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"Diversity of Species in Freshwater Systems"

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ONE
A WEALTH OF LIFE

A WEALTH OF LIFE

SPECIES DIVERSITY IN FRESHWATER SYSTEMS

Estelle Balian, Ian J. Harrison, Helen Barber-James, Stuart H. M. Butchart, Patricia Chambers, Jay Cordeiro, Neil Cumberlidge, Ferdy de Moor, Claude Gascon, Vincent Kalkman, Peter Paul van Dijk, Darren Yeo

Fresh water provides a thread of life and resources across the planet. It has been described as the spark of life that has allowed evolution and speciation to flourish over millennia through geographically isolated and protected freshwater ecosystems (McAllister et al., 1997). An understanding of the diversity and distribution of species in freshwater ecosystems can tell us much about how Earth has evolved, and how freshwater ecosystems support humans and all other life found not only within those waters, but also in adjacent terrestrial ecosystems. These freshwater and terrestrial ecosystems extend from the sources of rivers in the peaks of mountain ranges to the estuaries and wetlands along the continental coasts. Indeed, distributions of freshwater species have been used to interpret the historical patterns of plate tectonics and other geological processes on Earth. For example, the distribution patterns of a range of aquatic insects can be used to show the sequence of events that resulted in the breakup of Gondwana between 127 and 165 million years ago, and consequent isolation of today's southern continents (South America, Africa, Antarctica, Australia), along with more recent dispersal within the last 65.5 million years (Dingle et al., 1983; Briggs, 2003; Yoder and Nowak, 2006).

Previous Spread: Katydid drinking water in a river, Altas Cumbres, Tamaulipas, northeast Mexico. At least 126,000 species depend on fresh water for at least part of their life cycle. —Claudio Contreras-Koob

However, there is a more urgent concern to develop baseline information about the current patterns of diversity and distribution offreshwater species. This information forms the basis on which to assess how freshwater ecosystems are being directly changed over time by human activities; for example, by habitat modification, impacts of pesticides on species physiology and community structure, introduction of alien species, or overfishing, as well as the impacts of climate change (Revenga et al., 2005; Dudgeon et al., 2006; Heino et al., 2009; Hayes et al., 2010). Many freshwater species are sensitive to water quality or flow, and therefore good bioindicators of the environmental condition of aquatic systems and neighboring terrestrial ecosystems. Freshwater fishes, mollusks, crabs, and several groups of insects (e.g., dipterans, ephemeropterans, plecopterans, trichopterans, and odonates; see table 1.1 for English names) are well suited for use in evaluating long-term and short-term environmental change in aquatic and riparian ecosystems (Daniels, 2001; Revenga and Kura, 2003; Leclerf et al., 2006; Sterling et al., 2006; Dijkstra, 2007; Kalkman et al., 2008; Strong et al., 2008; Cumberlidge et al., 2009). Freshwater mollusks contribute to nutrient exchange and help maintain good water quality by controlling algal blooms and cleaning substrates for other benthic invertebrates (Dillon, 2000). Aquatic vegetation is important in promoting water clarity (Kosten et al., 2009), providing refuge for fishes and invertebrates (Petr, 2000), and

Opposite page: Entirely aquatic and tolerant of a wide range of salinity, the Florida manatee (*Trichechus manatus latirostris*) makes its home in rivers, estuaries, and shallow coastal waters. The closely related Amazonia manatee (*T. inunguis*) is adapted exclusively to freshwater habitats in the Amazon basin. —Art Wolfe altering water and sediment chemistry (Carpenter and Lodge, 1986). Aquatic vegetation may also be used as an indicator of water quality (Penning et al., 2008). Thus, each species in a freshwater ecosystem contributes to the overall biodiversity and complexity of that ecosystem. It is that complexity that results in what has been termed an "ecosystem service" to that community, and to the humans that depend on it (Reaka-Kudla et al., 1997).

WHAT IS A FRESHWATER SPECIES?

Before one can describe the diversity of species in freshwater systems, it is necessary to have a clear definition of what constitutes a "freshwater species." This is any species that lives at least part of its life cycle in fresh water (Balian et al. [2008a] refer to these as "real aquatic species"), or any species that shows a close and specific dependency on freshwater habitats (Balian et al. [2008b] refer to these as "water dependent" or "paraquatic" species). It is important to note that the ancestors of most "freshwater species" lived in marine environments; possible exceptions include aquatic spiders, mites, many insects, pulmonate gastropods, and perhaps rotifers, cladocerans, and phyllopodus branchiopods. Also, other than Echinodermata (starfish, sea urchins, sea cucumbers, and their relatives), all major phyla have at least some freshwater representatives, but only a select few (e.g., insects, rotifers) have a higher diversity in fresh water than in marine systems. Some aquatic species spend their entire lives in fresh water (e.g., fishes, some crustaceans, some mollusks, most algae), but other species may have only a specific phase of their life cycle completely restricted to fresh water (e.g., parasites that present an aquatic free-living form; many insects, including odonates, mayflies, stoneflies, caddisflies; and amphibians). However, species that are dependent on a water matrix within a terrestrial habitat (termed limno-terrestrial species) are generally not regarded as aquatic species, because they have a more specific dependency on the interface between these media. Microoganisms that live in the moisture between soil particles are an example of such limno-terrestrial species.

There are several definitions of aquatic species that have been specifically applied to plants. For example, Cook (1970) considered vascular aquatic plants to be those "whose photosynthetically active parts are permanently or, at least, for several months each year submerged in water or float on the surface of water." Subsequently, Denny (1985) and Pieterse (1990) defined aquatic plants as those whose vegetative parts actively grow either permanently or periodically (for at least several weeks each year) submerged below, floating on, or growing up through the water surface.

There are many water-dependent species (following Balian et al.'s [2008a] definition; see above) that are not restricted to fresh water at any stage of their life cycle, but are heavily dependent upon it for specific aspects of their ecology. For example, many reptiles and aquatic birds rely on freshwater ecosystems as a source of food (e.g., ospreys and snakes that feed on fishes; diving ducks that feed on aquatic plants). Other species rely on freshwater systems for their habitat. Certain hymenopteran insect species are dependent on mud and water for constructing nests. The hippopotamus, *Hippopotamus amphibious,* uses freshwater systems during the day to stay cool, and as a safe place to give birth to young. Many aquatic species of plants require seasonally flooded habitats to survive. (It is important to note that these various definitions of water-dependent species of plants and animals do not include the need for fresh water for ingestion to support cellular metabolism [i.e., the simple requirement of the water medium itself, rather than the ecosystem that the medium supports] because that would include all life on Earth.)

There are also freshwater species living in temporary water bodies and in transitional systems that link fresh water with terrestrial and marine environments. Some species of large branchiopods, such as fairy shrimp, clam shrimp, and tadpole shrimp (*Artemia monica, Lynceus brachyurus, Streptocephalus sealii*), occur in pools that never dry completely, or in wetland or vernal pools that dry completely and may not become wet again for years or even decades (e.g., *Branchinella, Thamnocephalus, Triops spp.*) (Brendonck et al., 2008). The water in these temporary pools, or in transitional systems linking rivers and wetlands to the sea, may change in salinity and become brackish or even hypersaline (see below and chapter 2). Freshwater species may also be found in these brackish waters, or in fully marine waters. From an evolutionary standpoint, it is in these brackish environments where adaptation toward or away from fresh water perhaps begins. Species that are tolerant of wide ranges in salinity are termed "euryhaline." Examples include many fishes that migrate between marine, brackish, and fresh waters. Many aquatic birds are also found in both marine and inland waters. Euryhaline species can also be classified as being freshwater species only if the majority of the individuals of the species rely on freshwater habitats for at least some stage of their life cycle or aspect of their ecology. Indeed, besides diadromous fishes that regularly migrate between marine and fresh water, species of fishes have been classified as primary or secondary freshwater fishes based on whether they are strictly intolerant of salt water (primary), or are usually confined to fresh water but may be tolerant of salt water for short periods (secondary) (Myers, 1951; Lévêque, 1997). However, species that spend all, or nearly all, of their lives in brackish or marine environments are excluded from the present discussion.

