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

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

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

Main Text

Freshwater ecosystems occupy less than 1% of the Earth's surface, make up only 0.01% of all water, yet host c. 10% of all known species, including a third of all vertebrates (*1*). They also deliver vital ecosystem services, such as climate regulation and the provision of food, fuel and fiber (*2*). Nevertheless, freshwater ecosystems are far more imperilled than their terrestrial or marine counterparts; since 1970, for example, populations of freshwater vertebrates have declined by 83% compared to a c. 40% decline of terrestrial and marine vertebrates (*3,4*). A range of threats have long been linked to this collapse in freshwater biodiversity, including habitat loss and degradation, overexploitation, eutrophication, flow modification, and the introduction of non-native species (*5*). These are now amplified by emerging stressors, including climate change and contamination from microplastics and biochemicals (*3*).

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

Here, we addressed these knowledge gaps using data from extensive terrestrial and freshwater biodiversity surveys in two biogeographically distinct regions of Brazilian Amazonia: Paragominas and Santarém (Fig. S1; *17*). With >40% of their forests having been converted to agricultural land-uses, these regions typify the agricultural-forest frontier in the Amazon (*18*). In terrestrial sites (n = 377; Fig. S2), we sampled plants (n = 812 species), birds (n = 327 species), and dung beetles (n = 141 species). In freshwater sites (n = 99 streams; Fig. S3), we sampled fish (n = 143 species); Odonata (i.e. dragonflies and damselflies; n = 134 species); and Ephemeroptera (mayflies), Plecoptera (stoneflies) and Trichoptera (caddisflies; hereafter, "EPT"), which are frequently used as a measure of freshwater ecosystem health (*19*). We could identify EPT individuals only to genus level (n = 59 genera; *17*). All taxa are referred to as "species" hereafter.

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

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

Differences in the incidental conservation outcomes can be explained by (i) the correlations in catchment priority rankings among species groups (Figs. S5 & S6) and (ii) the spatial distribution of conservation priorities (Fig. 2, S7 & S8). Terrestrial and freshwater groups act as good surrogates for, respectively, other terrestrial and freshwater groups because of the strong correlation in catchment priority rankings: a catchment with high marginal conservation value for one terrestrial group is likely to be of high marginal conservation value for other terrestrial groups, and the same holds for freshwater taxa. Catchment priority ranking correlations were somewhat weaker between terrestrial and freshwater groups, leading to smaller but nonetheless high incidental terrestrial benefits when focused on freshwater species. However, the failure to incorporate aquatic connectivity into terrestrial planning produced conservation network designs that were inadequate for freshwater species (Figs. 2, S7 & S8), resulting in poor freshwater outcomes from terrestrial planning.

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

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

While the freshwater gains we found for negligible reductions in terrestrial protection were substantial in both Paragominas and Santarém, there were large regional differences when using the joint planning approach that incorporates both terrestrial and freshwater biodiversity data (Fig. 3). These differences arise from variation in the spatial overlap of conservation priorities between regions. In Santarém, many of the highest priority catchments for terrestrial and freshwater groups were in the south-west (where the Tapajós National Forest is located; Fig. 2). In Paragominas, the same spatial overlap in priorities was not apparent (Fig. 2). Thus, in Paragominas, substantial deviation from the optimal catchment prioritization for terrestrial species was required to achieve the largest increases in freshwater benefits. In Santarém, by contrast, large freshwater gains were possible simply by selecting catchments in the region of high conservation value for both realms that produced the requisite aquatic connectivity. Therefore, the realized magnitude of the freshwater gains possible from integrated planning will depend on the underlying spatial covariance in species distributions, which determines the spatial overlap in conservation priorities.

