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 dominant 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 reconform 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 (km^2) 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 stepwise 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, astroblepid 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 Neoplecostomatinae, 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 km^2), 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 km^2, is Cocos Island (Costa Rica); the average ecoregion size is 311,605 km^2. 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.

North America
101 Alaskan Coastal
102 Upper Yukon
103 Alaska and Canada Pacific Coastal
104 Upper Mackenzie
105 Lower Mackenzie
106 Central Arctic Coastal
107 Upper Saskatchewan
108 Middle Saskatchewan
109 English–Winnipeg Lakes
110 Southern Hudson Bay
111 Western Hudson Bay
112 Canadian Arctic Archipelago
113 Eastern Hudson Bay–Ungava
114 Gulf of St. Lawrence Coastal Drainages
115 Canadian Atlantic Islands
116 Laurentian Great Lakes
117 St. Lawrence
118 Northeast US and Southeast Canada Atlantic Drainages
119 Scotia–Fundy
120 Columbia Glaciated
121 Columbia Unglaciated
122 Upper Snake
123 Oregon and Northern California Coastal
124 Oregon Lakes
125 Sacramento–San Joaquin
126 Lahontan
127 Bonneville
128 Death Valley
129 Vegas–Virgin
130 Colorado
131 Gila
132 Upper Rio Grande–Bravo
133 Pecos
134 Rio Conchos
135 Lower Rio Grande–Bravo
136 Cuatro Cienegas
137 Rio Salado
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 Ouachita 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 California
160 Sonora
161 Guzman–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 Coatzacoalcos
173 Grijalva–Usumacinta
174 Upper Usumacinta
175 Yucatan
176 Bermuda

Central America
201 Chiapas–Fonseca
202 Quintana Roo–Motagua
203 Mosquitia
204 Estero Real–Tempisque
205 San Juan (Nicaragua and Costa Rica)
206 Chiriqui
207 Isthmus Caribbean
208 Santa Maria
209 Chagres
210 Rio Tuira
211 Cuba–Cayman Islands
212 Bahama Archipelago
213 Jamaica
214 Hispaniola
215 Puerto Rico–Virgin Islands
216 Windward and Leeward Islands
217 Cocos Island (Costa Rica)

South America
301 North Andean Pacific Slopes–Rio Atrato
302 Magdalena–Sinu
303 Maracaibo
304 South America Caribbean Drainages–Trinidad
305 Orinoco High Andes
306 Orinoco Piedmont
307 Orinoco Llanos
308 Orinoco Guiana Shield
309 Orinoco Delta and Coastal Drainages
310 Essequibo
311 Guianas
312 Amazonas High Andes
313 Western Amazon Piedmont
314 Rio Negro
315 Amazonas Guiana Shield
316 Amazonas Lowlands
317 Ucayali–Urubamba Piedmont
318 Mamore–Madre de Dios Piedmont
319 Guapore–Itenez

320 Tapajos–Juruena
321 Madeira Brazilian Shield
322 Xingu
323 Amazonas Estuary and Coastal Drainages
324 Tocantins–Araguaia
325 Parnaiba
326 Northeastern Caatinga and Coastal Drainages
327 S. Francisco
328 Northeastern Mata Atlantica
329 Paraiba do Sul
330 Ribeira de Iguape
331 Southeastern Mata Atlantica
332 Lower Uruguay
333 Upper Uruguay
334 Laguna dos Patos
335 Tramandai–Mampituba
336 Central Andean Pacific Slopes
337 Titicaca
338 Atacama
339 Mar Chiquita–Salinas Grandes
340 Cuyan–Desaguadero
341 South Andean Pacific Slopes
342 Chaco
343 Paraguay
344 Upper Parana
345 Lower Parana
346 Iguassu
347 Bonaerensean Drainages
348 Patagonia
349 Valdivian Lakes
350 Galapagos Islands
351 Juan Fernandez Island
352 Fluminense

Europe and Middle East
401 Iceland–Jan Mayen
402 Northern British Isles
403 Cantabric Coast–Languedoc
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 Vardar
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 Sinai
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
447 Namak
448 Kavir and Lut Deserts
449 Esfahan
450 Turan Plain
451 Northern Hormuz Drainages
452 Caspian Marine
453 Volga Delta–Northern Caspian Drainages