WHAT IS A FRESHWATER ECOSYSTEM?

The preceeding discussion indicates that the definition of a freshwater species directly relates to how we define a freshwater ecosystem. Fresh water, which has less than 0.5 g per liter of dissolved salts, exists in many ecosystems both above and below ground. These freshwater ecosystems are highly diverse: temporary or permanent, large or small, stationary or flowing, intermittent or continuous, hot or cold, surface or subterranean (see chapter 2). As noted above, there are also transitional systems that link fresh water with terrestrial and marine environments. In the latter case, where fresh water mixes with seawater, for example in estuaries and coastal marshes, the water will be higher in salts and hence "brackish" (i.e., between 0.5 g per liter and 35 g per liter of dissolved salts). Although these brackish environments may include freshwater species that are tolerant of brackish conditions for at least part of their life cycle (see above), they are quite distinct from freshwater ecosystems and are not considered further in this chapter.

The majority of Earth's fresh water exists as ice, snow, and permafrost. This frozen water does not provide a habitable aquatic ecosystem for many organisms—although bacteria and other microorganisms may be present in viable states frozen into ice (Zhang et al., 2002), and fairy shrimp (*Branchinecta gaini*), can survive complete freezing of its habitat in Antarctica (Peck, 2005). Therefore, frozen fresh water can also be excluded from our definition of a freshwater ecosystem. Nevertheless, it is important to recognize that these frozen freshwater systems are upstream

The decline of stream-dwelling frogs in Central America is projected to have large-scale and lasting effects on the quality of water flowing downstream and on the function of the stream ecosystems.

Following Spread: Lake Kussharo on the Japanese island of Hokkaido is an important stopover for migrating whooper swans (*Cygnus cygnus*). When the lake is frozen over in winter, the swans exploit areas of open water created by volcanic hot springs. —Tim Laman

sources of meltwater that maintain flowing freshwater ecosystems downstream. Therefore, frozen fresh waters are essential physical components for persistence of freshwater ecosystems (See chapter 2 for further discussion of connectivity of freshwater systems.)

THREATS TO SPECIES

It is widely accepted that the human impacts on fresh waters are severe, causing profound declines in the resident freshwater biota (Harrison and Stiassny, 1999; Stiassny, 1999; Revenga et al., 2005; Dudgeon et al., 2006) (see chapter 3 for further discussion of threats to species). These changes in the diversity of species alter the way freshwater ecosystems function, and may eventually lead to totally different systems (through the loss of species that are major components of the food webs, energy flow, and chemical cycling, or that shape the physical structure of the freshwater ecosystem). Declines in freshwater crab populations in rivers in Kenya due to competition and replacement by introduced invasive crayfishes have resulted in declines in the populations of one of the crabs' predators, clawless otters (Cumberlidge et al., 2009). This is probably because of competition with predators of the crayfishes. It is projected that the decline of stream-dwelling frogs in Central America will have large-scale and lasting effects on the quality of water flowing downstream and on the function of the stream ecosystems. Moreover, the decline in frogs may affect the community structure of neighboring riparian ecosystems and the transfer of energy between the stream and riparian systems (Whiles et al., 2006; Colón-Gaud et al., 2008). Changes in the abundance and diversity of aquatic vegetation can also have profound effects on aquatic ecosystems. This is because aquatic plants serve as water filtration organisms (limiting pollution and sedimentation) and provide habitat for a variety of aquatic fauna. For example, declines in abundance of submersed plants in shallow lakes are associated with turbid water and, in turn, impairments to food-web dynamics and water quality (Scheffer et al. 1993; Kosten et al., 2009).

SPECIES RICHNESS IN FRESHWATER ECOSYSTEMS

Despite the importance of freshwater species to ecology and human well-being, there have been a lack of comprehensive, synthesized data on the total number of freshwater species in the world, their patterns of geographic distribution, and their regional and global evolutionary diversity (i.e., the number of genera, families, orders, etc., that are represented) (Revenga and Kura, 2003). Without these data, it is impossible to quantify the taxonomic scale and breadth of the anthropogenic impacts to freshwater ecosystems. Indeed, this dearth of easily accessible information on freshwater biodiversity has long been a major justification for the lack of appropriate conservation and management for freshwater systems (Stiassny, 2002; Lévêque et al., 2005). Meaningful attempts to provide a global overview of the biodiversity of freshwater systems have only been developed in the last decade (for example, see Revenga and Kura, 2003; Lévêque et al., 2005). The most recent study is the global overview provided by the Freshwater Animal Diversity Assessment (FADA) project (Balian et al., 2008a, b; and see table 1.1).

Although fresh water (e.g., in lakes, rivers, and wetlands) makes up less than 0.008% of the volume of all water on Earth, and covers only 0.8% of the surface area of the planet, freshwater ecosystems harbor exceptional diversity (Dudgeon et al., 2006). That diversity generates nearly 3% of the total net primary production on Earth (Alexander and Fairbridge, 1999). FADA estimates the number of known freshwater animal species to be about 126,000. This is about 7% of the total number of described species on Earth, which is estimated at 1.8 million (Hilton-Taylor et al., 2009). However, other studies have estimated that the percentage of freshwater

Taxonomic Group	Number of freshwater species	Number of freshwater species as percent of total described species for the taxonomic group	Number of freshwater species in taxonomic group as percent of all described freshwater species	Reference
Vascular macrophytes (plants)	2614	1	1.9	Chambers et al. (2008)
Porifera (sponges)	219	1.5	0.2	Manconi and Pronzato (2008)
Cnidaria	40	0.6	0.0	Jankowski et al. (2008)
Turbellaria (free-living flatworms)	1303	20	0.9	Schockaert et al. (2008)
Rotifera (rotifers)	1948	96	1.4	Segers (2008)
Nemertea (nemerteans)	22	1.8	0.0	Sundberg and Gibson (2008)
Nematoda (nematodes)	1808	6.7	1.3	Abebe et al. (2008)
Nematomorpha (hairworms)	326	16	0.2	Poinar (2008)
Bryozoa (bryozoans)	88	1.1	0.1	Massard and Geimer (2008)
Tardigrada (tardigrades)	62	6.8	0.0	Garey et al. (2008)
Annelida: Polychaeta (polychaetes)	168	1.9	0.1	Glasby and Timm (2008)
Annelida: Oligochaeta, Clitellata (oligochaetous clitellates)	1119	22	0.8	Martin et al. (2008)
Annelida: Hirudinea (leeches)	482	71	0.3	Sket and Trontelj (2008)
All Annelids	1769	12	1.3	Balian et al. (2008b)
Mollusca: Bivalvia	1026	6.8	0.7	Bogan (2008)
Mollusca: Gastropoda	3972	9.9	2.8	Strong et al. (2008)
All Mollusks	4998	4.3	3.6	Balian et al. (2008b)
Crustacea: Large branchiopods (Branchiopoda)	500	100	0.4	Brendonck et al (2008)
Crustacea: Cladocera	620	100	0.4	Forro et al. (2008)
Crustacea: Ostracoda	1936	6.5	1.4	Martens et al (2008)
Crustacea: Copepoda	2814	22	2.0	Boxhall and Defaye (2008)
Crustacea: Branchiura (fishlice)	113	100	0.1	Poly (2008)
Crustacea: Mysidae	72	6.8	0.1	Porter et al. (2008)
Crustacea: Spelaeogriphacea & Thermobaenacea	22	NA	NA	Jaume (2008)
Crustacea: Cumacea & Tanaidacea	25	1.1	0.0	Balian et al. (2008b)
Crustacea: Isopoda	994	9.9	0.7	Wilson (2008)
Crustacea: Amphipoda	1870	21	1.3	Vainola et al. (2008)
Crustacea: Syncarida	240	100	0.2	Camacho and Valdecasas (2008)
Crustacea: Decapoda, Anomura, Aeglidae (hermit crabs)	63	100	0.0	Bond-Buckup et al. (2008)
Crustacea: Decapoda, Brachyura (true crabs)	1280	20	0.9	Cumberlidge et al. (2009); De Grave et al., (2009)
Crusatcea: Decapoda, Caridea (shrimps)	655	20	0.5	De Grave et al. (2008, 2009)
Crustacea: Astacidae, Cambaridae, Parastacidae (crayfish)	638	100	0.5	Crandall and Buhay (2008)
All crustaceans	**11842**	**24**	**8.4**	Balian et al. (2008b)

