

CONSERVATION PLANNING

Integrated terrestrial-freshwater planning doubles conservation of tropical aquatic species

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Conservation initiatives overwhelmingly focus on terrestrial biodiversity, and little is known about the freshwater cobenefits of terrestrial conservation actions. We sampled more than 1500 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, by 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 that such gains can be achieved without compromising terrestrial conservation goals.

Freshwater ecosystems occupy less than 1% of the Earth's surface, make up only 0.01% of all water, yet host ~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 imperiled than their terrestrial or marine counterparts; since 1970, for example, populations of freshwater vertebrates have declined by 83% compared with a ~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, 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).

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 ($n = 377$ sites) (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 (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 (for example, fish) is protected under conservation strategies directed at another species group (for example, 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 used 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 (without socioeconomic

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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). Last, 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). An overview of all analyses is available in 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 to 29%) of the freshwater benefits achieved through freshwater conservation were secured through terrestrial conservation. By contrast, freshwater species prioritizations achieved on average 84% (range, 70 to 96%) of the terrestrial benefits achieved through terrestrial prioritizations. 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 optimizations were constrained by area or financial budgets (Fig. 1, A to C).

Differences in the incidental conservation outcomes can be explained by (i) the correlations in catchment priority rankings among species groups (figs. S5 and S6) and (ii) the spatial distribution of conservation priorities (Fig. 2 and figs. S7 and 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 (Fig. 2 and figs. S7 and 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 used both terrestrial and freshwater biodiversity data to determine a prioritization optimized for species from both realms (hereafter, “joint plan-