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

Identifying promising new approaches for biodiversity conservation is only the first step towards improving conservation outcomes. Given that evidence is lacking for the translation of systematic conservation planning exercises into tangible benefits (*23*), how best to turn our findings into meaningful action? First, while previous global conservation agendas – such as the UN's Sustainable Development Goals and the Convention on Biological Diversity – have recognized the need to conserve both terrestrial and freshwater ecosystems (SDG 15, Aichi target 11), recognition of their interdependence remains largely absent from conservation planning. As the world prepares to consider new, post-2020 conservation targets (*9*,*24*), we show that a truly integrated approach to conservation on land, which accounts for trade-offs and harnesses synergies among ecosystems and realms, can provide a cost-effective means to significantly improve outcomes. Understanding where such gains are highest and lowest should be a focus of future research efforts. Crucially, our findings from two biogeographically distinct regions with different biophysical drivers of species distributions (Fig. S11) suggest substantial freshwater gains ought to be attainable across the biodiverse agricultural frontier regions of the forested tropics. Second, conservation remains hampered by a severe lack of biodiversity data, especially in tropical regions (*11,25*). Resolving these data shortfalls will be necessary to unlock the benefits we document, and this will require more investment in large-scale ecological surveys and taxonomy (*16,26*). Third, to be effective and feasible, integrated terrestrial-freshwater strategies need to be aligned with or incorporated into current environmental policies and laws. In particular, freshwater-orientated planning should not come at the expense of existing protected areas, which often hold the last populations of endangered species and are coming under increasing pressure globally (*27*) and in the Amazon (*28*). Overcoming these challenges will be difficult, but the task is small compared to the enormous gains that can be made for the world's diverse and highly threatened freshwater biota.

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

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

Supplementary Materials:

