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Freshwater Ecoregions of the World: A New Map of Biogeographic Units for Freshwater Biodiversity Conservation

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We present a new map depicting the first global biogeographic regionalization of Earth's freshwater systems. This map of freshwater ecoregions is based on the distributions and compositions of freshwater fish species and incorporates major ecological and evolutionary patterns. Covering virtually all freshwater habitats on Earth, this ecoregion map, together with associated species data, is a useful tool for underpinning global and regional conservation planning efforts (particularly to identify outstanding and imperiled freshwater systems); for serving as a logical framework for large-scale conservation strategies; and for providing a global-scale knowledge base for increasing freshwater biogeographic literacy. Preliminary data for fish species compiled by ecoregion reveal some previously unrecognized areas of high biodiversity, highlighting the benefit of looking at the world's freshwaters through a new framework.

Keywords: freshwater, ecoregions, biogeography, fish, mapping

Growth of the human population, rising consumption, and rapid globalization have caused widespread degradation and disruption of natural systems, especially in the freshwater realm. Freshwater ecosystems have lost a greater proportion of their species and habitat than ecosystems on land or in the oceans, and they face increasing threats from dams, water withdrawals, pollution, invasive species, and overharvesting (MEA 2005, Revenga et al. 2005). Freshwater

ecosystems and the diverse communities of species found in lakes, rivers, and wetlands may be the most endangered of all (MEA 2005).

These stressed systems support an extraordinarily high proportion of the world's biodiversity. In terms of area, freshwater ecosystems occupy only 0.8% of Earth's surface, but they are estimated to harbor at least 100,000 species, or nearly 6% of all described species (Dudgeon et al. 2006). Each year,

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new freshwater species are described. For South America alone, about 465 new freshwater fish species have been described in the last five years (Eschmeyer 2006), a figure that corresponds to a new species every four days. The presence of species confined to small ranges is also unusually high in freshwater ecosystems; for example, 632 animal species have been recorded as endemic to Lake Tanganyika (Groombridge and Jenkins 1998).

Despite this combination of extraordinary richness, high endemism, and exceptional threat, few broadscale conservation planning efforts have targeted freshwater systems and their dependent species. This relative inattention derives in part from an acute lack of comprehensive, synthesized data on the distributions of freshwater species (Revenga and Kura 2003). The most exhaustive recent global inventory of freshwater taxa acknowledges serious survey gaps and assigns species distributions only to the level of continent (Lévêque et al. 2005). Such inventories are valuable for highlighting research priorities and providing a global picture of how taxonomic diversity compares across continents, but they have limited utility for conservation planning efforts, for which the largest planning unit is often the river basin or ecoregion.

A global freshwater regionalization

Ecoregions are a widely recognized and applied geospatial unit for conservation planning, developed to represent the patterns of environmental and ecological variables known to influence the distribution of biodiversity features at broad scales (Groves et al. 2002). Building on the work of Dinerstein and colleagues (1995), we define a freshwater ecoregion as a large area encompassing one or more freshwater systems with a distinct assemblage of natural freshwater communities and species. The freshwater species, dynamics, and environmental conditions within a given ecoregion are more similar to each other than to those of surrounding ecoregions, and together form a conservation unit. Ecoregion boundaries are not necessarily determined by the turnover of species ranges (McDonald et al. 2005) but are intended to describe broad patterns of species composition and associated ecological and evolutionary processes.

Ecoregion delineation benefits from the best available data describing species and systems ecology, but can proceed with imperfect information (Wikramanayake et al. 2002). Global ecoregion frameworks have already been developed for the terrestrial and, more recently, marine realms, both of which are characterized by their own data limitations (Olson et al. 2001, Spalding et al. 2007). In this article we demonstrate how the ecoregion concept has been applied to freshwater systems, and present the first global map of freshwater ecoregions—a starting point for conservation planning anywhere on Earth.

Ecoregions have typically been delineated to represent patterns of potential vegetation (Olson et al. 2001) and have at times been used to characterize regional differences in water quality as well (Omernik 1987). Terrestrial ecoregions are delineated largely on the basis of climate, physiography, and vegetation types, but different features are often domi-

nant in shaping the broadscale distributions of freshwater species. As Tonn (1990) described, the species occurring in a given river reach, lake, spring, or wetland will be a function of a hierarchy of continental-scale filters (including mountain building, speciation, and glaciation) that have defined large biogeographic patterns; regional-scale filters (such as broad climatic and physiographic patterns, and dispersal barriers such as regional catchments); and subregional and finer-scale habitat filters (e.g., distinct physiographic types and macrohabitats) acting on the regional species pool. Freshwater ecoregions capture the patterns generated primarily by continental- and regional-scale filters.

Of these filters, dispersal barriers in the form of catchment divides (also called watersheds) are distinctive to freshwaters. Unlike terrestrial species or those with aerial or wind-dispersed life stages, obligate freshwater species—those confined to the freshwater environment and unable to move via land, air, or sea—generally cannot disperse from one unconnected catchment to another. Furthermore, all species dependent on freshwater systems, whether or not they are confined to the aquatic environment, are to some extent affected by the hydrological and linked ecological processes of the catchments where they live. As a result, catchments strongly influence broad freshwater biogeographic patterns in most regions. There are exceptions, however. Tectonic movements have in some cases separated once-joined catchments, allowing for further speciation. Also, natural drainage evolution over geological time includes river piracy, which severs connections and provides new interdrainage links that reconfigure systems. The freshwater ecoregions of the world presented here reflect both the hydrological underpinning of freshwater fish species distributions as well as historical shifts in landmasses and consequent evolutionary processes.

