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Chapter 4

A Synopsis of Global Mapping of Freshwater Habitats and Biodiversity: Implications for Conservation[1]

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http://dx.doi.org/10.5772/intechopen.70296

Abstract

Accurately mapping freshwater habitats and biodiversity at high-resolutions across the globe is essential for assessing the vulnerability and threats to freshwater organisms and prioritizing conservation efforts. Since the 2000s, extensive efforts have been devoted to mapping global freshwater habitats (rivers, lakes, and wetlands), the spatial representation of which has changed dramatically over time with new geospatial data products and improved remote sensing technologies. Some of these mapping efforts, however, are still coarse representations of actual conditions. Likewise, the resolution and scope of global freshwater biodiversity compilation efforts have also increased, but are yet to mirror the spatial resolution and fidelity of mapped freshwater environments. In our synopsis, we find that efforts to map freshwater habitats have been conducted independently of those for freshwater biodiversity; subsequently, there is little congruence in the spatial representation and resolution of the two efforts. We suggest that global species distribution models are needed to fill this information gap; however, limiting data on habitat characteristics at scales that complement freshwater habitats has prohibited global high-resolution biogeography efforts. Emerging research trends, such as mapping habitat alteration in freshwater ecosystems and trait biogeography, show great promise in mechanistically linking global anthropogenic stressors to freshwater biodiversity decline and extinction risk.

Keywords: ecology, streams, rivers, lakes, wetlands, fish, crafyish, mussels, amphibians

[1]This manuscript has been authored by UT-Battelle, LLC under Contract No. DE-AC05-00OR22725 with the U.S. Department of Energy. The United States Government retains and the publisher, by accepting the article for publication, acknowledges that the United States Government retains a non-exclusive, paid-up, irrevocable, worldwide license to publish or reproduce the published form of this manuscript, or allow others to do so, for United States Government purposes. The Department of Energy will provide public access to these results of federally sponsored research in accordance with the DOE Public Access Plan (http://energy.gov/downloads/doe-public-access-plan).

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1. Introduction

Our knowledge of Earth's ecosystems and biodiversity is growing at rates that exceed our ability to accurately predict regional species pools [1]. Recent estimates of Earth's biodiversity suggest that the planet boasts a total of 8.7 million species, 87% of which are yet to be described [2]. Yet while our comprehension of the magnitude and appreciation of species diversity grows, many have suggested we are currently within the Earth's six mass extinction event [3, 4], in which rates of species loss are unprecedented compared to past extinction events. Indeed, cataloguing biodiversity is a catalyst for global conservation efforts. The International Union for the Conservation of Nature (IUCN) has assessed over 77,300 species, of which 29,530 (38%) are classified as threatened, endangered, or critically endangered, and >10,000 more (13%) species listed as vulnerable [5]. While only 0.01% of Earth's surface water occurs in rivers, lakes, and swamps, >126,000 (7%) of the Earth's described species are found in freshwaters [6, 7]. Therefore, freshwater species especially are in serious jeopardy of extinction.

Dudgeon et al.'s [6] review of threats and conservation challenges to global freshwater biodiversity came at a much-needed time and addressed information gaps limiting our knowledge of these systems. The authors suggested (correctly) that there was no global comprehensive analysis of freshwater biodiversity comparable to those conducted for terrestrial systems [8]. Additionally, there was no comprehensive mapping of inland waters. The lack of this information prohibited our collective ability to inform large-scale conservation and prioritizing species and habitat protection. Since that time, many have answered the call to map global freshwater habitats and biodiversity to inform large-scale conservation. Just 2 years later, in 2008, the first seamless high-resolution map of global river hydrography was developed [9], and the first global biogeographical regionalization of freshwater biodiversity was completed [10].

In more recent years, significant advances in mapping aquatic habitats—specifically rivers, lakes, and wetlands—have been made at the global scale (e.g., [11–13]). Much of the progress in spatially depicting freshwater ecosystems has been the result of new globally comprehensive remote sensing technologies [13], but also significant efforts by scientists to collate disparate data sources [14]. As new datasets and geospatial products emerge with increasing spatial resolution, estimates of the spatial extent and importance of freshwater ecosystems in global biogeochemical cycles have also increased [15–17]. While efforts to develop comprehensive inventories and maps of the distribution of the world's freshwater fauna have dramatically increased [18, 19], these efforts have remained separate from those of freshwater habitat mapping.

