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**Title:** Integrated terrestrial-freshwater planning doubles conservation of tropical aquatic species

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1 **Abstract:** Conservation initiatives overwhelmingly focus on terrestrial biodiversity and little is  
2 known about the freshwater co-benefits of terrestrial conservation actions. We sampled >1,500  
3 terrestrial and freshwater species in the Amazon and simulated conservation for species from both  
4 realms. Prioritizations based on terrestrial species yielded on average just 22% of the freshwater  
5 benefits achieved through freshwater-focused conservation. However, using integrated cross-realm  
6 planning, freshwater benefits could be increased by up to 600% for a 1% reduction in terrestrial  
7 benefits. Where freshwater biodiversity data are unavailable but aquatic connectivity is accounted for,  
8 freshwater benefits could still be doubled for negligible losses of terrestrial coverage. Conservation  
9 actions are urgently needed to improve the status of freshwater species globally. Our results suggest  
10 such gains can be achieved without compromising terrestrial conservation goals.

11 **One Sentence Summary:** Integrated conservation planning increases freshwater species protection  
12 by up to 600% without compromising terrestrial conservation.

## 13 Main Text

14 Freshwater ecosystems occupy less than 1% of the Earth's surface, make up only 0.01% of all water,  
15 yet host c. 10% of all known species, including a third of all vertebrates (1). They also deliver vital  
16 ecosystem services, such as climate regulation and the provision of food, fuel and fiber (2).

17 Nevertheless, freshwater ecosystems are far more imperilled than their terrestrial or marine  
18 counterparts; since 1970, for example, populations of freshwater vertebrates have declined by 83%  
19 compared to a c. 40% decline of terrestrial and marine vertebrates (3,4). A range of threats have long  
20 been linked to this collapse in freshwater biodiversity, including habitat loss and degradation,  
21 overexploitation, eutrophication, flow modification, and the introduction of non-native species (5).  
22 These are now amplified by emerging stressors, including climate change and contamination from  
23 microplastics and biochemicals (3).

24 Despite the freshwater biodiversity crisis (6), freshwater species are rarely considered in broad-scale  
25 conservation strategies (7-9). Although distributions of terrestrial and freshwater vertebrates display a  
26 degree of spatial congruence (10), there are three key reasons why freshwater conservation based on  
27 terrestrial priorities cannot be taken for granted. First, studies that reveal terrestrial-freshwater  
28 congruence rely on coarse-grained data, and such congruence might not occur at local scales where  
29 conservation decisions are implemented. Second, assessments of the distribution of freshwater biota  
30 are often restricted to small scales or specific taxonomic groups (11). Third, and most importantly,  
31 terrestrial prioritizations do not account for aquatic connectivity, which strongly affects the  
32 distribution of freshwater species, facilitates nutrient flows and mediates the cumulative effects of  
33 stressors along watercourses (12-15). Given these limitations, there is an urgent need to understand the  
34 extent to which freshwater biodiversity can benefit from terrestrial conservation actions, and whether  
35 freshwater protection can be increased through integrated planning for both realms. This is  
36 particularly critical in tropical regions, which harbor >80% of the world's freshwater fish and are  
37 undergoing the most rapid land-use changes on Earth (16).

38 Here, we addressed these knowledge gaps using data from extensive terrestrial and freshwater  
39 biodiversity surveys in two biogeographically distinct regions of Brazilian Amazonia: Paragominas  
40 and Santarém (Fig. S1; 17). With >40% of their forests having been converted to agricultural land-  
41 uses, these regions typify the agricultural-forest frontier in the Amazon (18). In terrestrial sites ( $n =$   
42 377; Fig. S2), we sampled plants ( $n = 812$  species), birds ( $n = 327$  species), and dung beetles ( $n = 141$   
43 species). In freshwater sites ( $n = 99$  streams; Fig. S3), we sampled fish ( $n = 143$  species); Odonata  
44 (i.e. dragonflies and damselflies;  $n = 134$  species); and Ephemeroptera (mayflies), Plecoptera  
45 (stoneflies) and Trichoptera (caddisflies; hereafter, "EPT"), which are frequently used as a measure of

46 freshwater ecosystem health (19). We could identify EPT individuals only to genus level ( $n = 59$   
47 genera; 17). All taxa are referred to as “species” hereafter.

