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Concordance of freshwater and terrestrial biodiversity

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Abstract

Efforts to set global conservation priorities have largely ignored freshwater diversity, thereby excluding some of the world's most speciose, threatened, and valuable taxa. Using a new global map of freshwater ecoregions and distribution data for about 13,300 fish species, we identify regions of exceptional freshwater biodiversity and assess their overlap with regions of equivalent terrestrial importance. Overlap is greatest in the tropics and is higher than expected by chance. These high-congruence areas offer opportunities for integrated conservation efforts, which could be of particular value when economic conditions force conservation organizations to narrow their focus. Areas of low overlap—missed by current terrestrially based priority schemes—merit independent freshwater conservation efforts. These results provide new information to conservation investors setting priorities at global or regional scales and argue for a potential reallocation of future resources to achieve representation of overlooked biomes.

Introduction

Global priorities for biodiversity conservation are only as robust as the data used to identify them. To date, these priorities have largely neglected freshwater biodiversity due to patchy information on freshwater species (Revenga & Kura 2003; Brooks *et al.* 2006). This omission has real implications for conservation investment; for instance, the Global Environment Facility's (GEF) 2005 Resource Allocation Framework, providing guidance on how the GEF spends over U.S. $1 billion each year on environmental projects, incorporates terrestrial biodiversity data but none for freshwater (Global Environment Facility 2005). The low profile of freshwater biodiversity in broad-scale priority-setting efforts stands in stark contrast to its degree of imperilment, with freshwater habitats and species worldwide being more threatened than their terrestrial counterparts (Millennium Ecosystem Assessment 2005; Revenga *et al.* 2005). This imperilment should raise concern beyond the conservation community, as human well-being is clearly and directly tied to freshwater systems, and to freshwater species specifically, via the ecosystem services they provide (Millennium Ecosystem Assessment 2005). Bringing freshwater biodiversity considerations into ongoing debates about conservation priority-setting (Marris 2007) requires a basic understanding of freshwater biodiversity patterns.

Given that many conservation priorities are currently driven by terrestrial biodiversity patterns, we asked how regions of exceptional freshwater biodiversity overlap with regions of equivalent terrestrial importance. A new global database of freshwater fish distributions enabled this analysis. Fish are the most speciose vertebrate group, and freshwater fishes comprise approximately one-fourth of all vertebrate species (Dudgeon *et al.* 2006). Our freshwater fish database records the presence of about 13,300 species in 426 freshwater ecoregions (Abell *et al.* 2008), affording the first systematic analysis of global freshwater fish biodiversity patterns. The analysis allows us to begin to answer the question of whether current conservation priorities are reasonably inclusive and representative of freshwater species, a major component of the world's biodiversity.

Methods

Data

The map of 426 freshwater ecoregions was delineated by a consortium of conservation organizations and ichthyologists, and the associated freshwater fish species database was populated simultaneously and subsequently updated with new distribution data for South America (Abell *et al.* 2008). An earlier consortium delineated the map of terrestrial ecoregions (Olson *et al.* 2001) and produced corresponding distribution data for over 26,000 terrestrial vertebrate species (Lamoreux *et al.* 2006). Assignments of major habitat types to freshwater ecoregions are available online (www.feow.org).

Rarity-weighted richness index

For each ecoregion, we calculated a rarity-weighted richness (RWR) index as a simple measure of biodiversity importance (Williams *et al.* 1996). RWR counts the number of species in a given ecoregion, weighting each species by the inverse of the number of ecoregions it occupies. Formally, the index is

$$RWR_i = \sum_{s=1}^{Si} 1/N_s,$$

where S_i is the number of species in ecoregion i and N_s is the total number of ecoregions occupied by species s.

This index integrates two common measures of biodiversity importance: the species richness (i.e., number of species) in a given place and the rarity of those species (i.e., their range extent) (Redford *et al.* 2003). Ecoregions that score high on this index tend to be those in which conservation actions are likely to safeguard a relatively large number of species, including those for which options for conservation are limited.

We calculated freshwater and terrestrial RWR for each of the world's freshwater and terrestrial ecoregions, respectively, using the ecoregion maps and associated databases described above. For each set of ecoregions (i.e., terrestrial and freshwater), we identified those in the top quartile of RWR scores and consider these ecoregions to be of extraordinary biodiversity importance for the purposes of this analysis. We also identified those in the top 5%, 10%, 15%, and 20% to assess the sensitivity of the results to the selected threshold.

