

# Exposure of Africa's freshwater biodiversity to a changing climate

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## Keywords

Africa; biodiversity; climate change; freshwater; fish; hydrological change; waterbirds.

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## Received

27 July 2009

## Accepted

24 March 2010

## Editor

Corey Bradshaw

## Abstract

Anthropogenic climate change and increased human water use are widely expected to place great stress on available water resources across Africa and Madagascar, but the effects of these changes on freshwater biodiversity have only begun to be considered. We used a comprehensive species database and a global hydrologic model to examine the exposure of freshwater biodiversity to discharge and runoff alterations across Africa and Madagascar. Our results show that by the 2050s, ecoregions containing over 80% of freshwater fish species and several outstanding ecological and evolutionary phenomena are likely to experience hydrologic conditions substantially different from the present, with alterations in annual discharge or runoff of more than 10%. We recommend early action to buffer these species and systems from the expected changes, including reducing nonclimate stresses and implementing measures that buy species time to adjust to novel ecosystem characteristics.

doi: 10.1111/j.1755-263X.2010.00120.x

## Introduction

The world is finally waking up to the paired consequences of anthropogenic climate change and increased human use on water resources (deWit & Stankiewicz 2006; Kundzewicz *et al.* 2008; Döll 2009), but the effects of these changes on freshwater biodiversity have only begun to be considered (Poff *et al.* 2002; Wrona *et al.* 2006). In developing regions like Africa where freshwater species and systems provide critical ecosystem services, the intersection of climate change and increased water use could have particularly wide-reaching impacts on those segments of the human population with the fewest options for meeting basic needs (FAO & World Fish Center 2009).

The flow regime—defined by the magnitude, frequency, duration, timing, and rate of change of flows—is the master variable in most running water systems, determining many elements of water quality and quantity (Poff *et al.* 1997). Around the world, changes to

flow regimes resulting from shifts in precipitation and evaporation patterns and increased water use have already been documented (Matthews *et al.* 2009). Yet high-confidence, quantitative projections about specific future impacts remain elusive (Kundzewicz *et al.* 2007; Bates *et al.* 2008). Changes of any kind to natural flow regimes will, however, likely affect native aquatic species adapted to those regimes. In this article, we use a comprehensive freshwater fish database and data on waterbird congregations to examine the expected extent of exposure of Africa and Madagascar's freshwater biodiversity to discharge and runoff alterations caused by climate change and by increased human water use.

Climate change has and will continue to affect freshwater ecosystems in a variety of ways (Poff *et al.* 2002; Wrona *et al.* 2006; Heino *et al.* 2009). When flow regimes shift, quantitative and qualitative changes to aquatic habitat result, indirectly influencing ecosystem productivity and biodiversity. Freshwater systems are expected to experience an increase in the frequency and

intensity of extreme events, such as droughts and floods (Kundzewicz *et al.* 2008); freshwater species adapted to different, historic flow regimes might be unable to complete their life histories under these conditions. Climate change-induced air temperature shifts are already altering water temperature and attendant biogeochemical processes, and changes in lake volume and thermal structure are expected (Lake *et al.* 2000; Mohseni *et al.* 2003). Coastal wetlands and the lower reaches of most rivers in many regions have been affected by sea-level rise for over a century (Bates *et al.* 2008).

Stresses from climate change are compounded by other anthropogenic disturbances. Obligate aquatic species have naturally limited dispersal options, which have been further constrained by widespread habitat fragmentation and water abstractions (Ward 1998). Synergies between climate-induced impacts and other environmental changes lead to high uncertainty about the manner in which specific species and ecosystems will respond to new hydrologic regimes (Poff *et al.* 2002). However, we know that such changes have the potential to push some species to extinction. Recent modeling suggests that decreased discharges from climate change and increased water withdrawals will cause fish extinctions in many river basins by 2070 (Xenopoulos *et al.* 2005).