48 Using these data, we first investigated the extent to which one species group (e.g. fish) is protected  
49 under conservation strategies directed at another species group (e.g. plants), which we refer to as  
50 “incidental conservation”. To do so, we built regional species distribution maps with an array of  
51 biophysical predictors (Table S1; 17). We then used the distribution maps and the Zonation  
52 conservation planning framework (20) to simulate terrestrial and freshwater conservation at the  
53 catchment scale, a natural landscape unit that integrates hydrological processes. Zonation selects  
54 catchments that maximize the weighted average proportion of species distributions under conservation  
55 while accounting for species complementarity, and we use this as our conservation benefit function  
56 (17). For the freshwater analyses, we used the *directed-connectivity* algorithm, which produces  
57 aquatically connected conservation networks appropriate for freshwater species (21). To focus on  
58 biodiversity (i.e. without socio-economic considerations), we first ran the optimization analyses  
59 constrained by the proportion of the landscape that could be conserved. We then tested the robustness  
60 of these findings to budget-constrained analyses by incorporating two region-specific estimates of  
61 agricultural opportunity costs (Fig. S4; 17). Finally, we undertook sensitivity analyses by varying  
62 available conservation resources. We report results for the area-constrained analysis in which 20% of  
63 landscape could be conserved, which aligns with the Aichi target to conserve at least 17% of  
64 terrestrial and inland water areas (4). For an overview of all analyses, see Fig. S1.

65 Terrestrially focused conservation planning provided limited incidental conservation benefits for  
66 freshwater species (Fig. 1). Among taxa and regions, on average just 22% (range: 14-29%) of the  
67 freshwater benefits achieved through freshwater conservation were secured through terrestrial  
68 conservation. In contrast, freshwater species prioritisations achieved on average 84% (range: 70-96%)  
69 of the terrestrial benefits achieved through terrestrial prioritisations. Within both freshwater and  
70 terrestrial realms, prioritizing for any one taxonomic group provided >92% of the maximum  
71 achievable benefits to other groups in the same realm. These results were similar whether the  
72 optimisations were constrained by area or financial budgets (Fig. 1A-C).

73 Differences in the incidental conservation outcomes can be explained by (i) the correlations in  
74 catchment priority rankings among species groups (Figs. S5 & S6) and (ii) the spatial distribution of  
75 conservation priorities (Fig. 2, S7 & S8). Terrestrial and freshwater groups act as good surrogates for,  
76 respectively, other terrestrial and freshwater groups because of the strong correlation in catchment  
77 priority rankings: a catchment with high marginal conservation value for one terrestrial group is likely  
78 to be of high marginal conservation value for other terrestrial groups, and the same holds for  
79 freshwater taxa. Catchment priority ranking correlations were somewhat weaker between terrestrial

80 and freshwater groups, leading to smaller but nonetheless high incidental terrestrial benefits when  
81 focused on freshwater species. However, the failure to incorporate aquatic connectivity into terrestrial  
82 planning produced conservation network designs that were inadequate for freshwater species (Figs. 2,  
83 S7 & S8), resulting in poor freshwater outcomes from terrestrial planning.

84 Next, we considered the extent to which freshwater benefits could be increased through conservation  
85 planning mechanisms targeted at both terrestrial and freshwater species. To do so, we developed two  
86 integrated planning techniques (17). Our first approach utilised both terrestrial and freshwater  
87 biodiversity data to determine a prioritisation optimized for species from both realms (hereafter, “joint  
88 planning”). Given the general paucity of freshwater biodiversity data, our second approach  
89 incorporated aquatic connectivity into the terrestrial optimizations to account for freshwater species  
90 habitat requirements (hereafter, “terrestrial-plus-connectivity”). Using these approaches, we  
91 undertook two trade-off analyses. We first determined the increase in freshwater benefits that could be  
92 achieved for a given reduction in terrestrial benefits from their optimum. We focus on this trade-off  
93 analysis in the main text. We also considered the increase in freshwater benefits for a given resource  
94 increase (e.g. increase in landscape covered or financial budgets) while maintaining terrestrial benefits  
95 at their optimum. As above, we focused on area-constrained optimizations in which 20% of a  
96 landscape could be conserved.