Materials and Methods

Figures S1-S13

Table S1

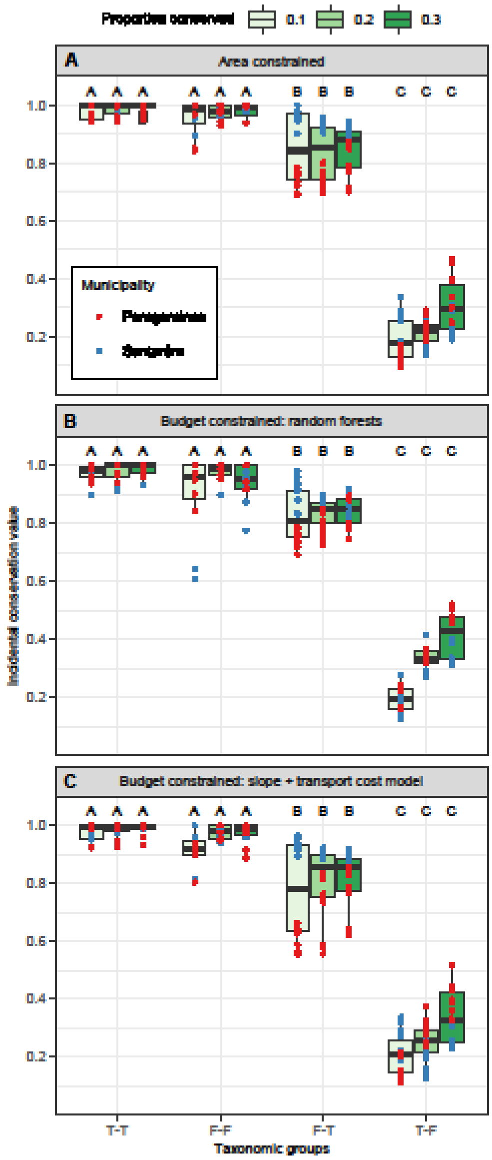
References 29-50

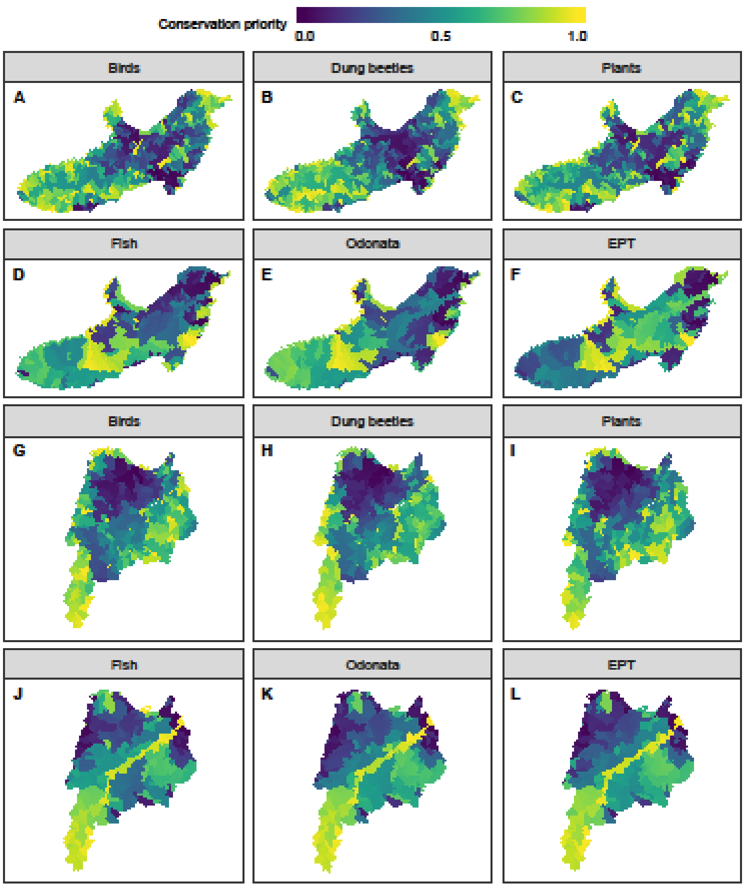
Figure legends

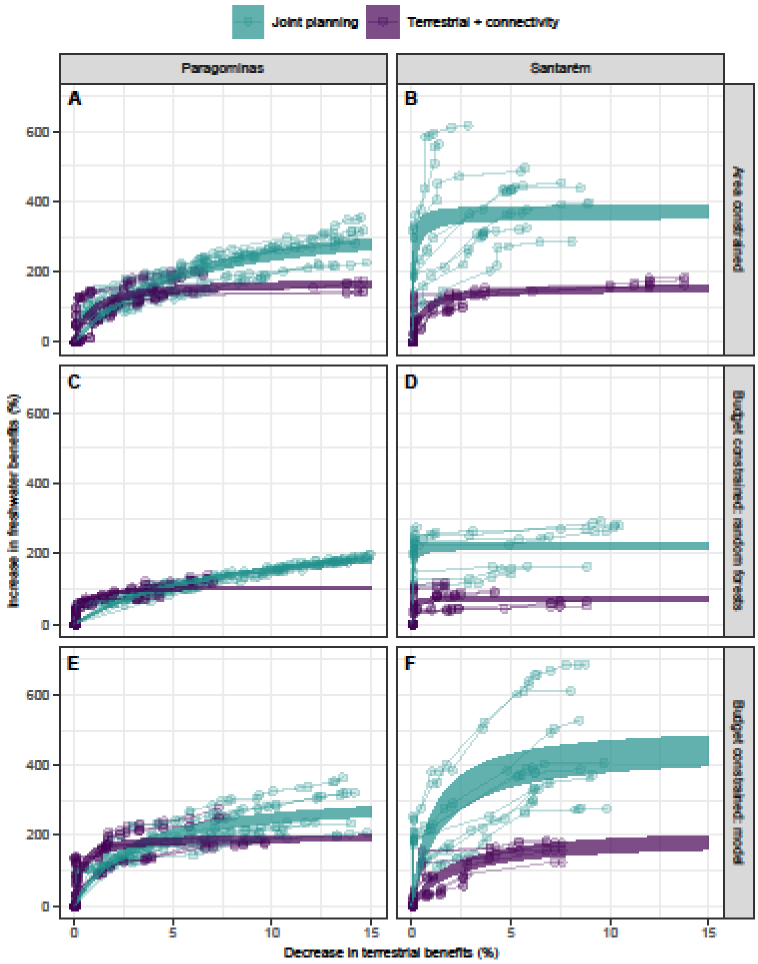
Fig. 1. Incidental conservation. The incidental conservation benefits achieved for one species group when focused on another. The *x*-axis ticks are labelled with the focal group first. For example, *T-F* shows the incidental conservation benefits achieved for a freshwater group when prioritizing for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

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

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


0.1
0.2
0.3
A
Area constrained
Municipality
B
Budget constrained: random forests
C
Budget constrained: slope + transport cost model
Incidental conservation value
1.0
0.8
0.6
0.4
0.2
A A A A A A B B B C C C
T-T
F-F
F-T
T-F
Taxonomic groups


Conservation priority
0.0
0.5
1.0
Birds
A
Dung beetles
B
Plants
C
Fish
D
Odonata
E
EPT
F
Birds
G
Dung beetles
H
Plants
I
Fish
J
Odonata
K
EPT
L



Joint planning
Terrestrial + connectivity
Paragominas
Santarém
A
B
C
D
E
F
Area constrained
Budget constrained: random forests
Budget constrained: model
Increase in freshwater benefits (%)
Decrease in terrestrial benefits (%)
0
200
400
600
0
5
10
15

336

337