Africa is expected to be hit hard by anthropogenic climate change, with broad declines in mean annual precipitation and runoff for a variety of scenarios (Bates *et al.* 2008). Acknowledging that evaporation projections are unreliable, assessments of potential future precipitation changes have nonetheless identified areas where water available for human use is likely to be diminished (deWit & Stankiewicz 2006). Regional and basin studies have also identified potential impacts on water resources and associated implications for human communities (e.g., Conway 2005; Matondo & Msibi 2006).

Currently, at least five climatic zones exist across the continent: equatorial, tropical, subtropical, Mediterranean, and mountain. The general precipitation pattern is one of highest rainfall near the equator in the Congo Basin and along the Gulf of Guinea, with progressively less at higher latitudes. Due to the high rainfall and low evaporation in the Congo basin, this river and its tributaries, which account for only about 13% of the surface area of the continent, carry about 30% of Africa's surface flow (FAO 1995). Arid, semiarid, and dry subhumid areas cover about 43% of Africa's surface area and include large deserts in the north and south (Björke 2002).

Accompanying this climatic variety is a diversity of freshwater species assemblages. Tropical communities in general are characterized by greater numbers of species in many taxonomic groups and more complex interactions compared to those in the temperate zone, and Africa's

freshwater systems are no exception (Lowe-McConnell 1987). Africa's freshwater fish diversity, at upward of 3,000 described species, rivals that of Asia (>3,500 species) and South America (>5,000 species) (Kottelat & Whitten 1996; Lundberg *et al.* 2000). However, Africa's evolutionary phenomena—its diverse species flocks (groups of two or more sister species that are endemic to a lake or river basin) and relictual “living fossils”—are what make its freshwater fauna particularly distinctive (Brown 1994; Lundberg *et al.* 2000). Africa has more archaic and phylogenetically isolated freshwater fishes than any other continent and outstanding species radiations among a variety of taxa in both rivers and lakes (Lowe-McConnell 1987; Brown 1994). Its archaic fauna is likely due to most of Africa being above sea-level since the Precambrian (Lévêque 1997).

Assessing the vulnerability of Africa's freshwater biodiversity to the combination of climate change and increased human water use is hampered by data gaps. Ideally, observational and projected data would provide high-confidence evidence of shifts in the natural flow regime, but data describing hydrologic regimes are typically unavailable. Instead, we use modeled changes in mean annual runoff and discharge values as an approximation of exposure to change, given that annual-scale shifts are likely to be accompanied by shifts in seasonality (Kundzewicz *et al.* 2007). Specifically, we evaluate the magnitude of change in discharge and runoff that Africa and Madagascar's freshwater systems may experience by the 2050s and determine the numbers of fish species, as well as regions supporting ecological and evolutionary phenomena, that would be exposed to these changes.

## Methods

To examine projected future changes in runoff and discharge, we used WaterGAP (Water—Global Assessment and Prognosis, version 2.1d), an integrated global discharge model that includes both water availability and human water use calculations (Alcamo *et al.* 2003; Döll *et al.* 2003). We chose to employ the “Global Orchestration” and “Order from Strength” scenarios as defined and used in the Millennium Ecosystem Assessment analyses (Alcamo *et al.* 2005a; Alcamo *et al.* 2005b; Sala *et al.* 2005) to highlight the general extent of climate and water use changes on African freshwater systems.

We define “runoff” strictly as spatial land surface and subsurface flow generated locally; “discharge” is then derived as the flow in river channels, representing the accumulated runoff after routing it downstream along a drainage network. We examined both runoff and discharge because runoff often plays a key role in creating

ephemeral or seasonal aquatic habitats, whereas discharge serves as a measure of the magnitude component of the flow regime. We refrained from analyzing other components of the flow regime (frequency, duration, timing, and rate of change of flows) as they are typically of much higher uncertainty when estimated with global-scale models.