97 Using the joint planning approach, freshwater benefits could be increased by on average 62% and  
98 345% in Paragominas and Santarém, respectively, for a negligible 1% reduction in terrestrial benefits  
99 relative to their optimum (Fig. 3). A 5% reduction in terrestrial benefits, on the other hand, resulted in  
100 an average increase in freshwater benefits of 184% in Paragominas and 365% in Santarém. The  
101 terrestrial-plus-connectivity approach generally produced lower freshwater conservation gains.  
102 Nonetheless, a 1% and 5% reduction in terrestrial benefits increased freshwater benefits by 75-100%  
103 and 130-175% in both Paragominas and Santarém. Alternatively, the freshwater gains we document  
104 for a 1% and 5% reduction in terrestrial benefits could be achieved without any terrestrial losses for,  
105 respectively, a <1% and <5% increase in conservation resources (Fig. S9). Trade-offs were  
106 qualitatively similar with the incorporation of opportunity costs (Fig. 3) and more and less  
107 pronounced for, respectively, lower and higher conservation resource levels (Fig. S10).

108 While the freshwater gains we found for negligible reductions in terrestrial protection were substantial  
109 in both Paragominas and Santarém, there were large regional differences when using the joint  
110 planning approach that incorporates both terrestrial and freshwater biodiversity data (Fig. 3). These  
111 differences arise from variation in the spatial overlap of conservation priorities between regions. In  
112 Santarém, many of the highest priority catchments for terrestrial and freshwater groups were in the  
113 south-west (where the Tapajós National Forest is located; Fig. 2). In Paragominas, the same spatial

114 overlap in priorities was not apparent (Fig. 2). Thus, in Paragominas, substantial deviation from the  
115 optimal catchment prioritization for terrestrial species was required to achieve the largest increases in  
116 freshwater benefits. In Santarém, by contrast, large freshwater gains were possible simply by selecting  
117 catchments in the region of high conservation value for both realms that produced the requisite  
118 aquatic connectivity. Therefore, the realized magnitude of the freshwater gains possible from  
119 integrated planning will depend on the underlying spatial covariance in species distributions, which  
120 determines the spatial overlap in conservation priorities.

121 These results provide compelling evidence that the protection of freshwater species can be vastly  
122 improved without undermining terrestrial conservation goals. However, there are factors for which we  
123 did not account that could lead to significantly different terrestrial-freshwater trade-offs than we  
124 found. First, we did not incorporate the many additional socio-ecological benefits of freshwater  
125 conservation, meaning our results are likely to be conservative. For example, in addition to the direct  
126 provisioning, supporting, regulating and cultural services freshwater ecosystems provide (2), by  
127 enhancing landscape connectivity, freshwater conservation can also promote movement of terrestrial  
128 species, recolonization of defaunated areas, and seed dispersal and pollination services (22). Second  
129 and conversely, where freshwater conservation imposes external opportunity costs beyond a loss of  
130 agricultural profits, by, for example, precluding the development of hydropower or imposing water-  
131 use restrictions in the surrounding landscape, the overall scope for conservation investment may be  
132 reduced, leading to fewer net benefits from integrated planning. The manifestation of these additional  
133 socio-ecological trade-offs that emerge when protecting freshwater ecosystems is likely to be highly  
134 dependent on local circumstances, but their consideration will be essential for designing effective and  
135 sustainable conservation projects. Finally, our optimization analyses were static. As freshwater  
136 biodiversity data were collected in different years in Paragominas (2011) and Santarém (2010), and as  
137 the regions experienced significantly different climatic conditions during this time (17), some of the  
138 observed regional differences in trade-offs could result from temporal variation. Understanding and  
139 incorporating environmentally mediated changes in species distributions will be important for  
140 estimating the long-term benefits of integrated terrestrial-freshwater planning.