Although size of both freshwater and terrestrial ecoregions significantly correlates with RWR, the variation in area explains only a small amount, 3% and 6%, respectively, of the variation (*FW*: log10(RWR) = 0.50 + 0.13 log10(area), R^2 = 0.033, P = 0.0002; *TERR*: log10(RWR) = 0.61 + 0.14 log10(area), R^2 = 0.058, P = 0.0002). The residuals of these regressions were highly correlated with RWR for both freshwater and terrestrial regions (*FW*: $r = 0.98$; *TERR*: $r = 0.97$). As a result, we conclude that area is not a major factor in determining RWR for either realm, and does not drive the spatial concordance we find between them.

We deliberately avoid any explicit recommendation of relative conservation priority among ecoregions. Such prioritizations often assess biodiversity value using measures in addition to species richness and rarity, such as large-scale ecological and evolutionary processes and biogeographic representation (Redford *et al.* 2003). They may also incorporate status information, through prioritizing especially intact or "wild" systems or, conversely, focusing on highly threatened areas and their biotas.

Overlap analyses

We used a geographic information system to intersect the terrestrial and freshwater ecoregion maps. For each top-quartile freshwater ecoregion, we calculated the area within it (if any) that overlaps with a top-quartile terrestrial ecoregion. We then summed these areas of overlap across all top-quartile freshwater ecoregions to quantify the global degree of spatial concordance between freshwater and terrestrial biodiversity.

To assess whether this observed degree of global overlap is greater than that expected by chance, we randomized the RWR values for terrestrial ecoregions (without replacement) and repeated the top quartile and overlap calculations described above 1,000 times. Diversity of both freshwater and terrestrial species tends to be higher in tropical latitudes. As a result, global randomization might not constitute an informative null model against which to compare our observed overlap. We therefore conducted a second randomization, this time stratified by 14 biomes into which terrestrial ecoregions are nested (e.g., tropical moist forests, temperate grasslands). We repeated the randomization tests using the RWR results from the top 5%, 10%, 15%, and 20% ecoregions to assess the sensitivity of the results to the top 25% threshold.

Results

Top-quartile freshwater ecoregions (Figure 1A) occur in all biogeographic realms and are concentrated between 30° S and 40° N latitudes. Two higher-latitude ecoregions