Africa and Madagascar
501 Atlantic Northwest Africa
502 Mediterranean Northwest Africa
503 Sahara
504 Dry Sahel
505 Lower Niger–Benue
506 Niger Delta
507 Upper Niger
508 Inner Niger Delta
509 Senegal–Gambia
510 Fouta–Djalon
511 Northern Upper Guinea
512 Southern Upper Guinea
513 Mount Nimba
514 Eburneo
515 Ashanti
516 Volta
517 Bight Drainages
518 Northern Gulf of Guinea Drainages–Bioko
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 Shebelle–Juba
532 Ogooue–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 Lualaba
546 Kasai
547 Mai Ndombe
548 Malebo Pool
549 Lower Congo Rapids
550 Lower Congo
551 Cuanza
552 Namib
553 Etosha
554 Karstveld Sink Holes
555 Zambezian Headwaters
556 Upper Zambezi Floodplains
557 Kafue
558 Middle Zambezi–Luangwa
559 Lake Malawi
560 Zambezian Highveld
561 Lower Zambezi
562 Mulanje
563 Eastern Zimbabwe Highlands
564 Coastal East Africa
565 Lake Rukwa
566 Southern Eastern Rift
567 Tana, Athi, and Coastal Drainages
568 Pangani
569 Okavango
570 Kalahari
571 Southern Kalahari
572 Western Orange
573 Karoo
574 Drakensberg–Maloti Highlands
575 Southern Temperate Highveld
576 Zambezian Lowveld
577 Amatolo–Winterberg Highlands
578 Cape Fold
579 Western Madagascar
580 Northwestern Madagascar
581 Madagascar Eastern Highlands
582 Southern Madagascar
583 Madagascar Eastern Lowlands
584 Comoros–Mayotte
585 Seychelles
586 Mascarenes
587 S. Tome and Principe–Annobon

Northern Asia
601 Irgyz–Turgai
602 Ob
603 Upper Irtysh
604 Chuya
605 Yenisei
606 Lake Baikal
607 Taimyr
608 Lena
609 Kolyma
610 Anadyr
611 East Chukotka
612 Koryakia
613 Kamchatka and Northern Kurils
614 Okhotsk Coast
615 Coastal Amur
616 Lower Amur
617 Middle Amur
618 Argun
619 Shilka (Amur)
620 Songhua 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 Qaidan
633 Upper Huang He
634 Upper Huang He Corridor
635 Huang He Great Bend
636 Lower Huang He
637 Liao He
638 Eastern Yellow Sea Drainages
639 Southeastern Korean Peninsula
640 Hamgyong–Sanmaek
641 Sakhalin, Hokkaido, and Sikhote–Alin Coast
642 Honshu–Shikoku–Kyushu
643 Biwa Ko

Southern Asia
701 Baluchistan
702 Helmand–Sistan
703 Lower and Middle Indus
704 Yaghistan
705 Indus Himalayan Foothills
706 Upper Indus
707 Tibetan Plateau Endorheic Drainages
708 Namuda–Tapi
709 Ganges Delta and Plain
710 Ganges Himalayan Foothills
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
723 Inle Lake
724 Upper Lancang (Mekong)
725 Er Hai
726 Lower Lancang (Mekong)
727 Khorat Plateau (Mekong)
728 Kratie–Stung Treng (Mekong)
729 Mekong Delta
730 Southern Annam
731 Eastern Gulf of Thailand Drainages
732 Chao Phraya
733 Mae Khlong
734 Malay Peninsula Eastern Slope
735 Northern Central Sumatra–Western Malaysia
736 Aceh
737 Indian Ocean Slope of Sumatra and Java
738 Southern Central Sumatra
739 Southern Sumatra–Western Java
740 Central and Eastern Java
741 Kapuas
742 Northwestern Borneo
743 Borneo Highlands
744 Northeastern Borneo
745 Eastern Borneo
746 Southeastern Borneo
747 Malukku
748 Lesser Sunda Islands
749 Sulawesi
750 Malili Lakes
751 Lake Poso
752 Mindanao
753 Lake Lanao
755 Northern Philippine Islands
756 Palawan–Busuanga–Mindoro
757 Western Taiwan
758 Eastern Taiwan
759 Hainan
760 Northern Annam
761 Song Hong
762 Yunnan Lakes
763 Xi Yiang
764 Upper Yangtze
765 Middle Yangtze
766 Lower Yangtze
767 Coastal Fujian–Zeijang
768 Andaman Islands
769 Nicobar Islands

Australia and Pacific
801 Southwestern Australia
802 Pilbara
803 Kimberley
804 Paleo
805 Arafura–Carpentaria
806 Lake Eyre Basin
807 Eastern Coastal Australia
808 Murray–Darling
809 Bass Strait Drainages
810 Southern Tasmania
811 New Zealand
812 Vogelkop–Bomberai
813 New Guinea North Coast
814 New Guinea Central Mountains
815 Southwest New Guinea–Trans-Fly Lowland
816 Papuan Peninsula
817 Bismarck Archipelago
818 Solomon Islands
819 Vanuatu
820 New Caledonia
821 Fiji
822 Wallis–Futuna
823 Samoas
824 Society Islands
825 Tubuai Islands
826 Marquesas Islands
827 Rapa
828 Hawaiian Islands
829 East Caroline Islands
830 West Caroline Islands