Table 1.1: Numbers of Freshwater Species for Major Taxonomic Groups. Continued on next page

Taxonomic Group	Number of freshwater species	Number of freshwater species as percent of total described species for the taxonomic group	Number of freshwater species in taxonomic group as percent of all described freshwater species	Reference
Acari: Hydrachnidia (water mites)	6000	100	4.3	Di Sabatino et al. (2008)
Acari: Halacaridae (halacarid mites)	56	5.3	0.0	Bartsch (2008)
Acari: Orabatida (orabatids)	90	0.9	0.1	Schatz and Behan-Pelletier (2008)
All Acari (mites)	6146	21	4.4	Balian et al. (2008b)
Insecta: Ephemeroptera (mayflies)	3138	100	2.2	Barber-James et al. (2008)
Insecta: Odonata (dragonflies and damselflies)	5680	100	4.0	Kalkman et al. (2008)
Insecta: Plecoptera (stoneflies)	3497	100	2.5	Fochetti and Tierno de Figueroa (2008)
Insecta: Heteroptera (true bugs)	4656	12	3.3	Polhemus and Polhemus (2008)
Insecta: Trichoptera (caddisflies)	13574	100	9.6	Morse (2010)
Insecta: Megaloptera (dobsonflies, fishflies, alderflies)	328	100	0.2	Cover and Resh (2008)
Insecta: Neuroptera (lacewings, antlions, snakeflies)	118	1.8	0.1	Cover and Resh (2008)
Insecta: Coleoptera (beetles)	12600	3.2	9.0	Jach and Balke (2008)
Insecta: Mecoptera (scorpioflies and hangingflies)	8	1.6	0.0	Ferrington (2008a)
Insecta: Diptera; Chironomidae (midges)	4147	28	2.9	Armitage et al., (1995); Ferrington (2008b)
Insecta: Diptera; Tipulidae (craneflies)	15178	99	11	de Jong et al. (2008)
Insecta: Diptera; Simuliidae (black flies)	2000	100	1.4	Currie and Adler (2008)
Insecta: Diptera; Culicidae (mosquitoes)	3492	100	2.5	Rueda (2008)
Insecta: Diptera; Tabanidae	5000	NA	3.6	Balian et al. (2008b)
Other Diptera	13454	NA	9.6	Wagner et al. (2008)
All Diptera	43271	22	31	Balian et al. (2008b)
Insecta: Lepidoptera (butterflies)	740	0.6	0.5	Mey and Speidel (2008)
Insecta: Hymenoptera	150	0.1	0.1	Bennett (2008)
Insecta: Orthoptera (grasshoppers, locusts, crickets)	188	0.8	0.1	Amedegnato & Devriese (2008)
All Insecta	87948	8.7	63	Balian et al. (2008b)
Pisces (fishes)	12740	44	9.1	Lévêque et al. (2008)
Amphibia (amphibians)	4245	66	3.0	IUCN (2010)
Reptilia: Lacertilia (lizards)	73	1.5	0.1	Bauer and Jackman (2008)
Reptilia: Crocodilia (crocodiles)	23	100	0.0	Martin (2008)
Reptilia: Chelonii (turtles)	268	80	0.2	Turtle Taxonomy Working Group (2009)
Reptilia: Serpentes (snakes)	153	5.1	0.1	Pauwels et al. (2008)
Mammalia (mammals)	145	2.6	0.1	IUCN (2010)
Aves (birds)	1979	20	1.4	BirdLife International (2010)
TOTAL	**140759**			

Table 1.1, continued

Opposite page: Duckweed (*Lemna sp.*), Iroquois National Wildlife Refuge, Niagara Region, New York, USA. —Carr Clifton

species is even larger, perhaps up to 12% of all species (Abramovitz, 1996; and see information compiled in table 1.1). The disproportionate relationship between high species numbers found in the relatively small habitable volume of fresh water on Earth has been termed "the paradox of freshwater biodiversity" (Martens, 2010).

Based on the results of the Freshwater Animal Diversity Assessment of 2008, more than 60% of the documented freshwater species that live in or are closely associated with fresh water are insects (table 1.1), because a large proportion of insects have aquatic larval phases. Almost half of the aquatic insects are dipterans, which play an important role in aquatic environments, particularly as a food source for many other species (Revenga and Kura, 2003). Some of the other important invertebrate groups include crustaceans (8% of documented freshwater species; decapods and copepods being the most species-rich groups), and mites (ca. 4%). Mollusks also represent about 4% of the aquatic species; in healthily functioning river systems, freshwater snails alone number in the millions (in terms of numbers of individuals) and serve as an important food source for other animals. Rotifers, annelid worms, nematode worms, and turbellarian flatworms each represent 1% to 2% of documented freshwater species. About 39% of all vertebrate species are dependent on fresh water, although these are mostly freshwater fishes (which represent 9% of the total number of documented freshwater plant and animal freshwater species). The 2,614 known species of freshwater vascular macrophyte plants represent about 1% of the total number of vascular plant species documented, and 2% of all known freshwater animal and vascular plant species.

Viruses, bacteria, simple eucaryotes (including a vast array of microorganisms that are often called protozoans, protists, and algae; see Tudge, 2000), and fungi are also critical components of freshwater communities, driving important biogeochemical cycles (Dudgeon et al., 2006). Although there was insufficient information to include these groups in the Freshwater Animal Diversity Assessment of 2008, some general estimates of overall species numbers exist. There are an estimated 2,390 species of free-living protozoans in freshwater ecosystems (Finlay and Esteban, 1998), along with 3,047 aquatic species of fungi, more than 500 species of meiosporic ascomycetes, 405 species of miscellaneous mitosporic fungi, and ninety species of aeroaquatic mitosporic fungi (Shearer et al., 2007). However, the total number of freshwater species could be much larger for protozoans and fungi, reaching as many as 10,000 to 20,000 species of protozoans and 1,000 to 10,000 species of fungi (Palmer et al., 1997); the same authors also estimated up to 20,000 freshwater species of algae. AlgaeBase (Guiry and Guiry, 2010) includes about 25,000 species of algae, of which about 11,000 are thought to be freshwater or terrestrial. However, because of the uncertainty of the classification of diatoms, the total number may be much greater. Six thousand species of diatoms are noted in AlgaeBase, but the actual species number may be greater than 100,000 species (M. Guiry, pers. comm.).

The species numbers and percentages given above are, nevertheless, probably underestimates of the total number of freshwater species, because many remain undiscovered or scientifically undescribed. For example, the number of recognized species of amphibians increased by 48% between 1985 and 2006 (Frost et al., 2006). A small proportion of these are cases where species were removed from synonymy with another species. Synonymy occurs when two or more species that were originally described as different are subsequently thought to be the same species (i.e., the differences between the species were considered to be insignificant). Thus, removal from synonymy occurs when the synonymized species are, even later, recognized once again as distinct and different species. Despite these cases of removal from synonymy, most of the newly recognized species of amphibians are genuine new discoveries of species (Köhler et al., 2008). Many more species are awaiting proper scientific description, and there is no doubt that many species remain to be discovered. Similarly, between 1976 and 1994 an average of 309 species of fishes were newly described or resurrected from synonymy each year (Stiassny, 1999). Eschmeyer and Fricke (2010) cited 500 new species of fishes in 2008, and 287 in 2009. Although these numbers are for both marine *and* freshwater fishes, a reasonable proportion of them can be expected to be freshwater fishes.

Global estimates of the species richness of freshwater invertebrates vary widely, and total species numbers are typically underrepresented, for many of the same reasons as noted above for vertebrates. Those reasons are compounded by the facts that the taxonomy of many of the invertebrate groups is less well known than for vertebrates, and that large parts of the world remain unexplored or undersurveyed for freshwater invertebrates. For example, a new species of freshwater leech was recently described based on collections made in 2006, just 50 km north of New York City (Hughes and Siddal, 2007). Nearly 25% of the approximately 500 globally known species of large branchiopods are represented by specimens from fewer than three localities (Belk and Brtek, 1995, 1997). In many cases those species are known only from a single collection point, the "type locality"; this is the collection locality for the "type specimens" on which the description of the species is based.