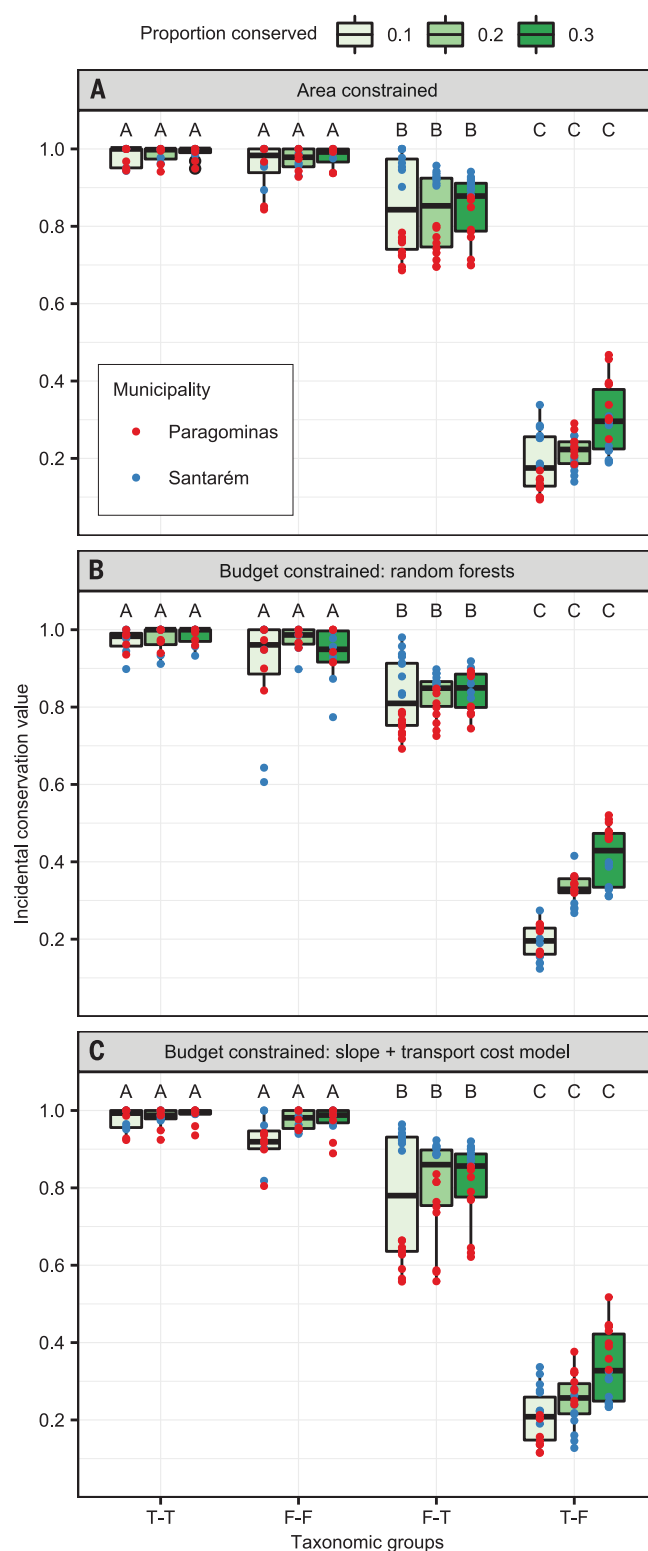


Fig. 1. Incidental conservation. (A to C) The incidental conservation benefits achieved for one species group when focused on another. The x axis ticks are labeled with the focal group first. For example, “T-F” shows the incidental conservation benefits achieved for a freshwater group when prioritizing 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 (A) the area-constrained analysis with the constraint that 10, 20, or 30% of landscape can be conserved, and [(B) and (C)] the budget-constrained analyses with two opportunity cost estimates and with budget levels so 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.

ning”). 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

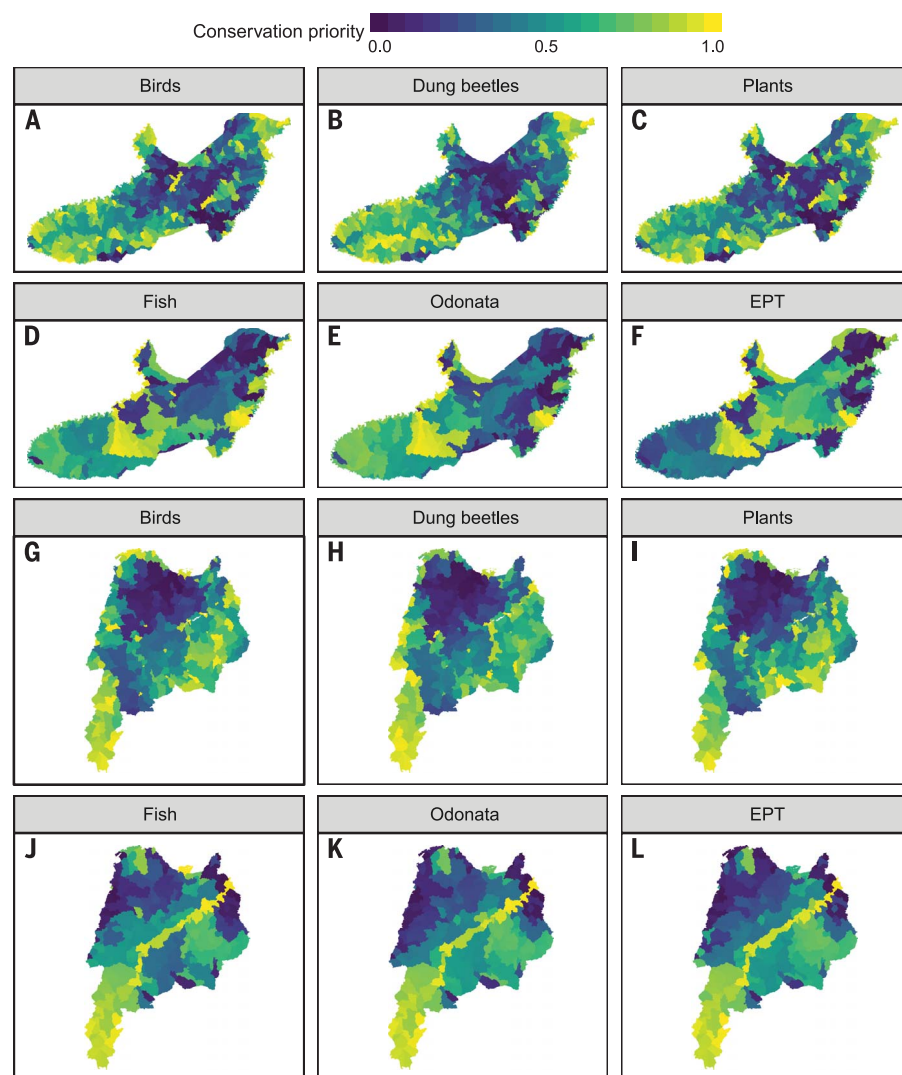


Fig. 2. Catchment prioritizations for terrestrial and freshwater biodiversity. (A to L) Catchment conservation priority rankings in [(A) to (F)] Paragominas and [(G) to (L)] Santarém for [(A) to (C) and (G) to (I)] terrestrial and [(D) to (F) and (J) to (L)] freshwater taxa. Rankings are based on catchment 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.

freshwater benefits for a given resource increase (such as an 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 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, 1 and 5% reductions in terrestrial benefits increased freshwater benefits by 75 to 100% and 130 to 175%, respectively, in both Paragominas and Santarém. Alternatively, the freshwater gains we documented for 1 and 5% reductions in terrestrial benefits could be achieved without any terrestrial losses for, respectively, <1 and <5% increases 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).