Ecoregion delineation and species list compilation

No global biogeographic framework for freshwater species was available as the foundation for our map. The applicability of Wallace's (1876) and Udvardy's (1975) zoogeographic realms to most freshwater taxa is unresolved (Berra 2001, Vinson and Hawkins 2003), and these divisions are too large for conservation planning endeavors. Several examinations of global freshwater biogeography (e.g., Banarescu 1990) provided information at somewhat finer scales but could not be clearly translated into seamless ecoregion delineations. Where appropriate, we adapted previous continental efforts. For North America, Africa, and Madagascar, we updated regionalizations outlined in two previously published volumes (Abell et al. 2000, Thieme et al. 2005), but we excluded a prior delineation for Latin America and the Caribbean (Olson et al. 1998) because the approach differed markedly from our current methodology, and data have improved substantially since its development (e.g., Reis et al. 2003). We examined but chose to exclude the 25 European regions of Illies's impressive *Limnofauna Europaea* (1978) because the approach for delineating those regions differed considerably from ours: those regions were based on the distributions of 75

different taxonomic groups and were drawn without reference to catchments. Moreover, neither ecological nor evolutionary processes figured in those delineations. A complete list of all references and experts consulted in the process of delineating ecoregions is available online (www.feow.org).

We assembled our global map of freshwater ecoregions using the best available regional information describing freshwater biogeography, defined broadly to include the influences of phylogenetic history, palaeogeography, and ecology (Banarescu 1990). We restricted our analyses to information describing freshwater fish species distributions, with a few exceptions for extremely data-poor regions and inland seas, where some invertebrates and brackish-water fish were considered, respectively. We focused on freshwater fish for several reasons. On a global scale, fish are the best-studied obligate aquatic taxa. Detailed information exists for other freshwater taxa in regions like North America and Europe, but the consideration of such groups in a global analysis would be difficult, given the wide variation in available data (Balian et al. 2008). Freshwater dispersant fish species—those unable to cross saltwater barriers—are better zoogeographic indicators than freshwater invertebrates, which can often disperse over land, survive in humid atmospheres outside water, or be transported between freshwaters (Banarescu 1990). Finally, the distributions of obligate aquatic invertebrate groups in general respond to ecological processes at localized scales that are too small to be meaningful for ecoregion delineation (Wasson et al. 2002). Therefore, fish serve as proxies for the distinctiveness of biotic assemblages. We recognize that analyses of other taxonomic groups would almost certainly reveal different patterns for some regions, and that our results are scale dependent (Paavola et al. 2006). Our near-exclusive focus on fish is a departure from earlier continental ecoregionalization exercises (Abell et al. 2000, Thieme et al. 2005), and we have updated the ecoregion delineations accordingly.

The available data for describing fish biogeography vary widely. In the United States, it is possible to map presence/absence data for all freshwater fish species to subbasins averaging about 2025 square kilometers (km²) in size (NatureServe 2006). But for many of the world's species, occurrence data are limited to a small number of irregularly surveyed systems. Large parts of the massive Congo basin remain unsampled, for instance, with most sampling occurring near major towns and most taxonomic studies of the region dating from the 1960s. Problems with taxonomy and species concepts hamper broadscale analyses even where systems have been reasonably well sampled (Lundberg et al. 2000). Although addressing many of these problems is beyond the scope of this project, in our analyses we have attempted to minimize nomenclatural errors by normalizing species names with Eschmeyer's *Catalog of Fishes* (2006; www.calacademy.org/research/ichthyology/catalog/).

Freshwater fish patterns were analyzed separately for different regions of the world to account for data variability. The geographic scope of major information sources largely defined those regions (table 1). Information sources were typically taxonomic works, some of which included biogeographical analyses. Leading ichthyologists delineated ecoregions primarily by examining the distributions of endemic species, genera, and families against the backdrop of an area's dominant habitat features and the presence of ecological (e.g., large concentrations of long-distance migratory species) and evolutionary (e.g., species flocks) phenomena. More than 130 ichthyologists and freshwater biogeographers contributed to the global map by either delineating or reviewing ecoregions.

Data gaps and biogeographic drivers resulted in the use of slightly different criteria among and even within some regions (table 2, box 1). Where fish species data were reasonably comprehensive and available at subbasin or finer scales, we attributed species distributions to catchments to facilitate evaluation of biogeographic patterns in a bottom-up

Table 1. Regional information sources used for ecoregion delineations.

Region	Primary information source
Africa	Roberts 1975, Skelton 1994, Lévêque 1997, Thieme et al. 2005
Middle East	No regional information sources available.
Former USSR	No regional information sources available.
Remainder of Eurasia	For Europe: Kottelat and Freyhof 2007; no regionwide information sources for Asia.
Australasia	McDowall 1990, Allen 1991, Unmack 2001, Allen et al. 2002
Oceania	Keith et al. 2002
Canada	Scott and Crossman 1998
United States	Maxwell et al. 1995, Abell et al. 2000
Mexico	Contreras-Balderas 2000, Miller et al. 2005
Central America	Bussing 1976, CLOFFSCA (Reis et al. 2003)
Caribbean	Rauchenberger 1988, Burgess and Franz 1989
South America	CLOFFSCA (Reis et al. 2003), Menni 2003

Note: In many cases, these same sources were used to compile species lists. A full bibliography with additional publications, which along with unpublished data often constituted the greater part of inputs to ecoregion delineations and species lists, is available at the Web site www.feow.org. Every region also benefited from expert input; individual contributors are listed in the acknowledgments section and at the Web site. Regions in some cases correspond to politically rather than biophysically defined units to take advantage of existing information sources and expertise.

approach. For example, a new high-resolution hydrographic dataset (HydroSHEDS; www.wwfus.org/freshwater/hydrosheds.cfm) for South America provided fine-scale catchment maps that, in conjunction with newly synthesized species data (Reis et al. 2003), aided in the assessment of biogeography. In regions without extensive species data, or where major basins support highly similar faunas as a result of recent glaciation, a top-down analysis used qualitative expert knowledge of distinctive species and assemblages to map major biogeographic patterns (table 2). Ecoregional boundaries resulting from either approach, therefore, largely coincide with catchment boundaries.