The total number of recorded Trichoptera (caddisflies) has risen from 11,532 in 2005 to 13,574 (Morse, 2010). This represents a 17.7% increase in species in a five-year period. Similarly, for the Ephemeroptera (mayflies), Brittain and Sartori (2009) indicated the addition of ten new families, ninety genera, and more than 500 species over the past twenty years. One mayfly family alone, the Baetidae, realized an 18% increase in species numbers and a 20.5% increase in the number of genera known globally (data derived from Gattolliat and Nieto, 2009). For Odonata (dragonflies and damselflies), an average of thirty-eight species have been described annually since 1970. In 2008 the number of described species of Odonata was 5,680, but it was estimated that well over a thousand species remain to be discovered and described (Kalkman et al., 2008). The taxonomic underrepresentation is greatest for the least-known invertebrate groups, fungi and microalgae. For example, in 1994 a new species of microorganism, *Limnognathia maerski*, was collected from a cold spring on Disko Island, West Greenland (Kristensen and Funch, 2000). This new species also represents an entirely new genus (*Limnognathia*), family (Limnognathiidae), class (Micrognathozoa), and order (Limnognathida). Some scientists, in fact, view the Micrognathozoa as a new phylum. Genomic analyses have shown that freshwater microbial diversity is likely to be much greater than presumed from nonmolecular analyses (Dudgeon et al., 2006).

> The number of recognized species of amphibians increased by 48% between 1985 and 2006

CRYPTIC SPECIES

There are frequent cases where a single, widespread species has been found to include several "cryptic species" that appear so similar morphologically that they were not previously recognized as distinct. The freshwater turtle fauna of Australia is rich in cryptics and has exceeded that of Brazil in total species number—at least for now, since Brazil also has a number of cryptic turtle species waiting to be described (R. A. Mittermeier, pers. comm.). A careful

Left: Great pond snail (*Lymnaea stagnalis*) in a hardwood forest pond at Gornje Podunavlje Ramsar site, Serbia. This species serves as host to the larvae of a number of cryptic species of flatworm. —Ruben Smit, Wild Wonders of Europe

mix of anatomical, biogeographic, and molecular analyses is often required to distinguish these cryptic species. Bain et al. (2003) used these techniques to identify six additional cryptic species of cascade frog from Southeast Asia that had previously been conflated as a single species.

Numerous examples of cryptic species of the freshwater snail family Hydrobiidae have recently been uncovered in the Great Basin of Australia (Ponder, 1997; Ponder and Walker, 2003) and the American West (Hershler, 1998, 1999). As recently as 1980, the primary North American reference for freshwater snails listed approximately thirty hydrobiid snail species in western North America (Burch and Tottenham, 1980), but subsequent surveys coupled with more modern taxonomic methods now recognize more than 300 species and subspecies (Hershler, 1998, 1999).

The distribution of these closely related, cryptic species is important for defining patterns of biodiversity and for planning conservation actions (Cook et al., 2008). Cryptic sibling species (i.e., those that are most closely related to each other) are particularly important to identify when one is dealing with mosquitoes and blackflies, for instance, which are vectors of parasites such as *Plasmodium* (which causes malaria) and *Onchocerca* (a roundworm that causes river blindness). Not accurately knowing the species can lead to an overly broad-scale control of the pest-vector species which, in some cases, can in turn lead to controling the harmless sibling and favoring the carrier of the disease (e.g., *Anopheles funestus*, studied in Malawi; Spillings et al., 2009). Detection of cryptic species is also critical when assessing the range extension of a species. Estimation of impacts and management actions will differ when the range extension is associated with a native species compared to a nonnative strain (for example, Saltonstall (2002) discussed cryptic invasion of the common reed, *Phragmites autralis*).

MAPPING FRESHWATER SPECIES

When mapping and analyzing patterns of species distributions, it is important to use methods that account for the ecological and environmental characteristics that define the species' ranges. This is necessary for any spatial analyses of overall numbers of species, numbers of endemic species, or species thought to be economically important, or threatened. The methods must also be appropriate for planning habitat conservation and for ecologically effective resource management. The patterns of species distributions across freshwater ecosystems on Earth are defined by historical processes of geology, extinction, and speciation, as well as current processes of species dispersal and, of course, the impacts of humans. These factors, when considered together, allow us to describe species distributions relative to the ecology and geography of Earth—that is, the "biogeography" of the species—rather than just relative to political boundaries, for example.

Freshwater species distributions are often described according to the river and lake basins, or subbasins, from which they have been collected. In practice, the ranges of the species may not always extend throughout an entire subbasin. For example, a waterfall or some other geological barrier may restrict the distribution of the species, but this is impossible to know without fine-scale biophysical and distribution data, which are often lacking. Also, the distributions of some species, such as dragonflies, mayflies, and stoneflies, often correspond less well with basins than with the dividing mountain ranges between the basins. Nevertheless, conservation planning for freshwater ecosystems, and management of these resources, are usually implemented for complete basins or subbasins, rather than partial subbasins (Abell et al., 2008). For these reasons, the method of describing species distributions by subbasins has been adopted by IUCN for the freshwater fishes, mollusks, crabs, dragonflies, and damselflies, and for aquatic plants included in the IUCN Red List of Threatened Species™ (Darwall et

Botswana

A baby Nile crocodile (*Crocodylus niloticus*) hides in an algal veil in the Okavango River Delta in Botswana. —David Doubilet

Dragonfly (*Libellula sp.*) in the Pantanal, Mato Grosso, Brazil. —Thomas Marent

Mato Grosso, Brazil

Ecuador

Marsupial frog tadpole (*Gastrotheca riobambae*) with back legs developed. Once common in the gardens and parks around Quito, Ecuador, their populations have declined. —Pete Oxford

A network of elephant (*Loxodonta africana*) trails crisscrosses the green grasses of Lake Amboseli, at the center of Kenya's Amboseli National Park. The elephants migrate from the dry surrounding plains almost daily in the dry season to drink and graze. —George Steinmetz