141 Identifying promising new approaches for biodiversity conservation is only the first step towards  
142 improving conservation outcomes. Given that evidence is lacking for the translation of systematic  
143 conservation planning exercises into tangible benefits (23), how best to turn our findings into  
144 meaningful action? First, while previous global conservation agendas – such as the UN’s Sustainable  
145 Development Goals and the Convention on Biological Diversity – have recognized the need to  
146 conserve both terrestrial and freshwater ecosystems (SDG 15, Aichi target 11), recognition of their  
147 interdependence remains largely absent from conservation planning. As the world prepares to  
148 consider new, post-2020 conservation targets (9,24), we show that a truly integrated approach to



149 conservation on land, which accounts for trade-offs and harnesses synergies among ecosystems and  
150 realms, can provide a cost-effective means to significantly improve outcomes. Understanding where  
151 such gains are highest and lowest should be a focus of future research efforts. Crucially, our findings  
152 from two biogeographically distinct regions with different biophysical drivers of species distributions  
153 (Fig. S11) suggest substantial freshwater gains ought to be attainable across the biodiverse  
154 agricultural frontier regions of the forested tropics. Second, conservation remains hampered by a  
155 severe lack of biodiversity data, especially in tropical regions (11,25). Resolving these data shortfalls  
156 will be necessary to unlock the benefits we document, and this will require more investment in large-  
157 scale ecological surveys and taxonomy (16,26). Third, to be effective and feasible, integrated  
158 terrestrial-freshwater strategies need to be aligned with or incorporated into current environmental  
159 policies and laws. In particular, freshwater-orientated planning should not come at the expense of  
160 existing protected areas, which often hold the last populations of endangered species and are coming  
161 under increasing pressure globally (27) and in the Amazon (28). Overcoming these challenges will be  
162 difficult, but the task is small compared to the enormous gains that can be made for the world's  
163 diverse and highly threatened freshwater biota.

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279 specific input from EB, ACL, RMH, LEOCA, JGB, NH, LJ, RPL, JL, NGM, JLN, JMBO, VHFO,  
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281 VHFO, VCO, LP, RRCS and JZ collected the field data or analyzed biological samples. SFBF and  
282 TAG processed the remote sensing data. GDL and CGL undertook the analyses with input from JB,  
283 JRT, RMN, RDG, TFM and SFBF. CGL, GDL and JB led writing with all authors contributing to  
284 reviewing and editing. **Competing interests:** Authors declare no competing interests. **Data and**  
285 **materials availability:** The data and computer code used in these analyses are available at:  
286 <https://doi.org/10.6084/m9.figshare.12423881>. The Zonation conservation planning software is  
287 available at: <https://github.com/cbig/zonation-core>.

288 **Ethics statement:** All biodiversity sampling was undertaken in compliance with Brazilian  
289 environmental regulations under the following licenses: (i) Sisbio license #24164 for collecting plants,  
290 issued by the Chico Mendes Institute for Biodiversity Conservation (ICMBio); (ii) Sisbio license

291 #10061-1 for collecting dung beetles, issued by the Institute of Environment and Renewable Natural  
292 Resources (IBAMA); (iii) Sisbio licenses #10199-2 and #24355-2 for collecting fish, both issued by  
293 ICMBio (iv) Sisbio license #10873-1 for collecting insects, issued by IBAMA; (v) Sisbio license  
294 #19102-4 for collecting Odonata, Ephemeroptera, Plecoptera and Trichoptera, issued by ICMBio. No  
295 license was required for bird sampling because the methods were observational and did not involve  
296 collecting or handling of specimens. Socio-economic data was collected following the UK Research  
297 Integrity Office Principles for Research involving human participants, human material, and personal  
298 data and was collected with informed consent. Further approval for opportunity cost data collection  
299 was obtained from the Brazilian Agricultural Research Corporation (Embrapa) under CAAE  
300 29054920.4.0000.5173 and Stanford University under IRB Protocol 19044.