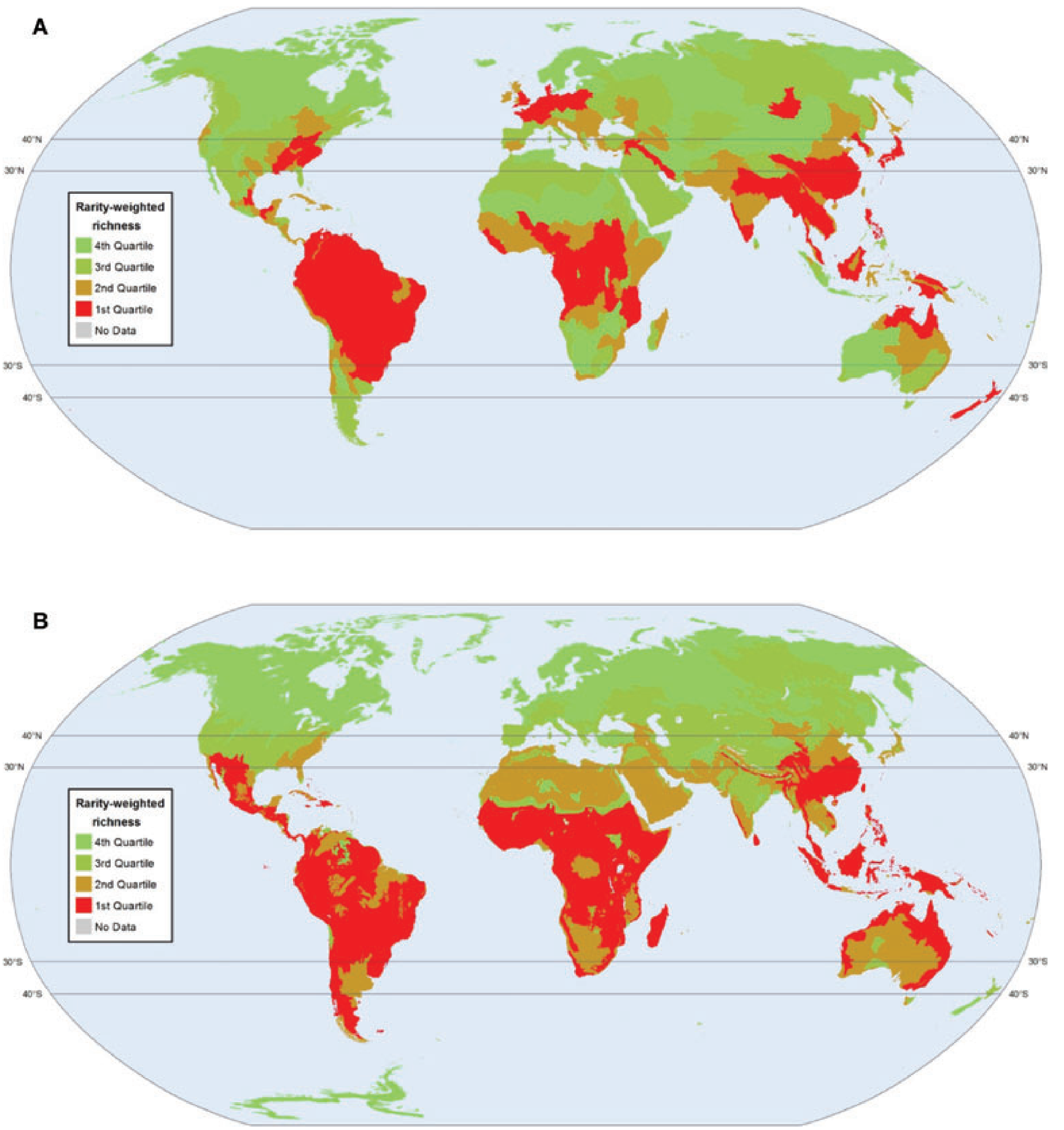

Figure 1 A: Freshwater ecoregion RWR. RWR values are based on freshwater fish species data for each ecoregion. There are 426 freshwater ecoregions. B: Terrestrial ecoregion RWR. RWR values are based on terrestrial vertebrate data for each ecoregion. There are 821 terrestrial ecoregions.

are in central and western Europe. Ten of 12 major habitat types are represented in the top quartile, with polar freshwaters and oceanic islands missing (Figure 2). Tropical and subtropical major habitat types have high representation; over 75% of tropical and subtropical upland river ecoregions are in the top quartile, followed by tropical and subtropical floodplain rivers and wetland complexes (57%).

Overlap between top quartile freshwater and terrestrial ecoregions is high (Figure 3). About 64% (22,862,110 km^2) of the area within top-quartile freshwater ecoregions overlaps with top terrestrial ecoregions. Of the