Runoff calculations of WaterGAP were analyzed in terms of their projected change between the “present” (long-term means of 1961 to 1990) and the “2050s” (long-term means of 2041 to 2070). Resulting monthly discharge values were routed along a global river network (Döll & Lehner 2002) including lakes and reservoirs and computed for every 0.5 degree grid cell. The values represent the maximum renewable water resources available within each cell after human water use has been taken into consideration.

WaterGAP calculates household, industrial, and agricultural water use. Globally, irrigation agriculture is by far the dominant water use sector (Postel *et al.* 1996), and the applied future irrigation scenario includes both climate-related effects (altered precipitation and evapotranspiration) and non-climate-related effects (altered extent and efficiency of irrigation). The inclusion of human water use in the model means that the projected changes reflect a change from “current” rather than “natural” conditions.

Runoff and discharge values were first calculated for each grid cell in WaterGAP. Cell values were then averaged by freshwater ecoregion, a broad-scale biodiversity conservation planning unit, and percent changes between current and future conditions were derived. Ecoregions were taken from the Freshwater Ecoregions of the World framework (Abell *et al.* 2008), which for Africa contains slightly modified units from an earlier continental assessment (Thieme *et al.* 2005). A freshwater ecoregion is defined as a large area encompassing one or more freshwater systems with a distinct assemblage of natural freshwater communities and species; in most cases these units follow basin boundaries (Abell *et al.* 2008).

Because of a lack of comprehensive data for most freshwater taxonomic groups, we used data on freshwater fish biodiversity and congregations of wetland birds as proxies of freshwater biodiversity more generally. We calculated species-level endemism and richness for each ecoregion after systematically comparing our ecoregion map with the estimated ranges of 3,048 described freshwater fish species (Abell *et al.* 2008). We controlled for area using the classic species-area relationship, but found that the results did not change the spatial pattern of richness or alter our conclusions, such that we present the raw data here (see Supporting Information for details on this analysis and the area-adjusted results). Endemic species were considered to be those occurring in a single ecoregion.