Whereas overall there is correspondence between catchments and ecoregion boundaries, unconnected neighboring catchments were in some cases grouped together, where strong biogeographic evidence indicates that landscape or other features overrode contemporary hydrographic integrity. For example, owing to historic drainage evolution and similarities in fauna, Africa's southern temperate highveld combines headwaters of coastal basins that drain to the Indian Ocean with those of the Atlantic-draining Orange basin. Considerable faunal exchange of the headwaters of the Orange River system with that of the coastal systems may have occurred as the coastal rivers eroded their basins at a faster rate than the adjacent Orange tributaries (Skelton et al. 1995).

These and other examples demonstrate that historical geographic events and current hydrology may have conflicting effects on the fish fauna of a particular region and thereby argue for different boundaries. The decision to weigh some effects more strongly than others was made on a case-by-case basis, and it is acknowledged that additional data may favor alternative delineations.

With the exception of islands, individual freshwater ecoregions typically cover tens of thousands to hundreds of thousands of square kilometers (Maxwell et al. 1995). Ecoregion size varies in large part because of landscape history. Regions with depauperate faunas resulting from recent glaciation events tend to have large ecoregion sizes, as do those dominated by very large river systems (e.g., much of South America). Regions with recent tectonic activity or smaller, more isolated freshwater systems often are divided into smaller ecoregions. For example, central Mexico has experienced intermittent isolation and exchange between basins owing to active mountain-building processes leading to small, fragmented systems with distinct faunas. We acknowledge that data quality may also influence the size of ecoregions; for instance, the entire Amazon is currently divided into only 13 ecoregions, but better data on species occurrences within major subbasins would most likely support finer delineations.

Table 2. Basic ecoregion delineation approaches for individual regions.

Region	Delineation approach
Africa	Using Roberts (1975) as a starting point, ecoregions were delineated using a top-down qualitative assessment that incorporated expert knowledge and divisions of major river basins. In a few cases where basin divides do not circumscribe species distributions or where basins contain internal barriers to dispersal, ecoregions straddle or divide basins.
Middle East	Species lists were generated for whole drainage basins, which were then either combined with smaller catchments that were very similar faunistically (minor desert basins, for example) or subdivided on the basis of different ecologies (e.g., the Tigris-Euphrates with lowland marshes and upland streams).
Former USSR	A species/genera/family presence/absence matrix was compiled for a hierarchy of hydrographic units, and cluster analysis and ordination techniques (Primer v.6 statistics software) were employed to assess biotic similarities among hydrographic units and to identify major faunal breaks.
Remainder of Eurasia	For Southeast Asia and southern Europe, a bottom-up approach employing both published and unpublished field data and expert assessment was used. East Asian, northern European, and eastern European ecoregions were delineated through a top-down process using major basins as a starting point and incorporating traditionally recognized zoogeographic patterns where appropriate.
Australasia	For Australia, ecoregions were adapted from Allen and colleagues' (2002) and Unmack's (1991) "freshwater fish biogeographic provinces"; provinces were derived through similarity analyses, parsimony analysis, and drainage-based plots of species ranges. For New Guinea, "subprovinces" of Allen (1991) were modified (primarily combined) on the basis of expert input. For New Zealand and other islands and island groups, islands were placed in ecoregions on the basis of expert input.
Oceania	Islands and island groups were placed in ecoregions on the basis of distinctive (endemic or near-endemic) fish faunas.
Canada	Separate cluster analyses were conducted on fish occurrence in the secondary watersheds in each of the nine primary watersheds in Canada.
United States	The "subregions" of Maxwell and colleagues (1995) were adopted, with relatively small modifications made following input by regional specialists, especially the Endangered Species Committee of the American Fisheries Society.
Mexico	Ecoregion delineations were based on qualitative similarity/dissimilarity assessments of major basins, using the standard administrative hydrographical regions of the Mexican federal government. Subregions within major basins were recognized as separate ecoregions when the fish fauna was sufficiently distinctive.
Central America	Fish provinces from Bussing (1976) were revised and subdivided on the basis of the application of the similarity index to subbasin fish presence/absence data.
Caribbean	Ecoregions from Olson and colleagues (1998) were modified on the basis of similarity analyses of island-by-island species lists and expert input.
South America	Ecoregion delineations were based on qualitative similarity/dissimilarity assessments of catchments, resulting in aggregation/disaggregation. See box 1 for additional information.

Note: Some of the variations resulting from differences in data quality and biogeographic drivers across and within regions are noted. For some regions, subecoregions (described at www.feow.org) were delineated to capture finer-scale patterns than could be represented by ecoregions.

Box 1. Example of criteria applied to ecoregion delineation: South America.

The delineation process for South America followed a step-wise process of subdivision of the continent's major drainage systems. Delineation started with the historically recognized major ichthyographic provinces exemplified in Gery (1969) and Ringuelet (1975) and proceeded with subdivision at finer scales using regionalized data on fish distributions.

The criteria for determining the merit of delineating an ecoregion were not uniform across the continent as a result of localized faunistic differences. In some areas, delineations were based on family-level data, whereas in others, faunistic turnover at lower taxonomic levels was the criterion. For instance, astrolepid catfishes are distinct components of high-elevation freshwaters along the Andes forefront, and that family's distribution was critical to informing the delineation of the high Andean ecoregions. On the other side of the continent along the Atlantic coast, we used the presence or absence of endemic assemblages of the genus *Trichomycterus*, several genera of the subfamily Neoplecostominae, and the presence or absence of annual killifish genera and species to distinguish distinct drainage complexes from one another.

In the piedmont zones and in contact areas between lowlands and geologic shield areas, we used indicator groups to determine where along the elevation/slope gradient the fauna was changing. The distribution of lowland forms was matched with forms found in higher-gradient systems to establish where one group was dropping out and the other started occurring. This transition zone was then established as the operational boundary between connecting ecoregions.