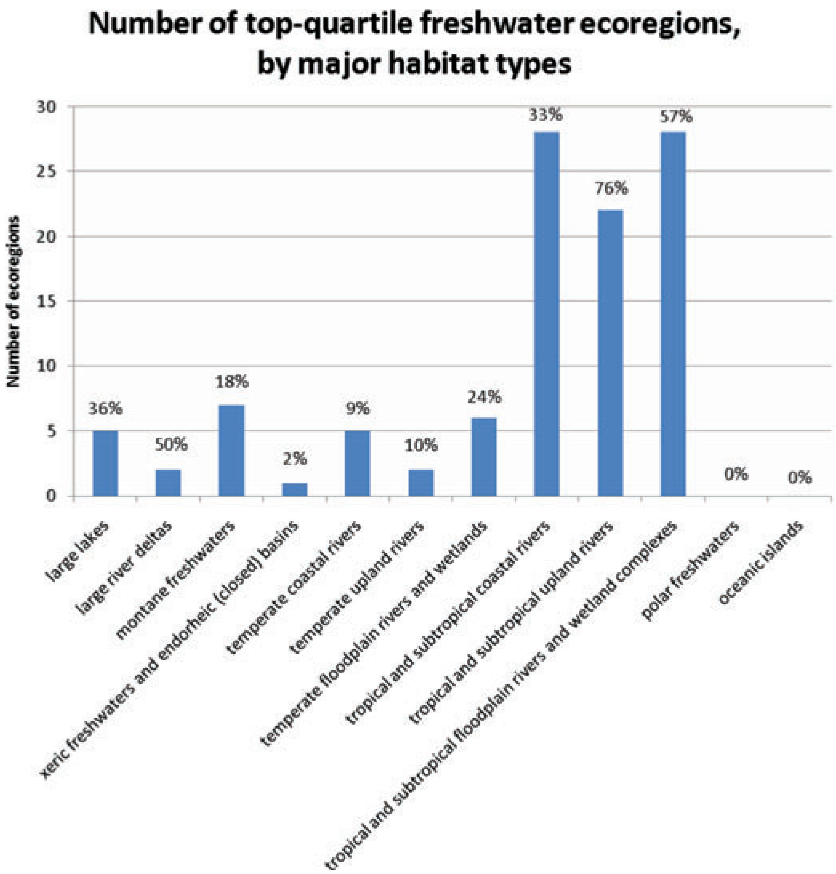

Figure 2 Representation of 12 major habitat types within the set of top-quartile freshwater ecoregions. Percentages of the total number of ecoregions in each habitat type are shown. Low RWR values are to be expected for polar ecoregions and oceanic islands, where climate and geographic isolation, respectively, as well as reduced habitat availability have restricted freshwater species diversity.

107 top-quartile freshwater ecoregions, 59 are "high-congruence" (75% or greater overlap). There is evidence that this overlap is greater than what would be expected by chance ($P < 0.001$, randomization tests; Figure 4). At 5%, 10%, 15%, and 20% levels, this result remains unchanged ($P < 0.001$, randomization tests; Tables S1 and S2). Overlap is markedly reduced when moving from the top 20% of ecoregions to the top 5% (Figures 5 and 6). About 40% of the area of top 5% freshwater ecoregions overlaps with top 5% terrestrial ecoregions, but only two freshwater ecoregions (Guianas and Upper Parana) qualify as high congruence.

Whereas endemism analyses treat species as either endemic or not, the rarity index weights species with limited distributions higher than species with widespread distributions, regardless of whether they are endemic. By combining richness and endemism into a single index, certain freshwater ecoregions are highlighted more strongly than they had been in previous separate analyses of richness and endemism (Abell *et al.* 2008). These include North America's Appalachian Piedmont, the Middle East's Upper Tigris and Euphrates, Africa's Lower Niger-Benue, Asia's Southeastern Ghats and Northern Philippines, and Australia's Arafura-Carpenteria. Additionally, improved data for South America show the importance of freshwater ecoregions like the Northeastern Caatinga & Coastal Drainages, the Xingu, the Tapajos–Juruena, and the Chaco.

Top-quartile terrestrial ecoregions occur almost nowhere beyond 30° N (Figure 1B). Several terrestrial ecoregions were also highlighted by the rarity index that had previously been overlooked in separate analyses of species richness and endemism (Lamoreux *et al.* 2006). These include several in southern South America (e.g., Patagonian Steppe, Argentine Monte), southwestern Madagascar (Madagascar Succulent Woodlands), and much of Australia's western and northern coastline (e.g., Pilbara Shrublands, Kimberly Tropical Savanna, Carpentaria Tropical Savanna).

Discussion

Our results highlight two types of ecoregions of special interest to conservation. First are areas of highest overlap between freshwater and terrestrial biodiversity