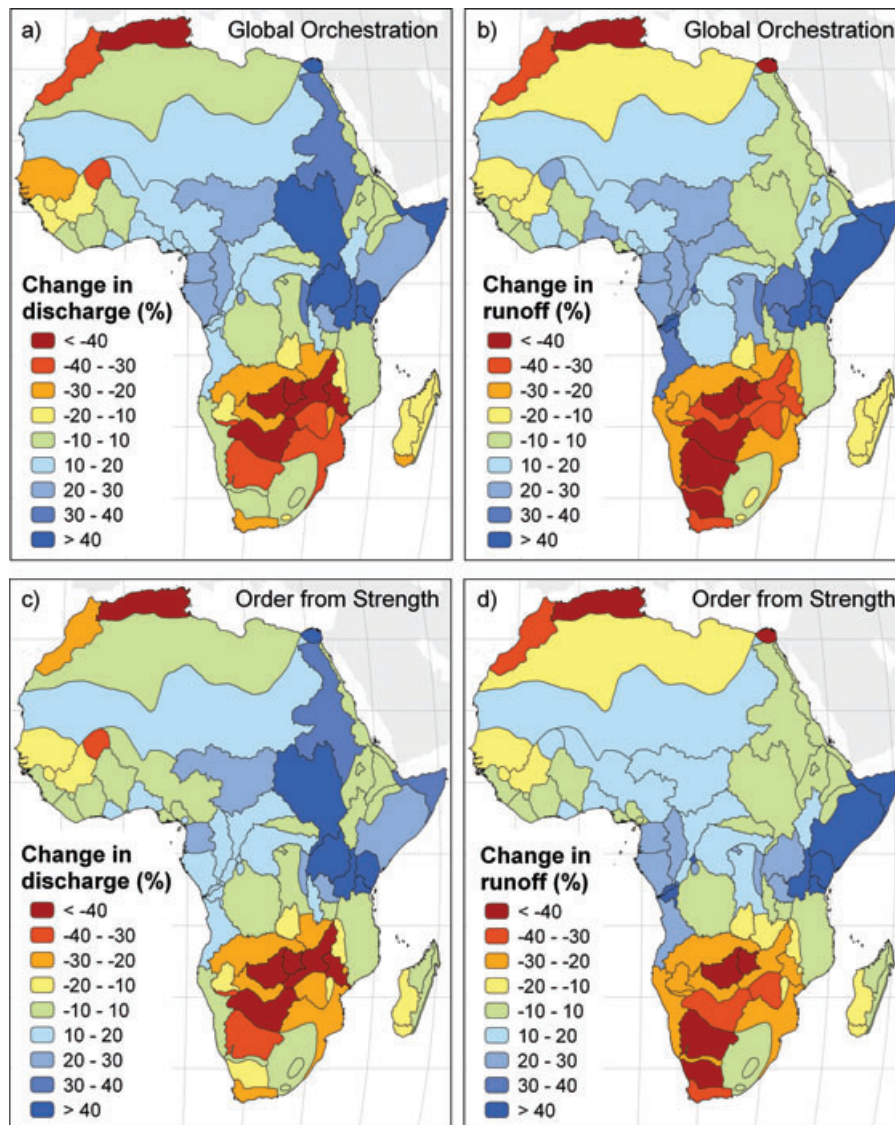
Ecoregions that contained the following were considered to have an ecological or evolutionary phenomenon: (1) greater than 25% of the fish genera endemic to that ecoregion; or (2) a fish species radiation judged to be unique at the continental or global scale by African freshwater experts; or (3) a congregation of  $\geq 1,000,000$  waterbirds (see Tables S1 and S2 in Supporting Information for details on data sources and phenomena by ecoregion). We then calculated the numbers of species, endemics, and phenomena located in ecoregions expected to experience changes in annual discharge or runoff of greater than 10% and 40%. These numbers provide a rough estimate of the exposure of Africa's freshwater biota to hydrologic changes associated with climate change and human water use.

Due to the inherent uncertainties of global modeling, the simulation of future conditions should not be interpreted as a precise forecast or prediction but only as a plausible path or “projection” of future development. Multiple runs with alternative climate and water use scenarios would likely identify some of our highlighted regions as outliers and add other regions.

## Results

Both scenarios show similar broad patterns of change in runoff and discharge across the continent (Figure 1). Decreased discharges are expected along the Mediterranean coast of North Africa, in parts of West Africa, in southern Madagascar, and in large parts of southern Africa. Increases are expected in much of the Nile Basin, Lake Chad, a large swath of the Guinean-Congolian forest, coastal Angola, the Horn of Africa, and several of East Africa's major freshwater lakes, swamps, and coastal rivers. Runoff shows a similar pattern except in the Nile Delta where runoff decreases while discharge increases. This is explained by the fact that discharge in the delta is generated almost exclusively in upstream areas where increases in runoff and discharge due to climate change are expected.

Independent of the direction of change, the magnitudes of changes across Africa are generally high. More than 80% (“Global Orchestration” scenario) and 75% (“Order from Strength”) of the African land surface shows a change in the long-term average discharge or runoff of  $\pm 10\%$  and above, with about 35% (“Global Orchestration”) and 30% (“Order from Strength”) of the region showing changes of more than 40%. In all, 73 and 63 out of 87 ecoregions are expected to experience an absolute change in discharge or runoff greater than 10% under the “Global Orchestration” and “Order from Strength” scenarios, respectively (Table 1).



**Figure 1** Average change in discharge (a and c) and runoff (b and d) by freshwater ecoregion. Percentage change is calculated as the average difference between WaterGAP calculations for the present (1961–1990) and the “2050s” under the “Global Orchestration” and “Order from Strength” scenarios of the Millennium Ecosystem Assessment.