For areas like Patagonia, the Titicaca altiplano, and the Maracaibo basin, the uniqueness of the fauna, often occurring within clearly defined geographic areas, permitted reasonably straightforward delineations. In the larger river basin systems where there are no clear boundaries, the ecoregional limits are the best approximation, given the current data.

The process of delineating ecoregions required compiling and synthesizing information on the distributions of fish species. A logical and practical extension of the delineations was the compilation of fish species lists for each ecoregion. For the United States, NatureServe provided presence/absence data for individual species, coded to eight-digit hydrologic unit codes (HUCs); these HUC occurrences were then translated to ecoregions, and the data were manually cleaned of erroneous occurrences derived from introductions and problematic records. These species lists were then merged with those from Canada and Mexico for transnational ecoregions. For all other ecoregions, data came from the published literature, as well as from gray literature and unpublished sources (see table 1; a full bibliography is available at www.feow.org). In all cases, experts served as gatekeepers of these data to ensure that lists were based on the best available information, both in terms of distributions and nomenclature. Introduced species were removed from the tallies presented here, as were

undescribed species. Confirmed extinct species (Ian J. Harrison, American Museum of Natural History, New York, personal communication, 29 March 2007) were excluded, but extirpated species were included to acknowledge restoration opportunities. Endemic species, defined as those occurring only in a single ecoregion, were identified first by experts and cross-checked using a species database constructed for this project, which includes more than 14,500 described fish species. Species were coded as freshwater, brackish, or marine using data from FishBase (www.fishbase.org), and species with only brackish or marine designations were omitted from the richness and endemism totals reported here.

Freshwater ecoregional map and species results

Our map of freshwater ecoregions contains 426 units, covering nearly all nonmarine parts of the globe, exclusive of Antarctica, Greenland, and some small islands (figure 1; a full legend is available at www.feow.org). There is large variation in the area of individual ecoregions. Large ecoregions, such as the dry Sahel (4,539,429 km²), tend to be found in more depauperate desert and polar regions exhibiting low species turnover. Smaller ecoregions are typically found in noncontinental settings where systems are by nature smaller and species turnover is higher, as in the Indo-Malay region. The smallest ecoregion, at 23 km², is Cocos Island (Costa Rica); the average ecoregion size is 311,605 km². Ecoregions ranged from those encompassing only 1 country to those straddling 16 countries (central and western Europe ecoregion).

In total, we assigned more than 13,400 described freshwater fish species to ecoregions, of which more than 6900 were assigned to single ecoregions (i.e., endemic). Examination of the fish species data synthesized by ecoregion confirms some well-known patterns and highlights others unknown to many conservationists, managers, and policymakers working at regional or global scales (figures 2a–2d). In agreement with previous global assessments (Groombridge and Jenkins 1998, Revenga et al. 1998), our analysis identifies as outstanding for both fish richness and endemism systems that include large portions of Africa's Congo basin, the southern Gulf of Guinea drainages, and Lakes Malawi, Tanganyika, and Victoria; Asia's Zhu Jiang (Pearl River) basin and neighboring systems; and large portions of South America's Amazon and Orinoco basins. Areas confirmed for globally high richness include Asia's Brahmaputra, Ganges, and Yangtze basins, as well as large portions of the Mekong, Chao Phraya, and Sitang and Irrawaddy; Africa's lower Guinea; and South America's Paraná and Orinoco. When richness is adjusted for ecoregion area, additional systems such as the Tennessee, Cumberland, Mobile Bay, Apalachicola, and Ozark highlands in the southeastern United States; portions of Africa's Niger River Basin; the islands of New Caledonia, Vanuatu, and Fiji; China's Hainan Island; and large parts of Sumatra and Borneo, among many other areas, are also especially noteworthy.

Numerous systems previously identified as highly endemic for fish were confirmed, as measured by either numbers of endemic species or percentage endemism. A subset includes



Figure 1. Map of freshwater ecoregions of the world, in which 426 ecoregions are delineated. An interactive version of this map that includes additional information is available at www.feow.org.

101	North America	170	Sierra Madre del Sur	216	Windward and Leeward Islands
102	Alaskan Coastal	171	Papaloapan	217	Cocos Island (Costa Rica)
103	Upper Yukon	172	Coatzacoalcas		
104	Alaska and Canada Pacific Coastal	173	Grijalva-Usumacinta		
105	Upper Mackenzie	174	Upper Usumacinta		
106	Lower Mackenzie	175	Yucatan		
107	Central Arctic Coastal	176	Bermuda		
108	Upper Saskatchewan				
109	Middle Saskatchewan				
110	English-Winnipeg Lakes				
111	Southern Hudson Bay				
112	Western Hudson Bay				
113	Canadian Arctic Archipelago				
114	Gulf of St. Lawrence Coastal Drainages				
115	Gulf of St. Lawrence Coastal Drainages				
116	Laurentian Great Lakes				
117	St. Lawrence				
118	Northeast US and Southeast Canada				
119	Atlantic Drainages				
120	Scotia-Fundy				
121	Columbia Glaciated				
122	Columbia Unglaciated				
123	Upper Snake				
124	Oregon and Northern California Coastal				
125	Oregon Lakes				
126	Sacramento-San Joaquin				
127	Lahontan				
128	Bonneville				
129	Death Valley				
130	Vegas-Virgin				
131	Colorado				
132	Gila				
133	Upper Rio Grande-Bravo				
134	Pecos				
135	Rio Conchos				
136	Lower Rio Grande-Bravo				
137	Cuatro Ciénegas				
138	Rio San Juan (Mexico)				
139	West Texas Gulf				
140	East Texas Gulf				
141	Sabine-Galveston				
142	Upper Missouri				
143	Middle Missouri				
144	US Southern Plains				
145	Quachita Highlands				
146	Central Prairie				
147	Ozark Highlands				
148	Upper Mississippi				
149	Lower Mississippi				
150	Teays-Old Ohio				
151	Cumberland				
152	Tennessee				
153	Mobile Bay				
154	West Florida Gulf				
155	Apalachicola				
156	Florida Peninsula				
157	Appalachian Piedmont				
158	Chesapeake Bay				
159	Southern California Coastal-Baja				
160	Sonora				
161	Guzmán-Samalayuca				
162	Sinaloa				
163	Mayran-Viesca				
164	Rio Santiago				
165	Lerma-Chapala				
166	Llanos El Salado				
167	Panuco				
168	Ameca-Manantlan				
169	Rio Balsas				
170	Sierra Madre del Sur				
171	Papaloapan				
172	Coatzacoalcas				
173	Grijalva-Usumacinta				
174	Upper Usumacinta				
175	Yucatan				
176	Bermuda				
177	Central America				
178	Chiapas-Fonseca				
179	Quintana Roo-Motagua				
180	Mosquitia				
181	Estero Real-Tempisque				
182	San Juan (Nicaragua and Costa Rica)				
183	Chiriqui				
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185	Santa Maria				
186	Chagres				
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195	Magdalena-Sinu				
196	Maracaibo				
197	South America Caribbean				
198	Drainages-Trinidad				
199	Orinoco High Andes				
200	Orinoco Piedmont				
201	Orinoco Llanos				
202	Orinoco Guiana Shield				
203	Orinoco Delta and Coastal Drainages				
204	Essequibo				
205	Guianas				
206	Amazonas High Andes				
207	Western Amazon Piedmont				
208	Rio Negro				
209	Amazonas Lowlands				
210	Amazonas Lowlands				
211	Ucayali-Urubamba Piedmont				
212	Manore-Madre de Dios Piedmont				
213	Guapore-Itenez				
214					
215					