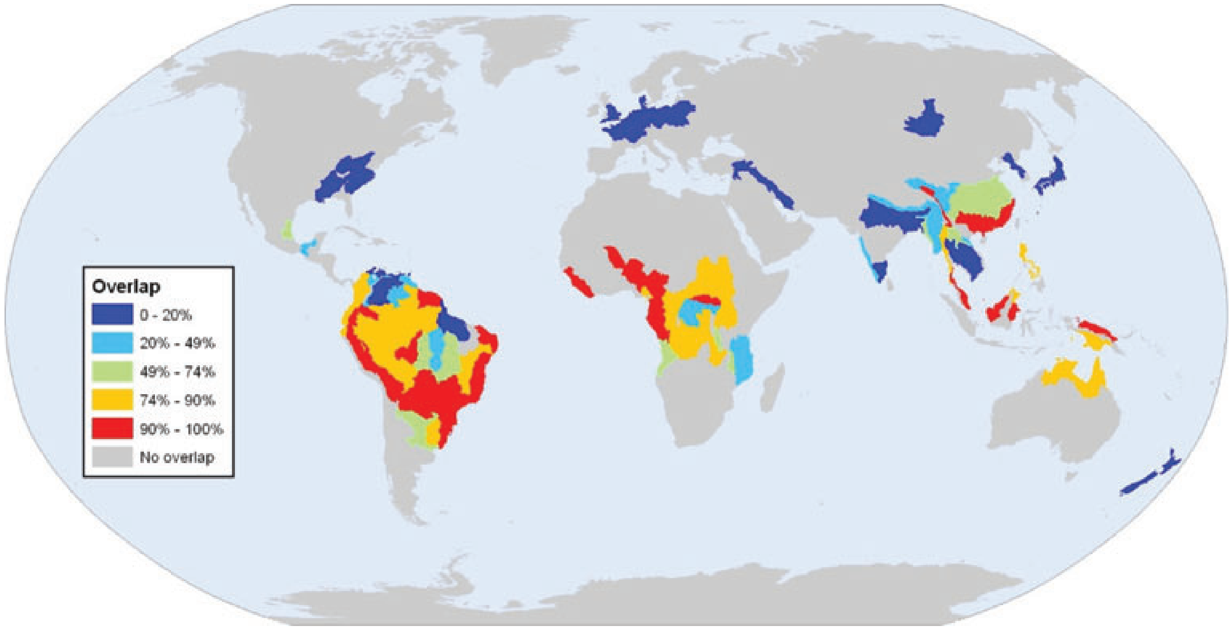

Figure 3 Spatial concordance between freshwater and terrestrial biodiversity. Colored areas represent freshwater ecoregions in the top quartile for rarity-weighted fish richness, and colors indicate degree of overlap with analogous terrestrial ecoregions based on rarity-weighted vertebrate diversity. In orange and red areas, integration of freshwater and terrestrial conservation strategies should be accelerated. Blue areas risk being missed if global investments focus only on terrestrial conservation.

("high-congruence" red ecoregions in Figure 3). While some regions (e.g., the Amazon) have already been recognized for their globally outstanding freshwater diversity (Groombridge & Jenkins 1998; Revenga *et al.* 1998; Olson & Dinerstein 2002), our results expand the list of high-congruence areas to include places like the Atlantic forests of Brazil. Other high-congruence places, like the Laguna dos Patos freshwater ecoregion of southeastern Brazil and Uruguay, and Africa's Lower Niger-Benue, have been recognized neither for their freshwater nor for their terrestrial biodiversity values in previous large-scale analyses (Olson & Dinerstein 2002; Mittermeier *et al.* 2004; Thieme *et al.* 2005).

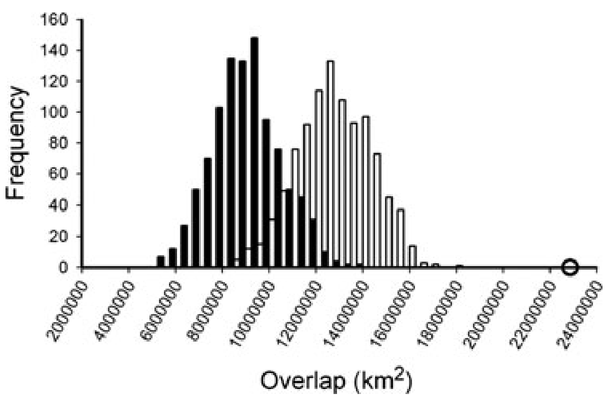

Figure 4 Randomization tests for overlap between important regions for terrestrial and freshwater biodiversity. Bars represent distribution from 1,000 spatial randomizations, both globally (black bars) and within each of the world's 14 terrestrial biomes (white bars). Circle marks the observed overlap. In both cases, the observed overlap is greater than that generated by all 1,000 randomizations ($P < 0.001$).