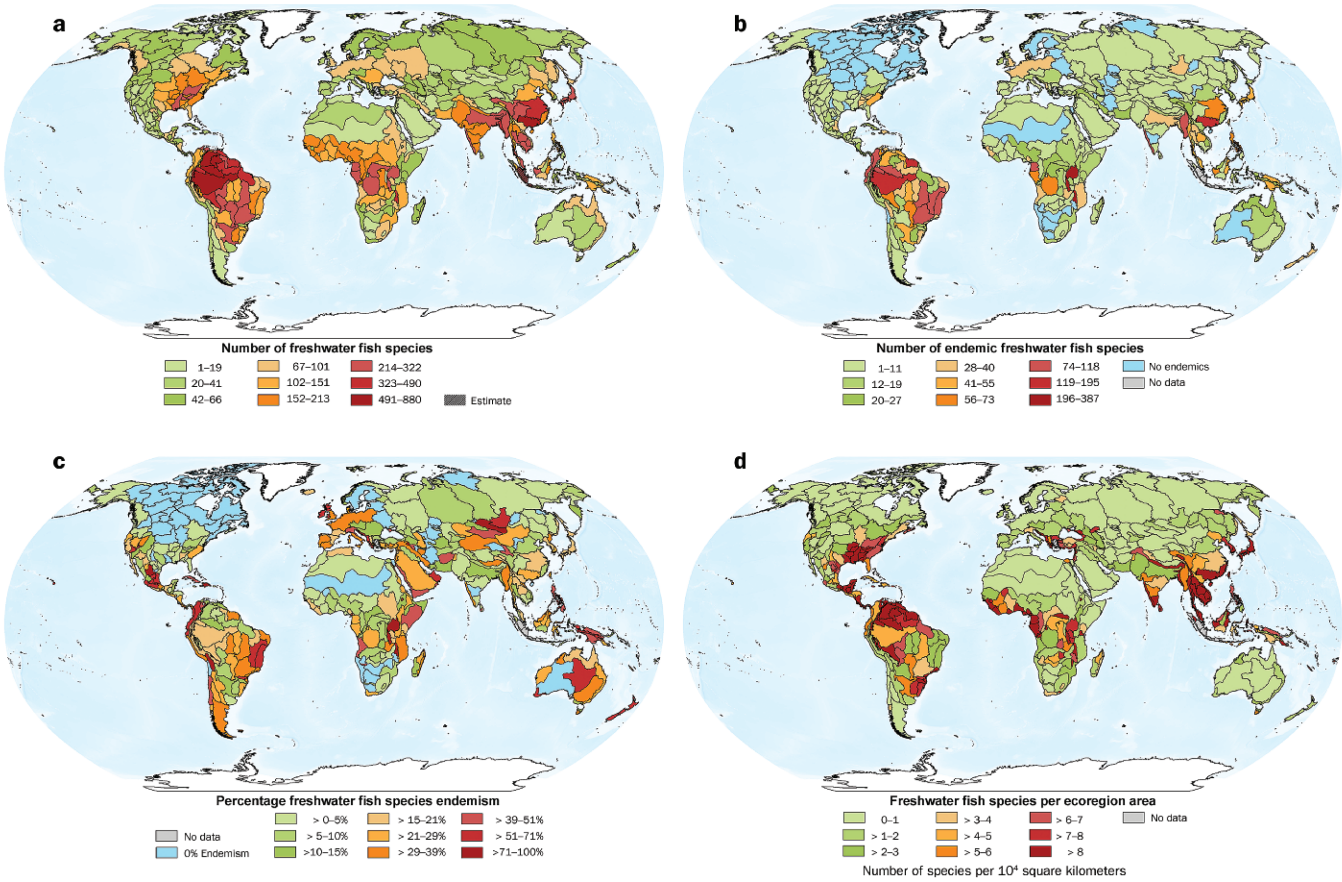

Figure 2. Preliminary freshwater fish species data for ecoregions: (a) species richness, (b) number of endemic species, (c) percentage endemism, and (d) species per ecoregion area. Numbers may be adjusted on the basis of an ongoing process to correct nomenclatural errors. Natural breaks (Jenk's optimization) was the classification method used for panels (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 Iguaçu 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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