320	Tapajos-Juruena	447	Namak	575	Southern Temperate Highveld	723	Inle Lake
321	Madeira Brazilian Shield	448	Kavir and Lut Deserts	576	Zambezi Lowveld	724	Upper Lancang (Mekong)
322	Xingu	449	Esfahan	577	Amatolo-Winterberg Highlands	725	Er Hai
323	Amazonas Estuary and Coastal Drainages	450	Turan Plain	578	Cape Fold	726	Lower Lancang (Mekong)
324	Tocantins-Araguaia	451	Northern Hornum Drainages	579	Western Madagascar	727	Khorat Plateau (Mekong)
325	Parnaiba	452	Caspian Marine	580	Madagascar Eastern Highlands	728	Kratie-Stung Treng (Mekong)
326	Northeastern Caatinga and Coastal Drainages	453	Volga Delta-Northern Caspian Drainages	581	Madagascar Eastern Highlands	729	Mekong Delta
327	S. Francisco			582	Southern Madagascar	730	Southern Annam
328	Northeastern Mata Atlantica			583	Madagascar Eastern Lowlands	731	Eastern Gulf of Thailand Drainages
329	Paraiba do Sul			584	Comoros-Mayotte	732	Chao Phraya
330	Ribeira de Iguaçu			585	Seichelles	733	Mae Khlong
331	Southeastern Mata Atlantica			586	Mascarenes	734	Malay Peninsula Eastern Slope
332	Lower Uruguay			587	S. Tome and Principe-Annohon	735	Northern Central Sumatra-Western Malaysia
333	Upper Uruguay						
334	Laguna dos Patos						
335	Tramandai-Mamutuba						
336	Central Andean Pacific Slopes						
337	Titicaca						
338	Atacama						
339	Mar Chiquita-Salinas Grandes						
340	Cuervo-Desaguadero						
341	South Andean Pacific Slopes						
342	Chaco						
343	Paraguay						
344	Upper Parana						
345	Lower Parana						
346	Iguassu						
347	Brasensean Drainages						
348	Patagonia						
349	Valdivian Lakes						
350	Galapagos Islands						
351	Juan Fernandez Island						
352	Fluminense						
401	Europe and Middle East						
402	Celtic-Iberian						
403	Northern British Isles						
404	Central and Western Europe						
405	Norwegian Sea Drainages						
406	Northern Baltic Drainages						
407	Barents Sea Drainages						
408	Southern Baltic Lowlands						
409	Lake Onega-Lake Ladoga						
410	Volga-Ural						
411	Western Caspian Drainages						
412	Western Iberia						
413	Southern Iberia						
414	Eastern Iberia						
415	Gulf of Venice Drainages						
416	Italian Peninsula and Islands						
417	Upper Danube						
418	Dniester-Lower Danube						
419	Dalmatia						
420	Southeast Adriatic Drainages						
421	Ionian Drainages						
422	Yardar						
423	Thrace						
424	Aegean Drainages						
425	Dnieper-South Bug						
426	Crimea Peninsula						
427	Don						
428	Kuban						
429	Western Anatolia						
430	Northern Anatolia						
431	Central Anatolia						
432	Southern Anatolia						
433	Western Transcaucasia						
434	Kura-South Caspian Drainages						
435	Sinal						
436	Coastal Levant						
437	Orontes						
438	Jordan River						
439	Southwestern Arabian Coast						
440	Arabian Interior						
441	Lower Tigris and Euphrates						
442	Upper Tigris and Euphrates						
443	Oman Mountains						
444	Lake Van						
445	Orumiyeh						
446	Caspian Highlands						
501	Africa and Madagascar						
502	Atlantic Northwest Africa						
503	Mediterranean Northwest Africa						
504	Sahara						
505	Dry Sahel						
506	Lower Niger-Benue						
507	Niger Delta						
508	Upper Niger						
509	Inner Niger Delta						
510	Senegal-Gambia						
511	Fouta-Djallon						
512	Northern Upper Guinea						
513	Mount Nimba						