High-congruence areas, which for the most part are already "on the map" for terrestrial values, offer opportunities to conserve species in both realms with strategies that integrate terrestrial and freshwater protection. For instance, protected areas have historically been a cornerstone of terrestrial conservation but integrating freshwater conservation objectives into terrestrially focused protected area management, and exploring appropriate protected area design that targets freshwater species and ecosystems, have hardly been investigated (Abell *et al.* 2007). Protected areas can be designed and managed to protect both sets of targets better, if not perfectly (Roux *et al.* 2008; Nel *et al.* 2009b). Similarly, terrestrial conservation can benefit from freshwater strategies like integrated catchment management, especially where land use can be managed to protect freshwater system dynamics and consequently ecosystem services like drinking water (Dudley & Stolton 2003). Efforts to identify smaller landscapes and watersheds of highest priority

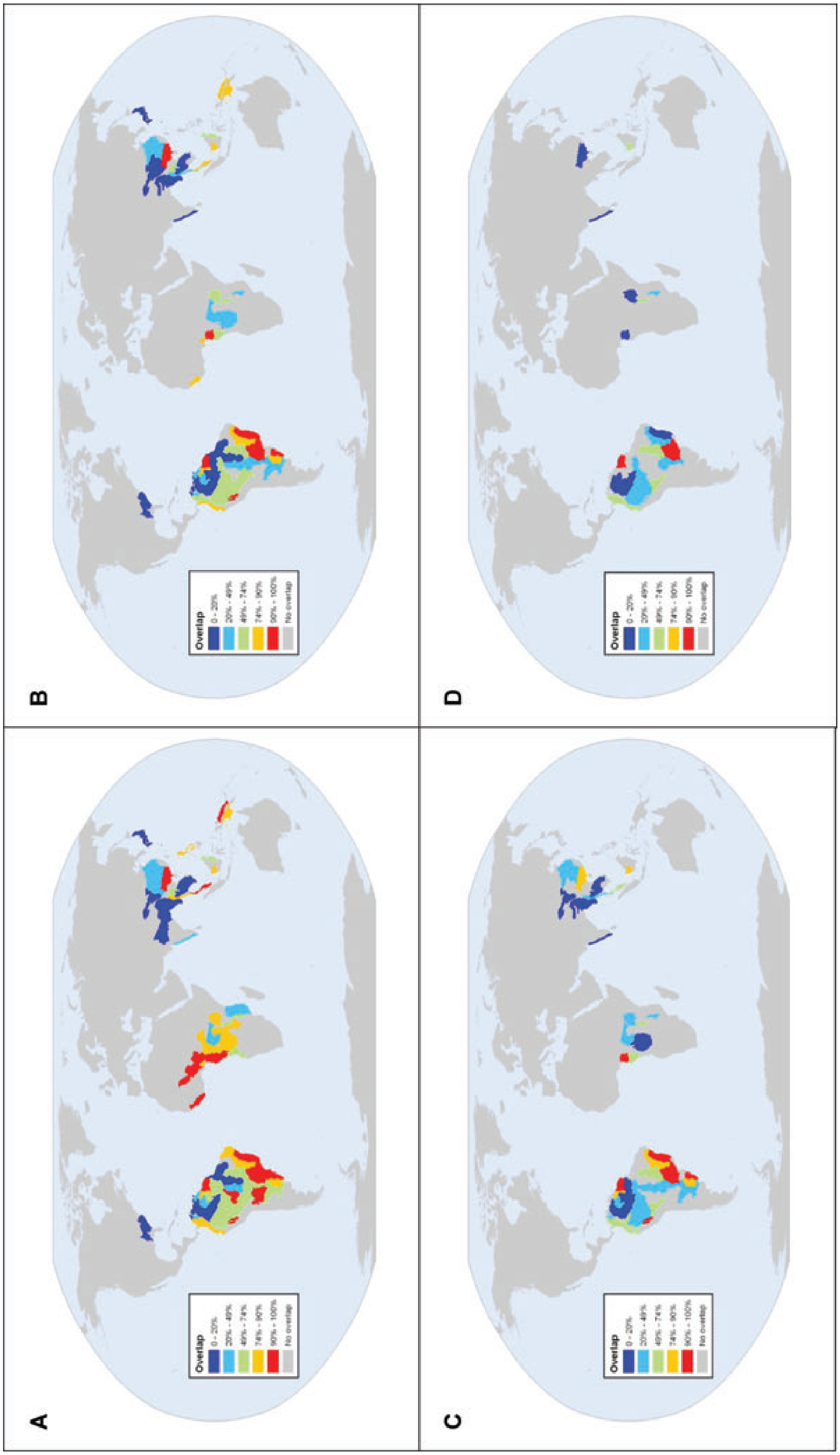

Figure 5 (A–D) Freshwater ecoregions with the top 20% (A), 15% (B), 10% (C), and 5% (D) rarity scores, colored by degree of overlap with terresterial ecoregions in the same levels. Colors change for individual ecoregions when overlapping terrestrial ecoregions fall out of the analysis.