These high-change ecoregions contain exceptional numbers of aquatic species, including many endemics whose loss from one ecoregion would mean global extinction. Fish species richness is highest in Central and Western Africa and in the large lakes of East Africa (Figure 2a), and exceptional levels of endemism occur in East Africa's large lakes as well (Figure 2b). Again, accounting for the affect of area did not change the basic pattern in species richness, in fact, richness and area-adjusted richness values are strongly positively correlated ( $R = 0.955$ ,  $N = 87$ ,  $P < 0.0001$ ; see Supporting

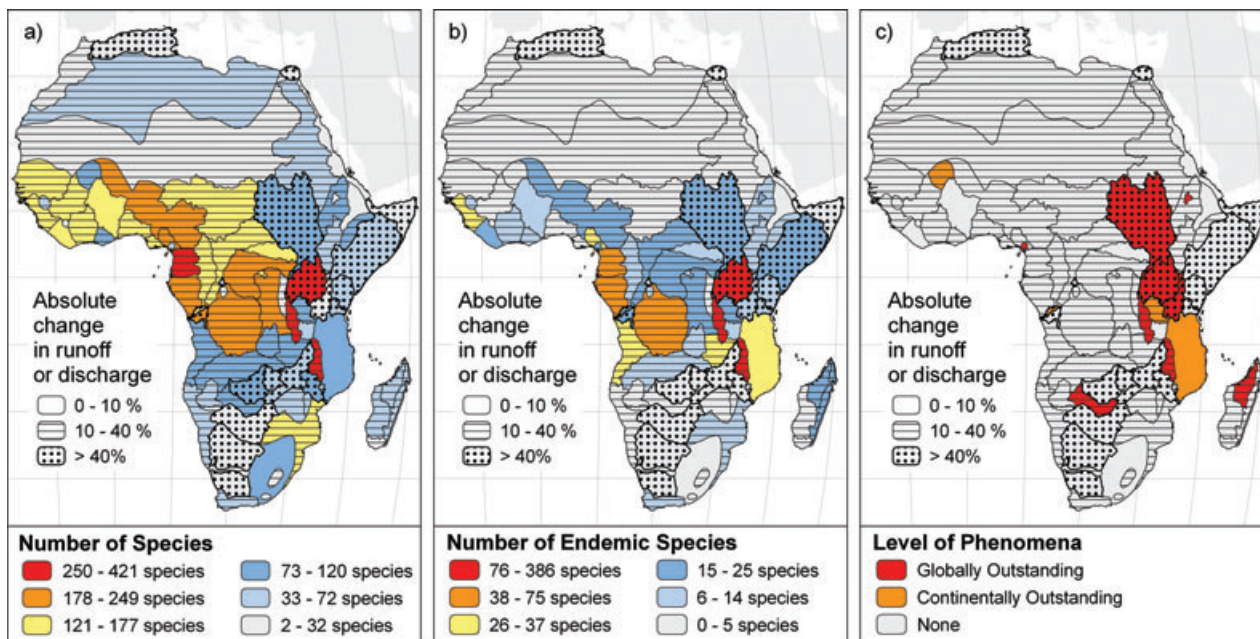
Information). Patterns of ecological and evolutionary phenomena are similar to that of richness and endemism, with the addition of waterbird congregations in ecoregions with large floodplains and wetlands (Figure 2c). Of the over 3,000 described freshwater fish species across the continent and Madagascar, about 95% (“Global Orchestration”) and 87% (“Order from Strength”) occur in ecoregions with a change in discharge or runoff greater than 10%. About 92% (“Global Orchestration”) and 82% (“Order from Strength”) of endemic species could be affected (Table 1). Under the “Order from

**Table 1** Numbers of ecoregions, fish species, endemic fish species, and ecoregions with ecological or evolutionary phenomena expected to experience a change in discharge or runoff greater than plus or minus 10% or 40% by the 2050s under the Global Orchestration (GO) and Order from Strength (OS) scenarios.