Although 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 southwest (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 substantially different terrestrial-freshwater trade-offs than we found. First, we did not incorporate the many additional socioecological benefits of freshwater conservation, meaning that our results are likely to be conservative. For example, in addition to the direct provisioning, supporting, regulating, and cultural services that 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—for example, by 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 socioecological 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. Last, our optimization analyses were static. Given that freshwater biodiversity data were collected in different years in Paragominas (2011) and Santarém (2010), and because the regions experienced substantially different climatic conditions during this time (17), some of

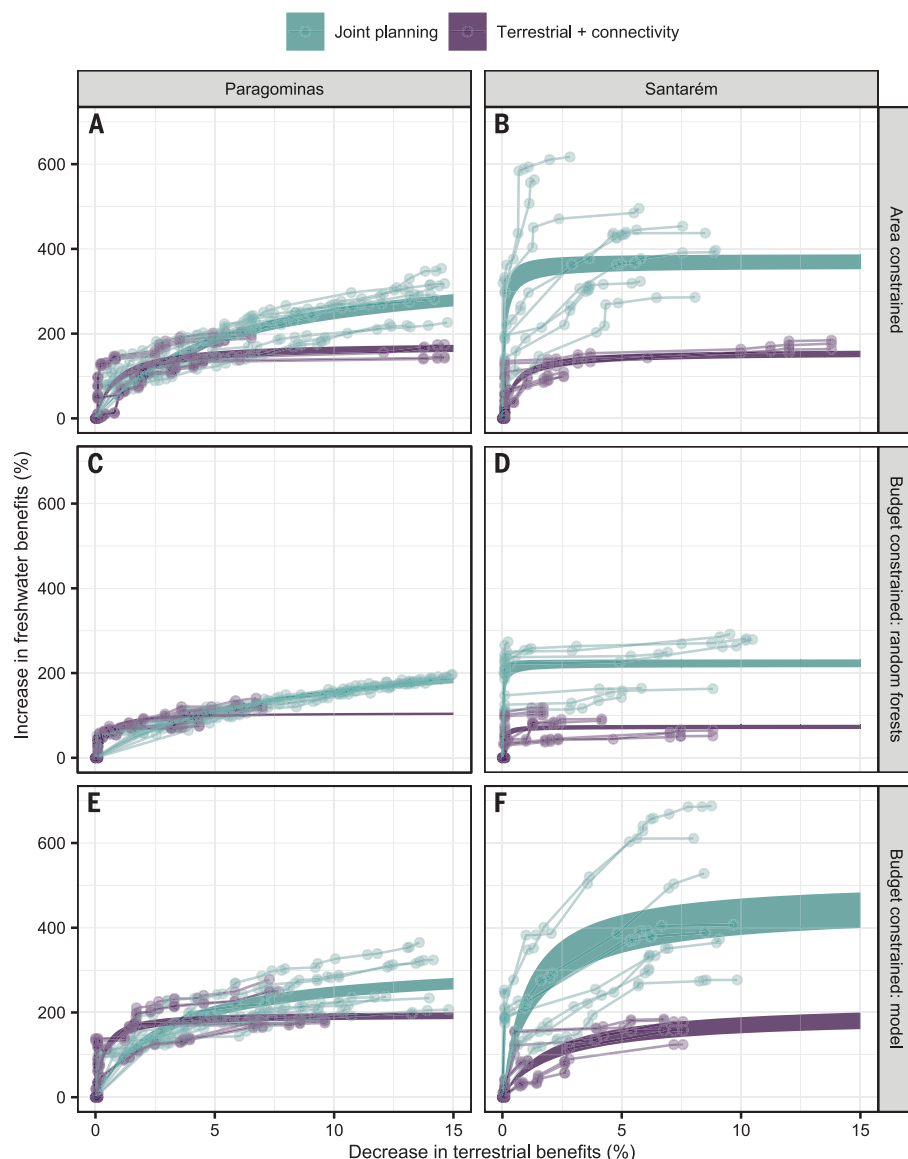


Fig. 3. Terrestrial-freshwater trade-offs. (A to F) The decrease in terrestrial benefits from their optimum required to achieve an increase in freshwater benefits through the joint-planning and the terrestrial-plus-connectivity approaches in [(A), (C), and (E)] Paragominas and [(B), (D), and (F)] Santarém. The thin lines show the results for each terrestrial-freshwater taxonomic pair. The thick lines show 1 SEM, where the mean was estimated by using Holling type-II curves, for each integrated planning approach. Results are shown for [(A) and (B)] the area-constrained analysis with the constraint that 20% of landscape could be conserved, and [(C) to (F)] the budget-constrained analyzes with two opportunity-cost estimates and with budget levels so that approximately 20% of the landscape could be conserved (17).