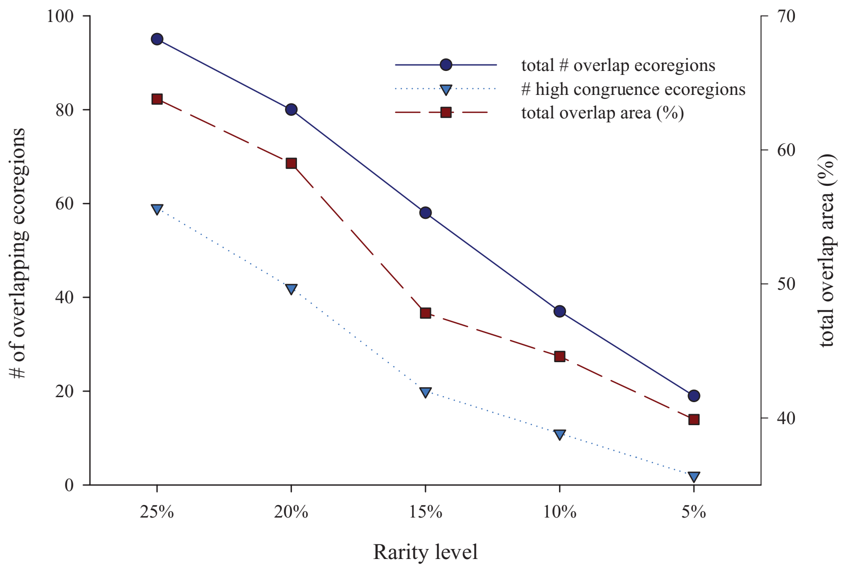

Figure 6 Numbers of high-congruence and total overlap ecoregions for each of the 5 rarity levels (top 25%, 20%, 15%, 10%, 5%), and percentage overlap area for each level.

within these high-congruence areas can utilize new data sets and methods that increasingly enable better integrated terrestrial and freshwater conservation planning (Amis *et al.* 2009; Nel *et al.* 2009c). In the current economic climate of shrinking conservation budgets, these high-congruence areas could hold special appeal for investment in more holistic land–water conservation efforts. A joint focus on conserving cooccurring terrestrial and freshwater targets cannot be taken for granted, however, as a strong tendency toward near-exclusive investment in terrestrial targets persists.

Of equal or greater interest are the 20 important freshwater ecoregions discordant with terrestrial equivalents ("low-overlap" blue ecoregions in Figure 3). Conservation priorities based solely on terrestrial data are likely to underemphasize or miss these ecoregions altogether. Low-congruence tropical ecoregions, like those of the Ganges and Mekong deltas, might lack globally significant terrestrial biodiversity but support rich fish faunas that are of critical importance to local human communities (Food and Agriculture Organization of the United Nations & WorldFish Center 2008).

Many additional low-congruence areas are outside the tropics. For example, the southeast United States features a rich, highly endemic fish fauna that evolved amid locally diverse habitats and glacial refugia (Isphording & Fitzpatrick 1992). Lake Baikal, the Upper Tigris-Euphrates, and other temperate freshwater ecoregions might not rival tropical ecoregions in terms of species richness, but their highly endemic fish faunas combined with relatively high species numbers result in high rarity values. Western Europe has rarely been considered a global conservation priority for either terrestrial or freshwater; it is highlighted here as a result of new taxonomic research concluding that its fish fauna, the Salmonidae and Cottidae families in particular, is far more diverse than previously thought (Kottelat & Freyhof 2007). The case of Western Europe in particular, and our temperate-zone results in general, underscore previous findings that greater taxonomic exploration has led to higher documented freshwater biodiversity in those regions (Balian *et al.* 2008). Tropical freshwaters remain poorly studied, and greater exploration of them could yield larger numbers of low-congruence tropical freshwater ecoregions.

Mobilizing conservation investment and attention in low-congruence freshwater ecoregions will be hard. The conservation community has often given relatively low priority to conserving freshwater biodiversity for its own sake. The rapidly growing interest in ecosystem services has the potential to generate new opportunities for freshwater conservation activities, especially if the prevailing tendency to focus on water resources and forested upper catchments shifts to better incorporate river-wide conservation and monitoring activities that include freshwater species and ecosystem processes (Dudgeon *et al.* 2006). The imperative of adapting to climate change impacts, which some human communities will principally experience through changes to freshwater systems, also offers new possibilities for freshwater conservation. Cross-sectoral climate change mitigation and adaptation policies that include water-related actions such as the conservation and restoration of wetlands and sustaining natural river flows to floodplains present opportunities to strengthen freshwater biodiversity conservation and minimize impact on local communities (Poff *et al.* 2002; Matthews & Wickel 2009).