514	Eburne						
515	Asanti						
516	Volta						
517	Bight Drainages						
518	Northern Gulf of Guinea Drainages-Bloko						
519	Western Equatorial Crater Lakes						
520	Lake Chad						
521	Lake Victoria Basin						
522	Upper Nile						
523	Lower Nile						
524	Nile Delta						
525	Ethiopian Highlands						
526	Lake Tana						
527	Western Red Sea Drainages						
528	Northern Eastern Rift						
529	Horn of Africa						
530	Lake Turkana						
531	Shabelle-Juba						
532	Ogoué-Nyanga-Kouilou-Niari						
533	Southern Gulf of Guinea Drainages						
534	Sangha						
535	Sudanic Congo-Oubangi						
536	Uele						
537	Cuvette Centrale						
538	Tumba						
539	Upper Congo Rapids						
540	Upper Congo						
541	Albertine Highlands						
542	Lake Tanganyika						
543	Malagarasi-Moyowosi						
544	Bangweulu-Mweru						
545	Upper Luabala						
546	Kasai						
547	Mal Ndombe						
548	Malebo Pool						
549	Lower Congo Rapids						
550	Lower Congo						
551	Cuanza						
552	Namib						
553	Etosha						
554	Karstfeld Sink Holes						
555	Zambesian Headwaters						
556	Upper Zambezi Floodplains						
557	Kafue						
558	Middle Zambezi-Luangwa						
559	Lake Malawi						
560	Zambesian Highveld						
561	Lower Zambezi						
562	Mulanje						
563	Eastern Zimbabwe Highlands						
564	Coastal East Africa						
565	Lake Rukwa						
566	Tana, Athi, and Coastal Drainages						
567	Pangani						
568	Okavango						
569	Kalahari						
570	Southern Kalahari						
571	Southern Orange						
572	Karoo						
573	Drakensberg-Maloti Highlands						
574							
601	Northern Asia						
602	Igizy-Turgai						
603	Ob						
604	Upper Irtysh						
605	Chuya						
606	Yenisei						
607	Lake Baikal						
608	Taimyr						
609	Lena						
610	Kolyma						
611	Anadyr						
612	East Chukotka						
613	Konakia						
614	Kamchatka and Northern Kurils						
615	Okhotsk Coast						
616	Coastal Amur						
617	Middle Amur						
618	Argun						
619	Shilka (Amur)						
620	Songma Jiang						
621	Inner Mongolia Endorheic Basins						
622	Western Mongolia						
623	Dzungaria						
624	Balkash-Alakul						
625	Tarim						
626	Lower and Middle Syr Darya						
627	Lake Issyk-Kul-Upper Chu						
628	Northern Central Asian Highlands						
629	Aral Sea Drainages						
630	Middle Amu Darya						
631	Upper Amu Darya						
632	Qaidam						
633	Upper Huang He Corridor						
634	Huang He Great Bend						
635	Lower Huang He						
636	Liao He						
637	Eastern Yellow Sea Drainages						
638	Southeastern Korean Peninsula						
639	Hangyong-Sammaek						
640	Sakhalin, Hokkaido, and Sikhote-						
641	Alin Coast						
642	Honshu-Shikoku-Kyushu						
643	Biwa Ko						
644							
701	Southern Asia						
702	Baluchistan						
703	Helmand-Sistan						
704	Lower and Middle Indus						
705	Yaghnistan						
706	Indus Himalayan Foothills						
707	Upper Indus						
708	Tibetan Plateau Endorheic Drainages						
709	Namuda-Tapi						
710	Ganges Delta and Plain						
711	Upper Brahmaputra						
712	Middle Brahmaputra						
713	Northern Deccan Plateau						
714	Southern Deccan Plateau						
715	Western Ghats						
716	Southeastern Ghats						
717	Sri Lanka Dry Zone						
718	Sri Lanka Wet Zone						
719	Chin Hills-Arakan Coast						
720	Sitang-Irawaddy						
721	Upper Salween						
722	Lower and Middle Salween						