Lake Amboseli, Kenya

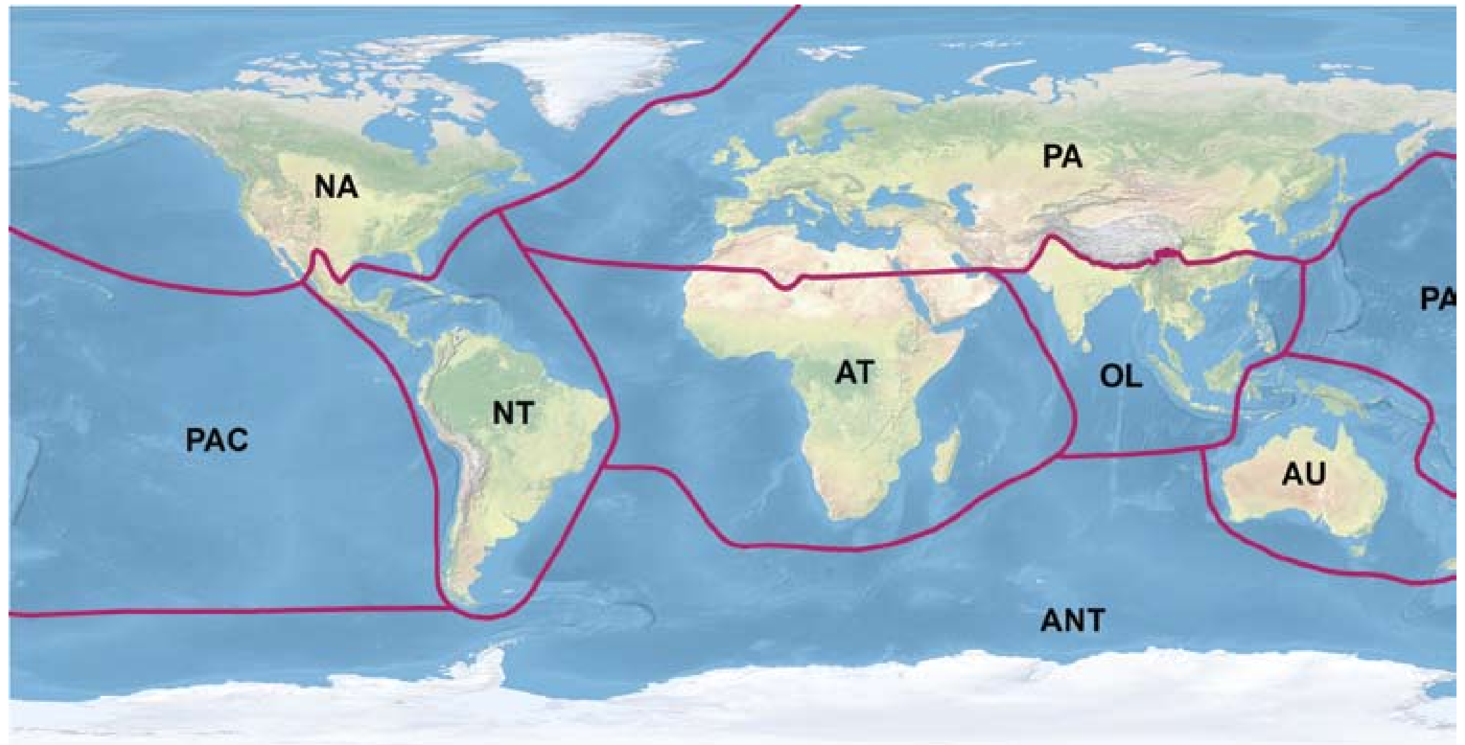


FIGURE 1.1 Zoogeographic regions used in the Freshwater Animal Diversity Assessment. PA: Palearctic Region; NA: Nearctic Region; AT: Afrotropical Region; NT: Neotropical Region; OL: Oriental Region; AU: Australasian Region; ANT:Antarctic Region; PAC: Pacific Region and Oceanic Islands. Based on Balian et al. (2008a). Created with Natural Earth datasets. Free vector and raster map data at naturalearthdata.com.

al., 2005, 2009; Smith and Darwall, 2006; Kottelat and Freyhof, 2007; IUCN, 2010). Similarly, NatureServe (2010) has used subbasins for mapping New World freshwater species.

WWF has proposed a slightly different spatial unit for mapping and analyzing the distribution of freshwater biodiversity, based on "freshwater ecoregions" (Abell et al., 2008). These ecoregions encompass one or more freshwater hydrological systems with a distinct assemblage of natural communities and species. Although the boundaries of freshwater ecoregions often match those of river basins, they are not constrained to them, because the ecoregions also account for various other factors, such as species composition and associated ecological and evolutionary processes. Currently, however, most of WWF's freshwater ecoregions are based only on fish distributions.

For these reasons, the distributions of many species can only be mapped at a much coarser level than basins. The 2008 Freshwater Animal Diversity Assessment mapped species numbers only to the level of eight large, zoogeographic regions (figure 1.1). These are:

The Palaearctic Region (PA)—Europe, Russia, North Africa (not the Sahara), the northern and central Arabian peninsula, and Asia to the southern edge of the Himalayas.

The Nearctic Region (NA)—North America, Greenland, and the high-altitude regions of Mexico.

The Afrotropical Region (AT)—Sub-Saharan Africa (south of the Sahara), the southern Arabian peninsula, and Madagascar.

Taxonomic Group	Region								Total for taxonomic group
	Afrotropical	*Antarctic*	*Australasian*	*Nearctic*	*Neotropical*	*Oriental*	*Pacific*	*Palearctic*	
Macrophytes	614	12	439	644	984	664	108	497	3962
Annelids	186	10	210	350	338	242	10	870	2216
Mollusks	483	0	557	936	759	756	171	1848	5510
Crustaceans	1536	33	1225	1755	1925	1985	133	4499	13091
Arachnids	801	2	708	1069	1330	569	5	1703	6187
Collembolans	6	1	6	49	28	34	3	338	465
Insects	14428	14	7510	9410	8594	13912	577	15190	69635
Vertebrates	3995	1	694	1831	6041	3674	8	2193	18437
Other phyla	1188	113	950	1672	1337	1205	181	3675	10321
Total for Region	23237	186	12299	17716	21336	23041	1196	30813	129824

Table 1.2. Number of Species by Zoogeographic Region, for Major Taxonomical Groups (based on Balian et al., 2008b).

The Neotropical Region (NT)—Southern and coastal parts of Mexico, Central America, the Caribbean Islands, and South America.

The Oriental Region (OL)—India and Southeast Asia south of the Himalayas to Indonesia, as far as Wallace's Line (passing between Borneo and Sulawesi, and through the Lombok Strait between Bali and Lombok [Wallace, 1876]); and including the Philippines, Taiwan, and Japan's Ryukyu Islands.

The Australasian Region (AU)—Australia and New Zealand, New Guinea, and Indonesian islands south and east of Wallace's Line.

The Antarctic Region (ANT)—the Antarctic continent, and the Antarctic and sub-Antarctic islands.

The Pacific Region and Oceanic Islands (PAC)—the islands in the North and South Pacific Ocean.

(See Balian et al. [2008a] for further information).

These data for large zoogeographic regions are of limited value for conservation planning, but are very useful for global analyses of patterns of species' abundance and endemism. De Moor and Ivanov (2008, fig. 4) had suggested a different approach when mapping Trichoptera (caddisflies). They identified an alternative set of regions to that used in the Freshwater Animal Diversity Assessment that more closely describe biogeographic characteristics and relationships of species within the group.

An important point to note is that most studies of freshwater species diversity are focused on species found in surface waters. Although groundwaters, those below Earth's surface, do not have the same extent of species richness as surface waters, their diversity should not be overlooked (Sket, 1999). Those subterranean ecosystems represent important conservation priorities. Further discussion on groundwater ecosystems and the species present is given in chapter 2.

BIOGEOGRAPHY AND SPECIES RICHNESS

Results of the Freshwater Animal Diversity Assessment (Balian et al., 2008b) indicate that the Palearctic Region is the richest in freshwater animal species, followed by the Afrotropical, Oriental, and Neotropical regions

Following Spread: Dalmatian pelican (*Pelecanus crispus*) at Lake Kerkini, Macedonia, Greece.
—Jari Peltomaki,
Wild Wonders of Europe

of the tropics, and then the mostly temperate Nearctic Region (table 1.2). The general trend, of a lower abundance of animal species in the tropical regions than at higher latitudes of the Palearctic, is in contrast to the usual pattern of latitudinal diversity of species (Gaston and Williams, 1996). Although some invertebrate groups are evidently rich in species in the Palearctic (see below), the overall trend of species abundance is probably biased by less extensive field sampling and taxonomic knowledge for freshwater species in the tropics than for the more northerly Neartic and Palearctic regions (Lundberg et al., 2000; Graf and Cummings, 2007; Balian et al., 2008b). Indeed, some well-sampled invertebrate groups, such as dragonflies and damselflies, as well as freshwater crabs, are richer in species numbers in the Neotropical, Australasian, and Oriental regions of the tropics than at higher latitudes.

Aquatic vascular plants are noted for having many species with a widespread distribution. Nevertheless, freshwater plants generally show greatest species richness in the tropical regions, especially the Neotropics. The Oriental, Nearctic, and Afrotropic regions are the next-most species-rich for aquatic plants, and lower numbers have been recorded from the Palearctic Region and from Australasia. Species richness is low in the Pacific Oceanic Islands (for reasons discussed below) and lowest, not surprisingly, in the Antarctic Region.