An investment in freshwater conservation is in many cases an investment in terrestrial (and marine) conservation as well, since protecting a freshwater system can be as much about protecting the integrity of its catchment as about protecting the aquatic system itself. At the same time, protecting land cover alone is insufficient. Extra investments are often required to restore natural flow regimes, mitigate point source pollution, prevent or remove barriers to connectivity, manage fisheries and invasive species, and undertake other activities designed specifically to reduce threats to freshwater species populations (Dudgeon *et al.* 2006). The private sector, which is demonstrating increased interest in reducing business risk by protecting freshwater resources, including through supporting watershed stewardship activities, may be one source of new investments (Nel *et al.* 2009a).

Our analysis confirms that, as with terrestrial vertebrates, freshwater fish diversity is largely concentrated in the tropics and subtropics (Leveque *et al.* 2008). However, biodiversity patterns for fish are not necessarily representative of those for other freshwater taxa (Heino *et al.* 2005). Global assessments of the distribution and conservation status of amphibians (IUCN, Conservation International, & Natureserve 2008), and more recently, freshwater turtles (Buhlmann *et al.* 2009) indicate that while there is considerable overlap between fish species distributions and these other taxa, some areas also stand out as unique for nonfish groups (IUCN, Conservation International, & Natureserve 2008; WWF & TNC 2008; Buhlmann *et al.* 2009). For instance, areas in much of Central America, north and eastern coastal Australia, and the North American drainages entering the Gulf of Mexico, while not outstanding for fish diversity, are all extremely rich in turtle species (Abell *et al.* 2008; Buhlmann *et al.* 2009). Similarly, the Upper Brahmaputra freshwater ecoregion, which is among the richest for freshwater turtle species, is not a hotspot for fish diversity (WWF & TNC 2008; Buhlmann *et al.* 2009). Amphibian richness, which also tends to be concentrated in the tropics, has a similar global pattern to fish diversity, with a few exceptions such as north and eastern coastal Australia, Madagascar, and parts of Central America, where amphibian richness stands out. Similar analyses for groups like aquatic invertebrates, once global distribution data are more comprehensive and accessible, might highlight additional ecoregions in higher latitudes (Rundle *et al.* 2000; Vinson & Hawkins 2003).

We have focused on ecoregions in the top quartile for rarity values, but shrinking the set to progressively narrower ranges of top ecoregions is revealing. Moving from the top 25% to the top 5%, there is a steep drop-off in the number of high-congruence ecoregions. Focusing conservation investments on the top quartile of terrestrial ecoregions then might benefit a number of top-quartile freshwater ecoregions, but the same is not the case for investments focused on a smaller subset of the highest scoring terrestrial ecoregions. We cannot take for granted that the world's most diverse freshwater places will incidentally be included in terrestrial priorities.

These results provide one of the most comprehensive global pictures of freshwater systems deserving increased conservation. Although fish might be imperfect surrogates for other aquatic taxa, this new global data set broadens previous terrestrial-focused frameworks and calls attention to important freshwater ecoregions that deserve conservation effort on their own. Additional criteria, such as representation across biomes and biogeographic realms, level of intactness or threat, or provision of ecosystem services could be applied to these new data to suggest a more balanced set of global conservation priorities. The priority-setting landscape may already be overcrowded (Marris 2007), but with the new availability of freshwater species data sets roughly comparable to those for terrestrial, and with an increasing understanding of the human dependence on freshwater resources, it may be worth taking another look at global conservation investments to ensure that blue areas are on the map.

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Results of randomizations. Each cell contains area of overlap (km^2) between freshwater ecoregions with the highest rarity-weighted-richness values (top X%) and randomized top X% terrestrial ecoregions. For those columns modified by "biome", the randomization was stratified by 14 biomes into which terrestrial ecoregions are nested (e.g., tropical most forests, temperate grasslands).

Table S2 Actual area of overlap of freshwater and terrestrial ecoregions with high rarity-weighted-richness values (top X%).

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