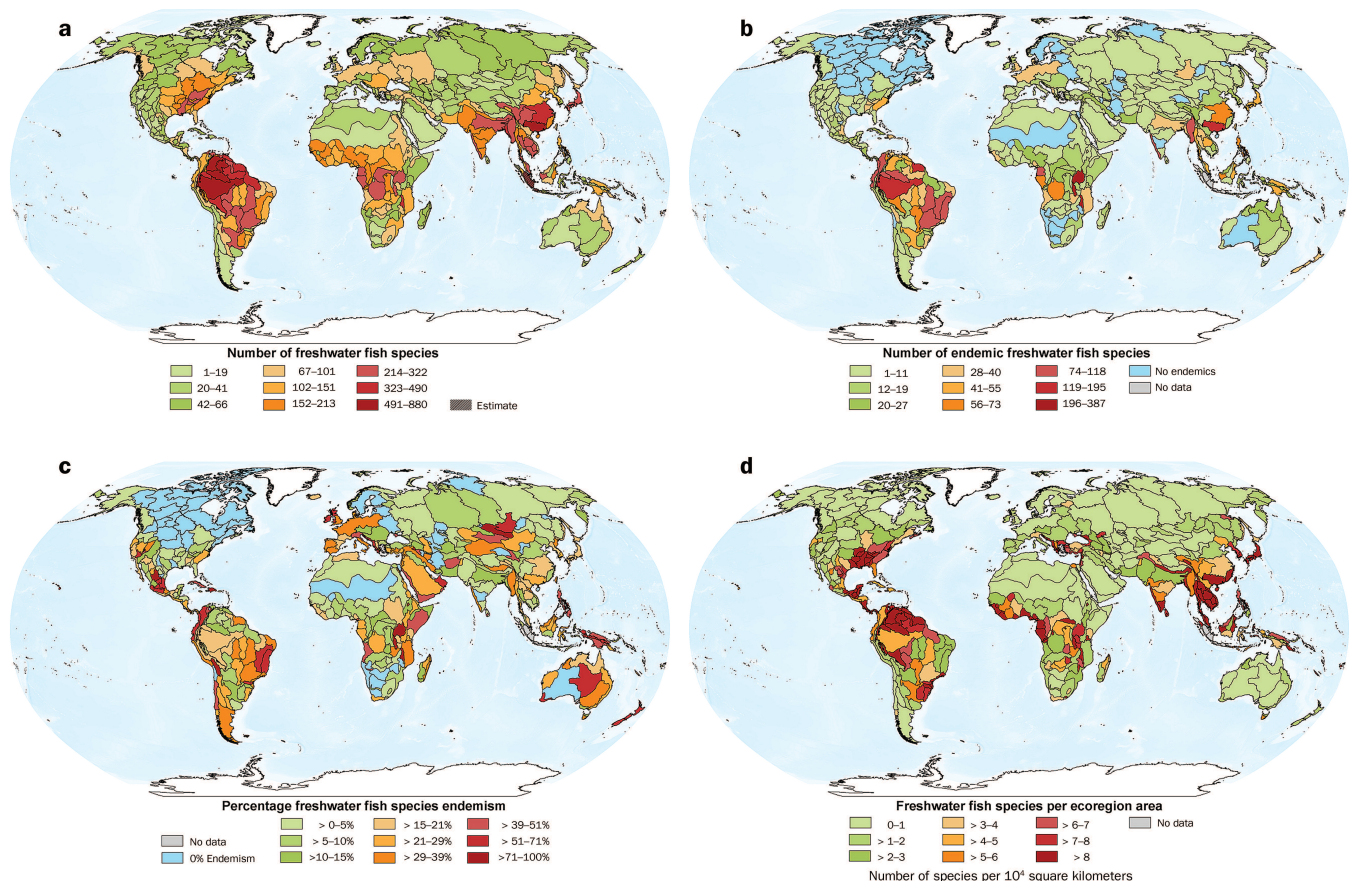


Figure 2. Preliminary freshwater fish species data for ecoregions: (a) species richness, (b) number of endemic species, (c) percentage endemism, and (d) species per ecoregion area. Numbers may be adjusted on the basis of an ongoing process to correct nomenclatural errors. Natural breaks (Jenks optimization) was the classification method used for figures (a)–(c). This method identifies breakpoints between classes using a statistical formula that identifies groupings and patterns inherent in the data.

highland lakes in Cameroon along with Africa's Lake Tana; northwestern and eastern Madagascar; freshwaters from Turkey's central Anatolia region, the northern British Isles, the Philippines, Sri Lanka, India's western Ghats, the southwestern Balkans, and northwest Mediterranean; southwestern Australia and nearly the entire island of New Guinea; Eurasian lakes, including Baikal, Inle, and Sulawesi's Lake Poso and Malili system; Death Valley in the United States and Mexico's Pánuco system; and South America's Iguazu River, Lake Titicaca, and the freshwaters of both the Mata Atlántica and the continent's northwestern Pacific coast. Additionally, newly available data show that some systems previously recognized for high endemism, such as those of South America's Guianas, also exhibit exceptional richness.

Because our ecoregions cover all nonmarine waters, and because they often exist as subdivisions of major river basins, our results also highlight a number of smaller systems for the first time in global analyses. Using finer-resolution data allowed us to identify the high richness of the Congo's Malebo Pool and Kasai basin. Cuba and Hispaniola stand out for endemism, along with the Amazon's western piedmont and

the Tocantins-Araguaia systems. The Tocantins-Araguaia, as well as the highly endemic São Francisco, were defined as units of analysis in Revenga and colleagues (1998), but fish data were unavailable for those basins when that study was done. Systems never before analyzed globally but recognized in our results as exceptionally rich for fish include those of the Malay Peninsula's eastern slope and Japan. A large number of ecoregions are identified for the first time for highly endemic faunas, measured as percentage endemism. Newly identified ecoregions with at least 50% endemism include Africa's Cuanza, Australia's Lake Eyre Basin, Mexico's Mayrán-Viesca, and New Zealand, as well as a large number of highly depauperate ecoregions such as Africa's karstveld sink holes, Turkey's Lake Van, the Oman Mountains, western Mongolia, and Hawaii.

Each of the biodiversity analyses that we offer here emphasizes different sets of ecoregions, suggesting that a single measure of species diversity might overlook ecoregions of important biodiversity value. In a comparative analysis of biodiversity value, ecoregions are probably best evaluated against others within the same region, with similar historical

and environmental characteristics, and of similar size to account for the typically positive relationship between river discharge and fish species richness (Oberdorff et al. 1995). Nonetheless, some systems, such as the Amazon and many of Africa's Rift Valley lakes, stand out by nearly any measure of fish biodiversity and are indisputable global conservation priorities.

Conservation applications

The ecoregion map and associated species data summarized here have a number of conservation applications. At global and regional scales the ecoregion map can be used to distinguish distinct units of freshwater biodiversity to be represented in conservation efforts. The Convention on Wetlands, for instance, requires that sites nominated as wetlands of international importance—with wetlands defined to include all freshwaters—be evaluated against a “biogeographic regionalization” criterion (Ramsar Bureau 2006). Lack of a global biogeographic scheme has stalled the application of this criterion, but our global map and database may provide a necessary framework for identifying broadscale gaps in protection. Similarly, progress toward the establishment of representative networks of freshwater protected areas, as called for by the third IUCN World Conservation Congress, the fifth World Parks Congress, and the seventh Meeting of the Conference of the Parties to the Convention on Biological Diversity, can now be measured using ecoregions as a proxy for finer-scale global species or habitat distribution data. At a regional level, the freshwater ecoregion map may be used as supplementary information for implementation of the European Union's Water Framework Directive (2000/60/EC), which requires a characterization of surface water bodies and currently uses regions defined by Illies (1978).