	Discharge			
	> $\pm 10\%$		> $\pm 40\%$	
	GO	OS	GO	OS
No. of Ecoregions	63	56	13	12
No. of Fish Species	2758	2554	625	618
No. of Fish Endemics	1549	1191	299	297
No. of Ecoregions with species radiations or endemic Genera/families	7	4	1	1
No. of ecoregions with wetland bird congregations (>1,000,000 birds)	4	3	2	2

	Runoff			
	> $\pm 10\%$		> $\pm 40\%$	
	GO	OS	GO	OS
No. of ecoregions	68	59	15	14
No. of fish species	2563	2354	568	566
No. of fish endemics	1363	1191	104	104
No. of ecoregions with species radiations or endemic Genera/families	6	4	1	1
No. of ecoregions with wetland bird congregations (>1,000,000 birds)	3	3	1	1



**Figure 2** (a) Fish richness, (b) number of endemic fish species, and (c) presence of ecological or evolutionary phenomena (endemic genera, species radiations, or large congregations of wetland birds) [Classification method for a and b: Natural breaks (Jenks optimization); this method identifies breakpoints between classes using a statistical formula that identifies groupings and patterns inherent in data]. Percentage change in runoff

and discharge is calculated as the average difference between WaterGAP calculations for the present (1961–1990) and the “2050s” under the “Global Orchestration” scenario of the Millennium Ecosystem Assessment; the “Order from Strength” scenario (results not shown) indicates similar but slightly lower changes.



Strength" scenario, 10 ecoregions with phenomena are expected to experience a greater than 10% change in discharge or runoff; under the "Global Orchestration" scenario the number would rise to 11 ecoregions. Under both scenarios about one-third of fish species and one-fifth of all endemics occur in ecoregions that will experience the extreme of a 40% change in discharge or runoff.

## Discussion

While the results presented here estimate the numbers of aquatic species that will experience hydrological change across the region, we cannot extrapolate specific impacts. The high uncertainty inherent in climate modeling and in the water balance component of the models makes it extremely difficult to project with accuracy the specific changes that will occur in any one ecoregion (Bates *et al.* 2008). Detailed projections might send a dangerous message anyway; Matthews and Wickel (2009) warn against assuming some future new climate stationarity to which we can tailor our management plans. Finally, there is also uncertainty in how human society will respond and adapt to future changes in water availability and the resulting effects on water resources. We have attempted to consider a range of projections by examining two scenarios that assume a world development of "globalization" ("Global Orchestration") versus "regionalization" ("Order from Strength"), but there remains large ambiguity in their long-term trajectories (Alcamo *et al.* 2005a).

We have treated all species equally, but effects are likely to be species-specific, given differing temperature tolerances and flow requirements, and the rate of environmental change relative to a species' adaptive capacity (Reist *et al.* 2006; Palmer *et al.* 2009). The ability of aquatic organisms to respond to climatic changes will also depend on their ability to move to more suitable habitats (e.g., entirely aquatic obligates may be more constrained than those with terrestrial life stages) and on changes within community-level interactions (Heino *et al.* 2009). Thus, predicting the responses of species or assemblages to climate change is beyond the scope of this article. Furthermore, many ecoregions encompass tens or hundreds of thousands of square kilometers and span a wide range of climatic and ecological conditions. Large variations in climate and hydrological changes would be expected within these regions, with associated variations in biotic responses.

Although the thresholds at which species are affected by changes to flow regimes are almost universally unknown, a safe assumption is that greater magnitudes of change carry greater risks for species' populations. Our

results show that, as a result of climate change and increased water use, by the 2050s over 80% of Africa's freshwater fish species are likely to experience hydrologic conditions substantially different from those in which they currently live. Existing conditions in turn are already often modified from natural conditions. Potential changes to thermal regimes and associated alterations in a range of biochemical and geomorphologic qualities, as well as compensatory actions undertaken by human communities to address changes in water availability (e.g., the construction of new water management infrastructure), were not explored in this analysis and are expected to affect aquatic systems further.

