,  
555 randomForest<sup>54</sup>, and e1071<sup>[55]</sup>.

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 km<sup>2</sup> 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 forests<sup>20</sup>. These  
563 biomes were defined based on a map of world ecoregions obtained from the Nature  
564 Conservancy<sup>56</sup>. Total annual precipitation was calculated by summing the individual monthly  
565 totals provided by WorldClim<sup>57</sup>. 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 WorldClim<sup>57</sup>, 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  $\text{AGB}_{20y}$  indicates the absolute biomass recovery potential over 20 years based  
575 on chronosequence models<sup>20</sup>. 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 Rainforest<sup>59</sup>. We  
584 believe this is a conservative assumption. A recent global study showing the impact of land-use

585 change on soil organic carbon<sup>60</sup> 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 gains<sup>22</sup>, 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 categories<sup>61</sup>.

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)<sup>62-63</sup>. 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)<sup>63</sup>.

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 biodiversity<sup>21</sup> 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

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

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 from<sup>30</sup>. 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 by<sup>64</sup>, 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  $\geq 3$  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

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



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 ( $A$ ;  $\text{km}^2$ ),  
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](http://www.iis-rio.org/ilup) from 2019.

704

705 **Methods References**

- 706 31. Lemes, P., Melo, A.S. & Loyola, R.D. Climate change threatens protected areas of the  
707 Atlantic Forest. *Biodiversity and Conservation* **23**(2), 357–368 (2014).
- 708 32. Global Biodiversity Information Facility database; GBIF; [www.gbif.org](http://www.gbif.org)
- 709 33. NeoTropTree and SpeciesLink, <http://splink.cria.org.br/>
- 710 34. NeoTropTree database, <http://prof.icb.ufmg.br/treetatlan/>
- 711 35. List of Species of the Brazilian Flora, <http://floradobrasil.jbrj.gov.br/>; Brazilian Flora 2020
- 712 36. Carvalho, G. Package “flora” 2016. Available on:  
713 <http://vps.fmvz.usp.br/CRAN/web/packages/flora/flora.pdf>, Accessed on 3 February 2017.
- 714 37. Robertson, T. *et al.* The GBIF integrated publishing toolkit: facilitating the efficient  
715 publishing of biodiversity data on the internet. *PLoS One*. **9**(8), 102623 (2014).
- 716 38. Stotz, D.F., Fitzpatrick, J.W., Parker III, T.A. & Moskovits, D.K. Neotropical Birds: Ecology  
717 and Conservation,, University of Chicago Press: Chicago, IL. (1996).
- 718 39. Hijmans, R.J., Cameron S.E., Parra, J.L., Jones, P.G. & Jarvis, A. The WorldClim  
719 interpolated global terrestrial climate surfaces. Version 1.3. (2004).
- 720 40. Jones, P.G. & Thornton, P.K.. Generating downscaled weather data from a suite of climate  
721 models for agricultural modelling applications. *Agricultural Systems*. 114:1–5 (2013);  
722 <https://www.usgs.gov/>
- 723 [41.](#) Dormann, C. F. et al. Collinearity: a review of methods to deal with it and a simulation study  
724 evaluating their performance. *Ecography*, **36**(1), 27-46 (2013).
- 725 42. Cruz-Cárdenas, G., López-Mata, L., Villaseñor, J. L. & Ortiz, E. Potential species  
726 distribution modelling and the use of principal component analysis as predictor variables. *Revista*  
727 *Mexicana de Biodiversidad* **85**(1), 189-199 (2014).