301 **Supplementary Materials:**

302 Materials and Methods

303 Figures S1-S13

304 Table S1

305 References 29-50

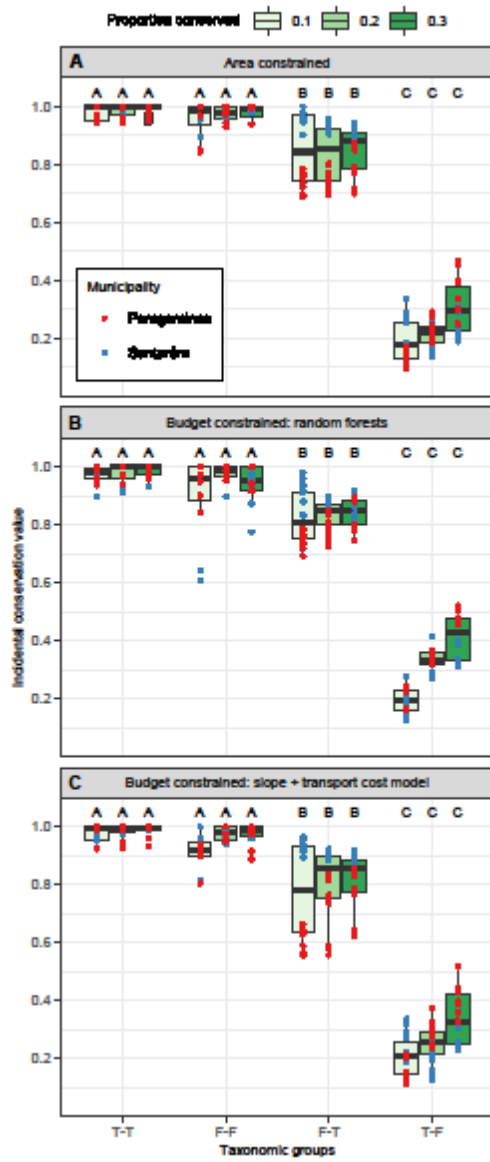
306 Figure legends

307 **Fig. 1. Incidental conservation.** The incidental conservation benefits achieved for one species group  
308 when focused on another. The *x*-axis ticks are labelled with the focal group first. For example, *T-F*  
309 shows the incidental conservation benefits achieved for a freshwater group when prioritizing for a  
310 terrestrial group. Points show results for each taxonomic pair. Boxplots show the interquartile range.  
311 The center line shows the median. Results are shown for the area-constrained analysis (**A**) with the  
312 constraint that 10%, 20% or 30% of landscape can be conserved, and the budget-constrained analyses  
313 with two opportunity cost estimates (**B-C**) and with budget levels such that approximately 10%, 20%  
314 and 30% of the landscape can be conserved (17). Letters next to the boxplots show results of pairwise  
315 comparisons of group means within resource levels (17). Variables not sharing a letter have  
316 statistically different means.

317 **Fig. 2. Catchment prioritizations for terrestrial and freshwater biodiversity.** Catchment  
318 conservation priority rankings in Paragominas (**A-F**) and Santarém (**G-L**) for terrestrial (**A-C, G-I**)  
319 and freshwater (**D-F, J-L**) taxa. Rankings are based on catchment marginal conservation value, with 1  
320 indicating the catchment with the highest marginal conservation value and 0 that with the lowest  
321 marginal conservation value. Results are shown for the area-constrained analysis.