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 toward 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, although previous global conservation agendas—such as the United Nations’ Sustainable Development Goals (SDGs) 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 substantially 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 that substantial freshwater gains ought to be attainable across the biodiverse agricultural frontier regions of the forested tropics. Also, 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). Last, 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 with the enormous gains that can be made for the world’s diverse and highly threatened freshwater biota.

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ACKNOWLEDGMENTS

We thank I. Vieira for coordinating the INCT Biodiversidade e Uso da Terra na Amazônia and the Large Scale Biosphere-Atmosphere Program (LBA) for logistical and infrastructure support during field measurements. **Funding:** This work was supported by grants from Brazil (CNPq 574008/2008-0, 458022/2013-6, and 400640/2012-0; CNPq-CAPES-PELD 441659/2016-0; Embrapa SEG:02.08.06.005.00; The Nature Conservancy–Brasil; and CAPES scholarships), the UK (Darwin Initiative 17-023; NE/F01614X/1; NE/G000816/1; NE/F015356/2; NE/I018123/1; and NE/K016431/1), Formas 2013-1571, and Australian Research Council grant DP120100797. Individual support included FAPESP funding (2017/25383-0 and 2019/05440-5, respectively) to C.G.L. and T.F.M.; H2020-MSCA-RISE (691053-ODYSSEA) funding to E.B. and J.B.; Fulbright Brasil funding to R.M.H.; NSF-Belmont Forum award (1852113) to L.C.; and CNPq funding (144452/2010-3, 307597/2016-4, 436007/2018-5, 303548/2017-7, 308970/2019-5, and 313183/2014-7, respectively) to V.C.d.O., L.J., R.P.L., P.S.P., N.H., and J.Z. Institutional support was provided by the Herbário

IAN in Belém, LBA in Santarém, and FAPEMAT. This is paper no. 76 in the Sustainable Amazon Network publication series. **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; and (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. Socioeconomic data were collected following the UK Research Integrity Office Principles for Research involving human participants, human material, and personal data and were 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. **Author contributions:** T.A.G., J.F., J.B., L.P., C.G.L., G.D.L., and S.F.B.F. designed the research with additional taxon-specific input from E.B., A.C.L., R.M.H., L.E.O.C.A., J.G.d.B., N.H., L.J., R.P.L., J.L., N.G.M., J.L.N., J.M.B.O.-J., V.H.F.O., V.C.d.O., P.S.P., R.R.C.S., and

J.Z.; C.G.L., E.B., A.C.L., R.M.H., J.G.d.B., N.H., L.J., R.P.L., J.L., N.G.M., J.L.N., J.M.B.O.-J., V.H.F.O., V.C.d.O., L.P., R.R.C.S., and J.Z. collected the field data or analyzed biological samples. S.F.B.F. and T.A.G. processed the remote sensing data. G.D.L. and C.G.L. undertook the analyses with input from J.B., J.R.T., R.M., R.D.G., T.F.M., and S.F.B.F.; T.F.M., T.A.G., L.P., and R.D.G. processed the socioeconomic data; C.G.L., G.D.L., and J.B. led the writing, with all authors contributing to reviewing and editing. **Competing interests:** Authors declare no competing interests. **Data and materials availability:** The data and computer code used in these analyses are available at <https://doi.org/10.6084/m9.figshare.12423881>. The Zonation conservation planning software is available at: <https://github.com/cbig/zonation-core>.

SUPPLEMENTARY MATERIALS

science.sciencemag.org/content/370/6512/117/suppl/DC1
Materials and Methods
Supplementary Text
Figs. S1 to S13
Table S1
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2 January 2020; accepted 10 August 2020
10.1126/science.aba7580

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Science, 370 (6512), • DOI: 10.1126/science.aba7580

Consider both water and land

When designing terrestrial reserves, it is common to consider the needs of species and systems from a terrestrial perspective, with an assumption that any freshwater systems will benefit as well. Leal *et al.* tested this assumption by analyzing data from two locations in the Brazilian Amazon and found that it is far from accurate: Terrestrial systems confer little benefit to freshwater systems (see the Perspective by Abell and Harrison). However, the authors also found that integrating the needs of freshwater species into overall reserve planning increased freshwater benefits by 600% while only decreasing terrestrial outcomes by 1%. They argue that reserve planning must take freshwater systems into account if they are to protect across both realms.

Science, this issue p. 117; see also p. 38

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