PALEARCTIC

Insects account for approximately half the total number of freshwater Palearctic species documented in the Freshwater Animal Diversity Assessment. For example, stoneflies (plecopterans), caddisflies (trichopterans), and various dipterans such as midges (chironomids) and craneflies (tipulids) show high levels of species richness in the Palearctic. However, high concentrations or hotspots of endemism in Trichoptera are to be found in high-rainfall montane ecosystems in both temperate and tropical regions worldwide (de Moor and Ivanov, 2008). Crustaceans, which have considerably more species in the Palearctic compared to other parts of the world, account for another 15% of the total number of freshwater Palearctic species. About 34% of the total documented freshwater species of mollusks are reported from the Palearctic (table 1.2), although particular evolutionary lineages of mollusks shower high diversity elsewhere (see "Biogeography and Species Endemism," below). Although vertebrates tend to show greatest species diversity in the tropics, the Palearctic realm supports a disproportionately large number of fresh water–dependent species of birds, reflecting the high diversity of migrant shorebirds that breed in wetland habitats at high latitudes.

AFROTROPICAL

The Afrotropical Region has 22% of the recorded freshwater vertebrate species diversity, making it the second richest region for vertebrate species after the Neotropics (see below). It also follows the Neotropics in being the second-most species-rich area for freshwater fishes. The Congo basin and Lakes Malawi, Tanganyika, and Victoria in the Rift Valley of East Africa are identified as areas of high species richness in freshwater fishes, mollusks, and freshwater crabs (Abell et al., 2008; Cumberlidge et al., 2009). These taxonomic groups, together with frogs, are also rich in species in the Lower Guinea region, roughly encompassing western Central African river basins from Cameroon to the Republic of Congo; (Stiassny et al., 2007; Abell et al., 2008).

The Afrotropical Region has relatively few families of dragonflies and damselflies, but relatively many recent evolutionary radiations within those families. Nevertheless, the region still has a relatively low total number of species of dragonflies and damselflies compared to the fauna of the Oriental and Neotropical regions. This relative species poverty has been attributed to the unstable climatological history of the Afrotropical Region, in which a sustained dry period in the past resulted in a strong contraction of tropical forest cover, which may have resulted in declines in species diversity (Dijkstra and Clausnitzer, 2006).

ORIENTAL

The Oriental Region is rich in several groups of insects, most noticeably dragonflies and damselflies, which have greatest species numbers in Indo-Malaya (Kalkman et al., 2008; Clausnitzer et al., 2009). This region also has the highest species richness for freshwater crabs, with more than 800 species known (Yeo et al., 2008; Cumberlidge et al., 2009). China and Southeast Asia in particular are centers of species richness for freshwater crabs and shrimps (Kottelat and Whitten, 1996; Dudgeon, 2000); there are at least 224 species of freshwater crabs and fifty species of shrimps in the southern half of China (more than any other country in Asia). There are about 219 species of freshwater mussels in the Oriental Region (Graf and Cummings, 2007). Twenty percent of recorded freshwater vertebrate species are found in the Oriental Region, with several river basins being especially rich in vertebrate species. The Mekong River supports an exceptional level of biodiversity. Estimates of the number of fishes in the Mekong River range from 500 to 2,000 species, with about 32% endemism (Kottelat and Whitten, 1996; Rainboth, 1996); only the Amazon and perhaps the Congo rivers have a greater diversity of freshwater fishes. The Lower Mekong has the greatest known species diversity of gastropod mollusks (ca. 140 species, 79% endemic) of any large river in the world (Strong et al., 2008), and the Mekong basin has 300 to 350 species of odonates (dragonflies and damselflies) and more than eighty-nine species of freshwater crabs (Cumberlidge et al., 2009). The annual inland fisheries production of the Mekong may be as much as 25% of the entire freshwater fish catch for the world (Baran et al., 2008). Lake Tonle Sap, on the Mekong, is Southeast Asia's largest and most productive lake (Motomura et al., 2002). Fishes provide an essential source of calcium and protein, and human consumption of fishes in the lower Mekong basin is one of the highest in the world. Tragically, the Mekong River is perhaps one of the most threatened freshwater ecosystems in Southeast Asia (see Kottelat and Whitten, 1996; Dudgeon, 2000; Roberts, 1995, 2001).

The Yangtze, Ganges, Brahmaputra, Chao Phyraya (in Thailand), and Kapuas (in Kalimantan) rivers also have high levels of species richness (Kottelat and Whitten, 1996; Abell et al., 2008). Indeed, globally high richness of freshwater fishes is reported from both the Yangtze and Pearl rivers in China (Abell et al., 2008). The Yangtze has an estimated 360 species and subspecies of freshwater fishes, of which 177 species (i.e., about half) are endemic (Fu et al., 2003). The lowland plains and modest elevations of the mainland Oriental Region (the Ganges plains to South China and to Peninsular Malaysia) are the world's most species-rich area for freshwater turtles (Buhlmann et al., 2009). However, as noted above for the Mekong River, many of these other rivers and associated wetlands of the Oriental Region are also highly impacted through river fragmentation and flow regulation caused by dams, and the attendant habitat loss (see chapter 3).

NEOTROPICAL

The Neotropics are especially diverse in freshwater vertebrates (which are the most comprehensively and consistently analyzed group at a global level); 33% of the total number of species of freshwater vertebrates are found in this region (table 1.2). Amphibians are generally richest in species in the Neotropics: Central America, the Andes, the Amazon basin, and the Atlantic Forest of Brazil (Stuart et al., 2008). There are also about 4,500 species of freshwater fishes in the Neotropics (more than any other region), with Characiformes (characins and their relatives) and Siluriformes (catfishes) being large components of this fauna (Lundberg et al., 2000; Reis et al., 2003; Ortega et al., 2007). The Neotropics are also rich in dragonfly and damselfly species (Kalkman et al., 2008; Clausnitzer et al., 2009), and vascular plants (Chambers

India

A tigress crosses a creek in Bandhavgarh National Park, India. Tigers (*Panthera tigris*) are powerful swimmers; some populations, especially those of Southeast Asia, spend much of their time in rivers or wetlands, feeding on fish and turtles. —Theo Allofs

Eastern long-neck turtle (*Chelodina longicollis*) at Piccaninnie Ponds Conservation Park, South Australia. —David Doubilet

South Australia

et al., 2008). The high diversity of freshwater species is supported by the networks of large rivers, tributaries, and extensive wetlands. For example, the Pantanal, which is the largest wetlands on the planet, covers between 140,000 and perhaps 210,000 km2 of lowland floodplain and incorporates many different habitats (Harris et al., 2005; Mittermeier et al., 2005a). The Amazon basin contains Earth's most diverse riverine fish fauna, with about 2,500 species described and another 1,000 species that may be present but not yet discovered (Junk et al., 2007). Some other large, Neotropical rivers flowing to the Atlantic are also rich in fish species, including the Orinoco (with about 1,000 species) and the Paraguay-Parana-Rio de la Plata system (about 400 species) (Lundberg et al., 2000; Quirós et al., 2007; Rodríguez et al., 2007). Brazilian inland waters are also rich in species of freshwater algae (with 25% of the world's species), Porifera (Demospongiae, 33%), Annelida (12%), Rotifera (25%), Cladocera (Branchiopoda, 20%), freshwater Decapoda (10%), and parasites of aquatic organisms (Agostinho et al., 2005; and see table 1.1 for English names of taxonomic groups).

NEARCTIC

The Nearctic Region is less species-rich than the Neotropical, Afrotropical, and Oriental regions, but has some groups with notably high species numbers. For example, 77% of the world's diversity of crayfishes is from North America (particularly the southeastern United States, contained within the Nearctic Region). Mollusks, especially, show high species richness and endemism (see below for discussion on endemism). North America contains about 302 of the world's 840 to 1,000 known species of freshwater mussels (Unionioda) (Lydeard et al., 2004; Strayer et al., 2004; Graf and Cummings, 2007); this represents as much as 36% of the world's freshwater mussel species richness, compared to 1.3% of the richness in Europe (Graf and Cummings, 2007). The world's greatest diversity of pleurocerid snails occurs in rivers and streams of the southeastern United States (Neves et al., 1997; Brown et al., 2008). Also, high levels of species richness of hydrobiid snails are reported from the American West (see "Cryptic Species," above).