A primary use of ecoregions is as conservation planning units (Higgins 2003). Our attribution of freshwater fish species data to ecoregions is an important first step for data-poor regions. Organizations or agencies with regional mandates may choose to compare biodiversity values across ecoregions in the process of setting continental priorities (Abell et al. 2000, Thieme et al. 2005). At the basin scale, ecoregions can help to introduce biodiversity information into water-resource or integrated-basin management activities (Gilman et al. 2004). Where major basins are divided among multiple freshwater ecoregions, whole-basin exercises can use ecoregions as stratification units to ensure adequate representation of distinct biotas. Where unconnected drainages are combined into a single freshwater ecoregion, planners may choose to consider a counterintuitive planning unit to incorporate biogeographic patterns. Freshwater ecoregions defined in previous exercises have already been put to use by the Nature Conservancy and WWF in numerous conservation planning efforts across North America (e.g., Upper Mississippi; Weitzell et al. 2003), South America (e.g., the Pantanal; de Jesus 2003), and Africa (e.g., the Congo basin; Kamdem-Toham et al. 2003).

Caveats and limitations

Ecoregions are delineated based on the best available information, but data describing freshwater species and ecological processes are characterized by marked gaps and variation in quality and consistency. Data quality is generally considered high for North America, Australia, New Zealand, Japan, western Europe, and Russia; moderate for Central America, the southern cone of South America, southern and western Africa, Oceania, and the Middle East; and poor for much of southeastern Asia, central and eastern Africa, and South America north of the Paraná River basin.

Freshwater ecoregions are not homogeneous units. Within individual ecoregions there will be turnover of species along longitudinal gradients of river systems and across different habitats such as flowing and standing-water systems. The inclusion of multiple macrohabitat types within a given freshwater ecoregion is a marked departure from terrestrial ecoregions, which typically encompass a single vegetation-defined biome (e.g., deciduous forests, evergreen forests, or scrub; Wikramanayake et al. 2002).

Ecoregions are imperfect units for highlighting certain highly distinct and highly localized assemblages occurring at subecoregion scales. Examples include many peat swamps or subterranean systems. Underground systems such as caves and karsts may require their own planning framework, as groundwater catchments may not correspond with the surface-water catchments upon which our ecoregions are built.

For reasons of practicality and scale, our ecoregion framework does not take into account the distributions of freshwater species such as invertebrates, reptiles, and amphibians. This is a limitation of the ecoregional approach presented here, which is especially problematic for places such as isolated islands where freshwater fish provide little information to inform biogeographic delineation. We hope this taxonomic omission will serve as motivation for generating and synthesizing global data for other taxonomic groups to provide complementary information for conservation planners, particularly when working at subecoregional scales. We recognize that improved information in the future may warrant map revisions, and we highlight areas of greatest data uncertainty in part to encourage enhanced research investment in those places. We believe that the critical state of freshwater systems and species argues against waiting for ideal biodiversity data to be developed before generating urgently needed conservation tools like the ecoregion map.

Shifting transition zones for species are common, and we recommend that ecoregions be viewed as logical units for more detailed analyses and strategies. Ecoregions are intended to depict the estimated original extent of natural communities before major alterations caused by recent human activities, but original distributions can be difficult to reconstruct. As new species are described, our understanding of distribution patterns may also change. Ecoregional delineation is an iterative process, and changes to ecoregion boundaries should be incorporated as new information becomes available.

There is no definitive, error-free data source for classifying fish species as freshwater, brackish, or marine. We chose to use the global FishBase habitat assignments, which are derived from the literature, to ensure that any given species in our database would be classified consistently wherever it occurred. We recognize that errors of omission or commission may derive from inaccuracies in the FishBase assignments as well as from the habitat plasticity of some species. All species information provided to us by experts, regardless of habitat assignment, is retained in our database for future analyses.

The preliminary richness and endemism numbers presented here are in some cases markedly different from existing estimates in the literature. For example, our tally for Lake Malawi contains 431 described fish species, but other estimates run as high as 800 or more (Thieme et al. 2005). Our omission of undescribed species, as well as the conservative approach taken by experts in using only robust species occurrence data, account for many of these lower-than-expected numbers. Numbers of endemics may in some cases be higher than expected because endemics were identified strictly through a database query for unique occurrences, and many species lists are undoubtedly incomplete or use synonyms. We anticipate that many tallies will change with further refinement of species lists but that the broad patterns presented here will hold.

Conclusions

The newly available species data attributed to ecoregions has important implications for prioritizing conservation investments. As one illustration, in 2005 the Global Environment Facility (GEF), which spends more than \$1 billion each year on environmental projects, adopted a new resource allocation framework. Terrestrial ecoregion maps and biodiversity data were notable inputs to the framework, but parallel freshwater information to help guide investments was lacking. The GEF framework fortunately leaves open the possibility of incorporating freshwater ecoregions and biodiversity data at a later date (GEF 2005).

In addition to providing data for scientific and conservation purposes, we aim to give the largest possible number of people access to the ecoregion-level information collected in association with the global map. The information will be freely available on the Internet (www.feow.org) as well as in brochures, posters, and other publications. The freshwater ecoregion map covers virtually all land surfaces on Earth, so people around the globe will have the opportunity to learn about the freshwater systems where they live.

For most policymakers, water resource managers, and even conservationists, freshwater biodiversity is more of an afterthought than a central consideration of their work. The freshwater ecosystem services that support the lives and livelihoods of countless people worldwide are a far larger concern. Yet freshwater biodiversity and ecosystem services are linked through ecological integrity, and better-informed efforts to conserve freshwater biodiversity should benefit human communities as well. The freshwater ecoregions of the world map

and associated species data begin to improve access to previously dispersed and difficult to access freshwater biodiversity information. We hope that this set of products catalyzes additional work toward a better understanding of freshwater species distributions and—of equal if not more importance—leads to a ramping up of freshwater conservation activity and success.

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