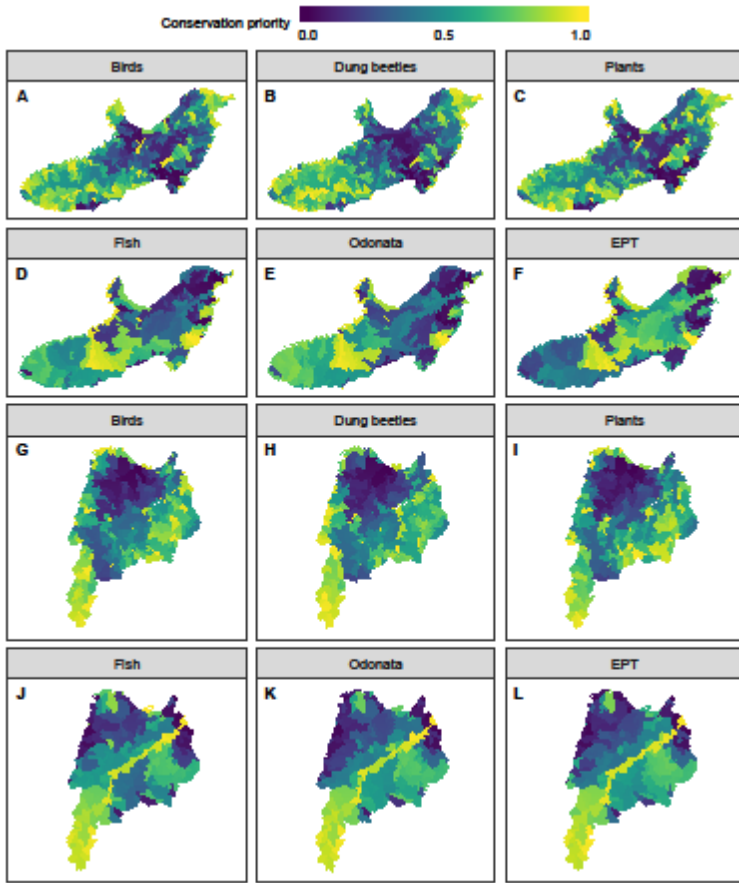
322 **Fig. 3. Terrestrial-freshwater trade-offs.** The decrease in terrestrial benefits from their optimum  
323 required to achieve an increase in freshwater benefits through the joint-planning and the terrestrial-  
324 plus-connectivity approaches in Paragominas (**A, C, E**) and Santarém (**B, D, F**). The thin lines show  
325 the results for each terrestrial-freshwater taxonomic pair. The thick lines show one s.e.m., where the  
326 mean was estimated using Holling type-II curves, for each integrated planning approach. Results are  
327 shown for the area-constrained analysis (**A-B**) with the constraint that 20% of landscape could be  
328 conserved, and the budget-constrained analyzes with two opportunity cost estimates (**C-F**) and with  
329 budget levels such that approximately 20% of the landscape could be conserved (17).

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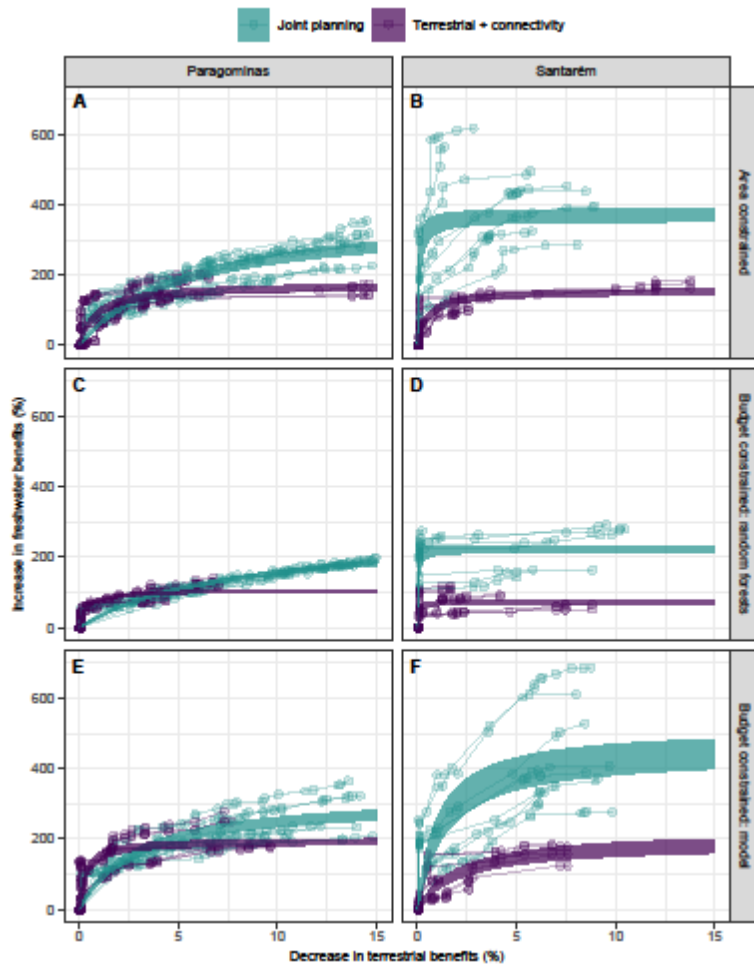
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