- 728 43. Allouche, O., Tsoar, A. & Kadmon, R. Assessing the accuracy of species distribution  
729 models: prevalence, kappa and the true skill statistic (TSS). *Journal of applied ecology* **43(6)**,  
730 1223–1232 (2006).
- 731 44. Barbet-Massin, M., Jiguet, F., Albert, C. H. & Thuiller, W. Selecting pseudo-absences for  
732 species distribution models: how, where and how many?. *Methods in Ecology and*  
733 *Evolution* **3(2)**, 327-338 (2012).
- 734 45. Barve, N. *et al.*. The crucial role of the accessible area in ecological niche modelling and  
735 species distribution modelling. *Ecological Modelling* **222(11)**, 1810–1819 (2011).
- 736 46. Stokland, J.N., Halvorsen, R. & Støa, B. Species distribution modelling—Effect of design  
737 and sample size of pseudo-absence observations. *Ecological Modelling* **222(11)**, 1800–1809  
738 (2011).
- 739 47. Araújo, M. B. & New, M. Ensemble forecasting of species distributions. *Trends in ecology &*  
740 *evolution* **22(1)**, 42-47 (2007).
- 741 48. Sánchez-Tapia, A. *et al.* Model-R: A Framework for Scalable and Reproducible Ecological  
742 Niche Modeling. In High Performance Computing - Fourth Latin American Conference,  
743 CARLA 2017. *Communications in Computer and Information Science* **796** (2017) (in press).
- 744 49. Lang, D.T. *et al.* XML: Tools for parsing and generating XML within R and S-Plus.. R  
745 package version 3.98-1.1. CRAN, Vienna, Austria (2013).
- 746 50. Hijmans, R.J., Phillips, S., Leathwick, J., Elith, J., Hijmans, M.R.J. Package “dismo”.  
747 *Circles9:1* (2016).
- 748 51. Bivand, R., Keitt, T. & Rowlingson, B. rgdal: Bindings for the Geospatial Data Abstraction  
749 Library. R package version 0.8-16. URL <http://CRAN.R-project.org/package=rgdal> (2014).

750 52. Becker, R., Wilks, A., Brownrigg, R., Minka, T. & Deckmyn, A. Maps: Draw Geographical  
751 Maps R package version 3.1. 0. (2016).

752 53. Bivand, R. & Rundel, C. rgeos: Interface to Geometry Engine-Open Source (GEOS). h ttps.  
753 CRAN R-project org/package= rgeos, r package version 03-8 (2014).

754 54. Liaw, A. & Wiener, M. Classification and regression by randomforest. R News 2 (3): 18–22.  
755 URL: <http://CRAN.R-project.org/doc/Rnews>. (2002).

756 55. Meyer, D., Dimitriadou, E., Hornik, K., Weingessel, A. & Leisch F. e1071: Misc Functions  
757 of the Department of Statistics (e1071), TU Wien, 2014. R package version, 1–6 (2015).

758 56. TNC Maps; [http://maps.tnc.org/gis\\_data.html](http://maps.tnc.org/gis_data.html)

759 57. WorldClim – Global Climate Data; <http://www.worldclim.org/current>

760 58. Chave, L. et al. Improved allometric models to estimate the above ground biomass of tropical  
761 trees. *Global Change Biology*. DOI: 10.1111/gcb.12629 [\(2014\)](#)

762 59. Mendes, M.S. et al. Look down – there is a gap – the need to include soil data in Atlantic  
763 Forest restoration. *Restoration Ecology*, *in press*.

764 60. Sanderman, J., Tomislav, H., & Gregory, J. F. "Soil carbon debt of 12,000 years of human  
765 land use." *Proceedings of the National Academy of Sciences* 114.36 (2017): 9575-9580.

766 61. FNP. Anuário da Agricultura brasileira: Agriannual 2015, Informa Economics FNP, São Paulo  
767 (2014).

768 62. Chazdon, R. L. Beyond deforestation: restoring forests and ecosystem services on degraded  
769 lands. *Science* **320**, 1458–1460 (2008).

770 63. Holl, H. D. & T. M. Aide. When and where to actively restore ecosystems? *For. Ecol.*  
771 *Manage.* **261**, 1558–1563 (2011).

772 64. SOS Mata Atlântica and INPE (2011)