AUSTRALASIAN

The freshwater species richness of Australasia is generally low, considering the size of this region (table 1.2), with less than 4% of the total numbers of freshwater vertebrate species. The land surface area of Australasia is comparable to that of Brazil, with a similar percent coverage of fresh water (about 0.8% of the land area; CIA, 2010), but it has only about 26% of the number of species of fishes compared to Brazil (Froese and Pauly, 2010). This difference is partly because of the extraordinary species richness of the Amazon basin, with its combination of large channel rivers and minor tributaries, and partly because the freshwater fauna of Australasia is incompletely documented (Lundberg et al., 2000). There are, however, some notable exceptions to this documented pattern. For example the diversity of odonates (dragonflies and damselflies) is relatively high in Australasia, and so is freshwater turtle diversity.

PACIFIC ISLANDS

The Pacific Islands have relatively low freshwater species richness for all groups (fewer than 1,200 species in total, according to the Freshwater Animal Diversity Assessment (Balian et al., 2008b; see table 1.2.). This might be an underestimate; for example, the Assessment records only eight species of vertebrates, which is much lower than other published estimates (see Mittermeier et al., 2005b). Nevertheless, the low overall species numbers on the Pacific Islands is not surprising, because of the small surface area of these islands, the restricted size of any freshwater systems, and the isolation of many of the islands from large land masses. However, most of the islands have been colonized by species of dragonflies flying from the Oriental Region, and these species are typically widespread. Several of the islands or island groups are home to endemic dragonfly species. There are several cases in which a large portion of the dragonfly diversity of an island comprises a large radiation of species within a single genus (Polhemus, 1997). If one estimates freshwater species richness relative to freshwater ecoregion area, then New Caledonia, Vanuata, and Fiji in the Pacific become especially noteworthy as regions of high species density within their small areas (Abell et al., 2008).

BIOGEOGRAPHY AND SPECIES ENDEMISM

A species whose distribution is restricted to a particular region is said to be "endemic" to that region. For example, a small species of carp-like fish, *Squalius keadicus*, is known to be endemic to just one river, the Evrotas River, in southeastern Greece (IUCN, 2010). One should note that a species can be "native" to a region without being endemic to it, because it may also be found elsewhere. For example, a species of dragonfly, *Oxygastra curtisii*, is native to southwestern Europe (i.e., it is naturally distributed there), but it is not endemic there because small populations also naturally occur in Morocco (Kalkman et al., 2010). Thus, the proportion of truly endemic species found in a region is an indication of the biological uniqueness (and hence irreplaceability) of the fauna or flora in that region.

Global patterns of species endemism vary for different taxonomic groups. For example, distributions of aquatic insects are quite variable; some species tend to show greater tendency for flight dispersal and may be more widespread (e.g., some dragonflies and damselflies [Odonata]; Dijkstra, 2007), whereas mayflies (Ephemeroptera) have a weak dispersal ability that, along with the antiquity of the order, has resulted in their generally high endemism. Similarly, amphibians and freshwater reptiles show high levels of endemism because of their reduced ability to disperse. Several regions of the southeastern United States are important areas of endemism for salamanders and freshwater turtles (Buhlmann et al., 2009). Many islands host only endemic species of amphibians: Jamaica, São Tomé and Principé, New Zealand, Fiji, Palau, and the archipelago of Seychelles where all caecilians and frogs are endemic.

Madagascar is an example of a much larger island with high endemism. It has long been recognized as one of the world's most important biodiversity hotspots (Myers et al., 2000; Groombridge and Jenkins, 2002), mainly due to the unique species found on the island and to the high level of threat they encounter. Of the natural habitats present on Madagascar before human settlement, about 2,000 years ago, only 10% remain intact. Despite extreme habitat loss, Madagascar has a surprisiningly high rate of new species discovery for many taxa, even for some well-known groups such as amphibians; a recent study suggests that the number of known species of frogs may still be an underestimate, and that between 129 and 221 new species of frogs could be added to the total known species from the island (Vieites et al., 2009). In addition to a high species richness, the level of endemism in Madagascar is tremendous. According to Goodman and Benstead (2003, 2005), endemism for several taxonomic groups is as follows: all species of Ephemeroptera (mayflies) except for one (>100 species); 73% of Odonata (dragonflies and damselflies; 132 of the 181 described species); 100% of Plecoptera (stoneflies; twelve species); 100% of freshwater crabs (fifteen species); 65% of freshwater fishes (ninety-three of 143 species); 99% of frogs (197 of 199 species). Among the other endemic vertebrates are the aquatic tenrec, *Limnogale mergulus*, from a family of insectivorous mammals; the rare turtle, *Erymnochelys madagascariensis;* and a large aquatic lizard, *Scelotes astrolabi*. In addition, at least twenty species of atyid shrimps, five species of palaemonid shrimps, seven species of freshwater crayfish, and fifteen species of potamonautid crabs inhabit the island's rivers and streams. All seven genera of freshwater crabs and the single genus of crayfish found in Madagascar are endemic (Cumberlidge, 2008; Cumberlidge et al., 2009).

Australia

The platypus (*Ornithorhynchus anatinus*) has declined in parts of its historic range because of urban development, agriculture, and other human activities. Yarra River, Victoria, Australia. —David Doubilet

The common kingfisher (*Alcedo atthis*) is an indicator of freshwater ecosystem health across Europe and Asia. The sparrow-sized birds hunt most successfully in habitats with good water clarity. —Laszlo Novak, Wild Wonders of Europe

Europe & Asia

Yucatán Peninsula, Mexico

Ghost crab (*Ocypode quadrata*) sheltering in a cenote, one of numerous karst caves and sinkholes in Sian Ka'an Biosphere Reserve, Yucatán Peninsula, Mexico. —Claudio Contreras-Koob

The freshwater pearl mussel (*Margaritifera margaritifera*), native to Europe and eastern North America, has disappeared from much of its historic range due to habitat loss and over-harvesting for the occasional pearl. Umeälven tributary, Sweden. —Michel Roggo

Sweden

As noted above for Madagascar, often those areas that are rich in species numbers also have a high percentage of endemism. Some lakes may have high levels of endemism because these habitats are more isolated than river networks. For example, fishes, mollusks, and crustaceans show high levels of endemism in lakes. Several ancient lakes are centers of endemism, a phenomenon that reflects their greater age and relative isolation compared to rivers. In the Palearctic Region, Lake Biwa, in Japan, is about four million years old and has endemic plankton and thirty-eight species of gastropod mollusks, of which 50% are endemic (see also Kottelat and Whitten, 1996). Lake Baikal in Russia and Lake Tanganyika in Africa, both older than Lake Biwa and with high levels of endemism, are discussed in more detail in chapter 2. Several of the other African Rift Valley lakes besides Tanganyika are well known for their high levels of species endemism for cichlids and gastropods. There are more than 800 species of cichlids in Lake Malawi, 99% of them endemic (Thieme et al., 2005). Fresh water–dependent birds, amphibians, and some reptiles (turtles and crocodiles are an exception) also tend to show great levels of endemism in the Afrotropical Region (Balian et al., 2008b).

Although fresh waters cover less than 1% of Earth's surface, they provide habitat for more than 10% of the known animals and about one-third of all known vertebrate species.