The high proportion of endemic species in ecoregions with significantly altered hydrological conditions is of particular concern. A recent review found that range-restricted species exhibit more severe range contractions than other groups and that they are the first species to have gone extinct due to recent climate change (Parmesan 2006).

Runoff and discharge both play a role in shaping aquatic habitats. Runoff is a better indicator of changes in ephemeral endorheic (closed-basin) habitats, since these rely primarily on local rainfall and groundwater flow patterns. Ecoregions experiencing large reductions in both discharge and runoff are located within parts of the continent (i.e., southern and northern Africa) that are already dry. Ephemeral or seasonal aquatic habitats within these regions will be under great stress and could disappear altogether. Although it is often assumed that more water is a positive or neutral change, if that water arrives as flood events or otherwise significantly alters the flow regime, it also can have detrimental consequences for aquatic systems and adjacent human communities.

Several strategies will be key to improving the freshwater species' survival prospects. Primary among these is reducing nonclimate stresses on aquatic ecosystems. Management actions that minimize water quality perturbations, approximate the historical flow regime as closely as possible, and prevent the spread of species from distant regions can help maintain resiliency (Poff *et al.* 2002). Dispersal opportunities should also be maximized by maintaining connectivity, particularly across environmental gradients, and by protecting spatial and thermal refugia (Ficke *et al.* 2007). Enhancing connectivity to facilitate range shifts may provide additional time for some species to autoadapt, such as through altered phenological behaviors. However, in lentic and lotic systems with uniform climates and altitudinal ranges, opportunities for strict aquatic obligates to disperse to more favorable environments might be rare.

New approaches to "climate-aware" water management are required in many basins across Africa and the

globe, as are governance structures with sufficient capacity and authority to deliver that management (Matthews *et al.* 2009). Flexibility and adaptability will be needed as water managers deal with ever-greater climatic and eco-hydrological uncertainty (Milly *et al.* 2008; Matthews & Wickel 2009).

This study shows that despite this uncertainty, we can be relatively confident that freshwater species will face changes in the hydrology of the systems to which they are adapted. Like freshwater systems, human communities that depend on them may be similarly stressed by future climate conditions and resulting impacts to water resources, including diminished freshwater biodiversity. Fortunately, some of the tools that we have for managing and protecting today's freshwater systems are the same ones that we can use to build resilience for the future.

## Acknowledgments

We thank the many scientists who contributed to the synthesis of fish species data: L. De Vos, I. Doadrio, A. Getahun, A. Konings, C. L  v  que, M. Oliver, A. Ribbink, U. Schliewen, L. Seegers, O. Seehausen, P. Skelton, J. Sparks, M. Stiassny, G. Teugels, D. Tweddle, D. van den Audenaerde. We also acknowledge Lincoln Fishpool at BirdLife who kindly provided the data on waterbird congregations. Additionally, W. Eschmeyer and S. Blum have provided critical support toward improving our fish species database. This work was supported in part by grants from The Coca-Cola Company, Johnson-Diversey, Inc., and HSBC.

## Supporting Information

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

**Table S1:** Ecological and evolutionary phenomena by ecoregion.

**Table S2:** Data sources for fish species richness and endemism (1–23), congregations of wetland birds (23), and expert evaluation of fish species radiations (8–22).

**Table S3:** Freshwater ecoregions of Africa and Madagascar with raw, log-transformed and area-adjusted fish richness values. Richness is estimated from the number of described fish species (see Table S1 for data sources).

**Figure S1:** Correlation between area-adjusted fish richness values and log (fish species richness). The two variables are strongly positively correlated ( $R^2 = 0.955$ ,  $N = 87$ ,  $P < 0.0001$ ).

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