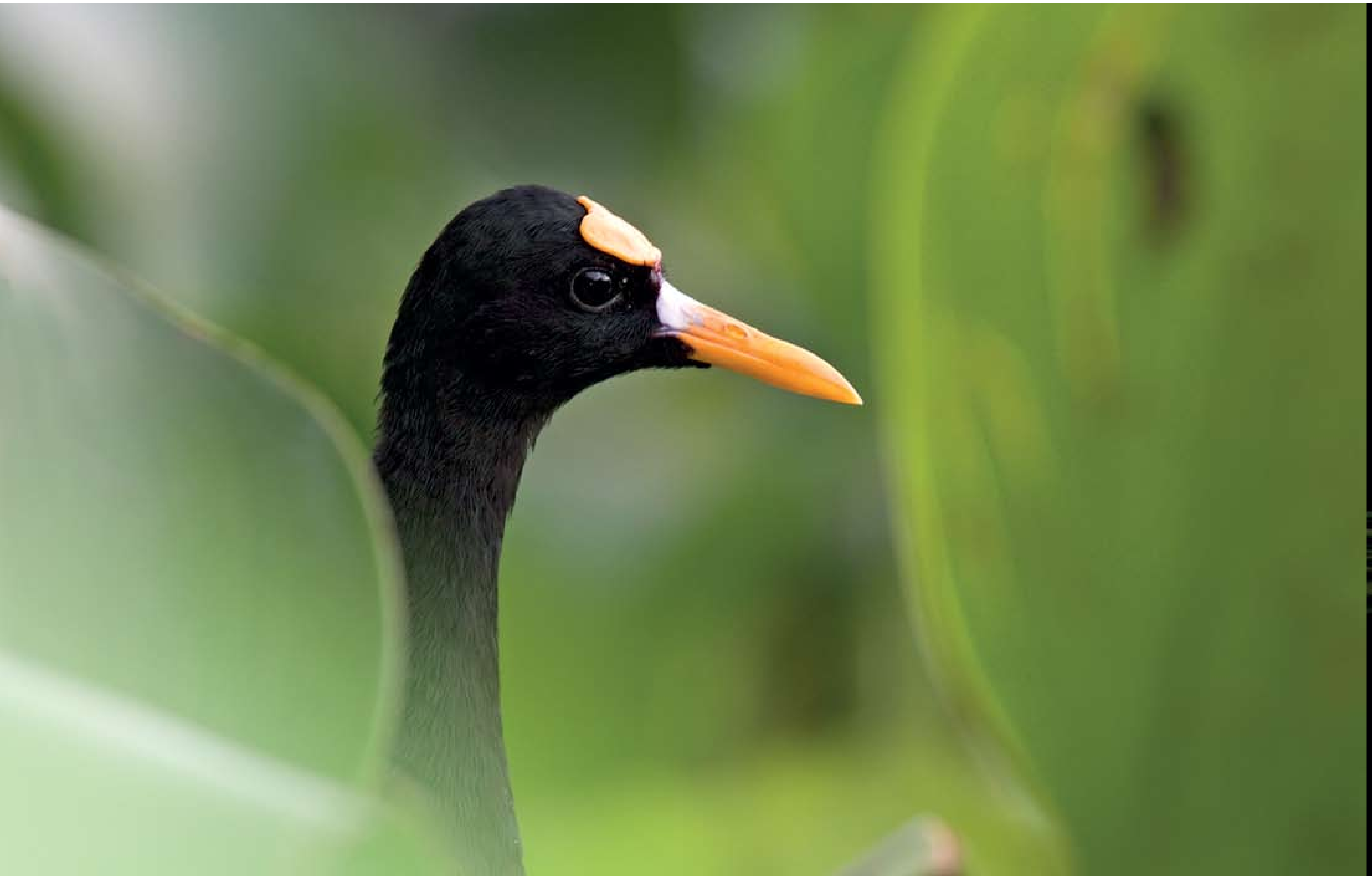
In Lake Titicaca in South America, 63% of the twenty-four gastropod species are endemic. The lake is also an area of endemism for fishes (Abell et al., 2008), where at least one endemic cyprinodontid fish has become extinct due to the introduction of exotic fishes (Harrison and Stiassny, 1999). Freshwater endemism has also been noted for several lakes in the Oriental and Australasian regions. Many lakes of the mountainous Yunnan region of China are of special interest because of their large numbers of endemic fishes and invertebrates (Kottelat and Whitten, 1996; Dai, 1999). In Sulawesi, the Malili lake system includes endemic radiations of crabs, shrimps, mollusks, and fishes, in particular small sailfin silversides (Herder et al., 2006), several of which are listed as threatened in the IUCN Red List (IUCN, 2010). Nearby, in Lake Poso, endemic species of halfbeak and goby fishes are threatened or may already be extinct (Harrison and Stiassny, 1999; IUCN, 2010). Similarly, Lake Lanao in the Philippines was a center of endemism, with a species flock of eighteen cyprinid fishes, fourteen of which may be extinct (due to the introduction of a species of goby). In the case of Lake Lanao, the cyprinid fishes disappeared from the lake even before their taxonomy could be fully investigated (Harrison and Stiassny, 1999).

Endemism is also found in other freshwater ecosystems. The relative importance of wetlands, rivers, and creeks, in terms of endemism, is much greater, proportionately, than would be suggested by their global water volume. Many of the approximately forty-nine genera and 330 species in the aquatic vascular plant family, Pdostemaceae, are found in rapids and waterfalls and are endemic to small geographic areas—even a single river or waterfall (Rutishauser, 1997). Freshwater fishes show high levels of endemism in the geographically isolated headwaters and small tributaries of the Neotropics (Junk et al., 2007; Quirós et al., 2007). The Atlantic Forest and Guianas ecoregions in South America are noted for high species endemism and richness of fishes. Many of the freshwater crabs and shrimps in the Oriental Region are restricted to single streams, or to a small group of streams associated with a single hillside or a small range of hills (Kottelat and Whitten, 1996; Cumberlidge et al., 2009). China has 96% freshwater crab endemism, and Southeast Asia has 69% to 98% freshwater crab endemism. Also in the Oriental Region, high levels of endemism for mollusks are reported from the Lower Mekong River. Similarly, the Congo River basin in Africa has high mollusk endemism (Strong et al., 2008).

The freshwater springs and groundwater of several parts of Australia show high species richness and endemism of hydrobiid snails (Strong et al., 2008; and see "Cryptic Species"). Of the numerous species of mollusks found in North America (see "Biogeography and Species Richness"), many are restricted to only one or a few river basins of the United States; for example, the basins of the Tennessee, Cumberland, and Apalachicola rivers, as well as drainages to Mobile Bay, and in the Ozark highlands (Abell et al., 2008). The basins of the southeastern United States are also a focus of threat and extinction for these species (Bogan, 2008; and see chapter 3).

Several wetlands of Southeast Asia, including the tropical peatland systems of Indonesia and Malaysia, have a large amount of freshwater endemism (Ng, 1994; Kottelat and Whitten, 1996). The small river networks found in Korea and Japan have high proportions of range-restricted species. About 42% of the 211 species or subspecies of freshwater fishes in Japan are endemic (Yuma et al., 1998). Among groups such as dragonflies and aquatic bugs, most species with a small range inhabit rivers or streams, often in tropical forest in mountainous areas. These range-restricted species are less commonly endemic to lakes. Trichopterans (caddisflies), which show some similarities to odonates in species distributions, have high levels of endemism in the Neotropical and Australasian regions, where 73% and 69% of the genera and subgenera are endemic (de Moor and Ivanov, 2008). The Ephemeroptera (mayflies) have their highest generic endemicity (90%) in the Australasian Region, yet this region has the lowest number of mayfly species per biogeographical realm. In contrast, the Palaearctic has the highest number of recorded mayfly species, but the lowest percentage generic endemism (Barber-James et al., 2008). This trend is true whether considering the order as a whole, or one particular family in detail; for example, Gattolliat and Nieto (2009) show the lowest number of Baetidae species in the Australasian Region when compared with other realms, but the highest endemicity. This implies that the lineages in the Australasian are old and stable, with little recent speciation, whereas the Palearctic species have been shaped by more recent extreme climatic conditions such as glaciation, resulting in higher species numbers.

The discussion above cannot do justice to the enormous range of species diversity and endemism in the freshwater ecosystems of the world. But it highlights some general trends and some important considerations for ensuring that we continue to conserve this biodiversity and safeguard the important ecosystem services it provides to humans. Readers who wish to find more comprehensive discussion of any of the taxonomic groups discussed above should consult the references cited, and especially the publications of the Freshwater Animal Diversity Assessment.



Veracruz, Mexico

The northern jacana (*Jacana spinosa*), seen here at Catemaco Lake, Veracruz, Mexico, is a common wading bird. —Claudio Contreras-Koob

Panama

Exploiting a nocturnal niche that is more commonly the domain of diurnal birds, a greater bulldog bat (*Noctilio leporinus*) in Panama swoops low over water and uses echolocation to detect ripples on the surface made by its prey—small fish. —Frans Lanting

Following Spread: Lake Baikal, Russia

A relative of the Arctic ringed seal, the nerpa (*Pusa sibirica*), endemic to Russia's Lake Baikal, is the only pinniped adapted exclusively to a freshwater habitat. —Boyd Norton