Herein, we briefly review the status and recent history of global mapping of freshwater habitats, their biodiversity, and human disturbances. First, we provide an overview of the efforts and datasets to empirically map rivers, lakes, reservoirs, and wetlands at the global scale, and compare these to theoretical estimates of the spatial coverage of unobserved features. This provides an assessment of the accuracy and comprehensiveness of global freshwater habitat mapping. Secondly, we discuss the current state of global freshwater biodiversity mapping and provide sources of information and various approaches used. We compare the spatial scales and resolution of biodiversity and freshwater habitat mapping to identify potential

http://dx.doi.org/10.5772/intechopen.70296

overlap and information gaps. Additionally, we discuss various approaches to map the global extent of human disturbances in freshwater systems. Finally, we discuss emerging themes, but also gaps and research needs for continuing to improve our knowledge of patterns in freshwater species and their habitats. We also present summaries of the various databases used in supporting these efforts, which to our knowledge have not been previously summarized in one publication.

2. Global freshwater habitat mapping efforts

Global estimates of freshwater ecosystem coverages have been developed through both theoretical [20] or empirical means [21], or a combination of both [11]. Theoretical constructs, for example, might assume relationships between the size, distribution, and bifurcation of rivers (i.e., network theory) to quantify size and distribution of rivers within a region [20]. Likewise, theoretical relationships of size versus distribution are commonly used to estimate the frequency and size of unobserved waterbodies [22]. In contrast, empirical estimates typically rely on spatial observations from remote sensing data. Because the geospatial representation of waterbodies is limited to the spatial fidelity of mapping efforts, the number and areas of waterbodies provided through empirical observation is consistently smaller than that estimated theoretically. This comparison is important, however, in that it yields insights into the current state (i.e., comprehensiveness and granularity) of global freshwater mapping efforts. In the following sections, we review and compare approaches to obtaining global scale estimates of three different freshwater ecosystem types: rivers and streams, lakes and reservoirs, and wetlands. Estimation methods and datasets vary for each of these aquatic ecosystem types and influence their respective global estimates. We also devote particular attention to trends in freshwater mapping efforts within the United States.

2.1. River and streams

Global estimates of river and stream mileage and area range widely, with aerial estimates provided more frequently than distances. The latest and largest estimates of river length and area are over 88.3 million km and 662,100 km^2, respectively [20]. To provide these estimates, Downing et al. [20] used two approaches, one reliant on stream network theory and empirical data on stream widths and the other estimating the fraction of continental area occupied by streams while correcting for the unresolved small stream portion. The authors first estimated global river number, length, and area according to stream order by relying on relying on river geometry and scaling laws [23, 24] and known bifurcation ratios and stream length-order equations [25]. Stream widths among different order streams were obtained from literature or aerial imagery and applied to the number and lengths of streams. In the second method, estimates of the fraction of river area per land for well-studied landscapes were extrapolated to the global land area, which led to a very close second approximation, 640,400 km^2.

Empirical estimates of global river length and area from mapping efforts are far less than the maximum theoretical estimates [20]. The Digital Chart of the World (DCW) estimates global

stream length at 16.6 million km [26, 27]. HydroSheds (basins and stream networks) were developed from global digital elevation models (DEMs) which increased the estimate to 27.3 million km (derived from 15 arc-second resolution) (**Figure 1**) [9]. The Hydro1K database is currently the highest resolution empirical estimates of global stream length [28], which constitutes 53% of the highest theoretical estimates [20]. Previous estimates of global river area range from 360,000 to 510,000 km^2 (**Table 1**). The Global Lakes and Wetlands Database (GLWD) is a compilation of at least 17 different datasets of regional to global registers, inventories, and digital maps according to different spatial extents [21]. Their estimate of 360,000 km^2 of global river area was dependent upon aerial and satellite imagery of >5th order rivers and streams [20].

The spatial distribution and quantification of global river and stream mileage is limited to the resolution of widespread DEMs and, in turn, derived stream networks [31, 32]. Increased spatial resolution [33] and new algorithms for deriving stream networks [31] have continually increased the accuracy of spatial representations of global rivers (**Figures 1** and **2**). The finest resolution of consistent global-extent elevation grids is >90 m [9, 28], which will grossly underrepresent small stream systems. According to the DCW, the length of streams and rivers within the conterminous-US (CONUS) totals 727,326 km (almost 29,000 reaches) whereas the HydroSheds database (15 arc-second) estimates the same distance as almost 1.9 million km (238,405 reaches) (**Figure 3**). In contrast, the total mileage is 5.7 million km (2.98 million reaches) according to the NHD plus medium resolution dataset (1:100k scale) [34], which was constructed on the basis of 30-m DEM resolution [35]. The NHD High-Resolution Dataset (1:24k scale), however, estimates stream length for the CONUS at 1.2 million km (**Figure 3**) [36]. While mapping perennial systems seems straightforward, accurately mapping ephemeral systems from flow accumulation thresholds is difficult. Even the NHDplus dataset under-represents the small headwater systems apparent in the high-resolution National Hydrography Dataset (1:24k scale), which also under-represents potential ephemeral systems (**Figure 2**).

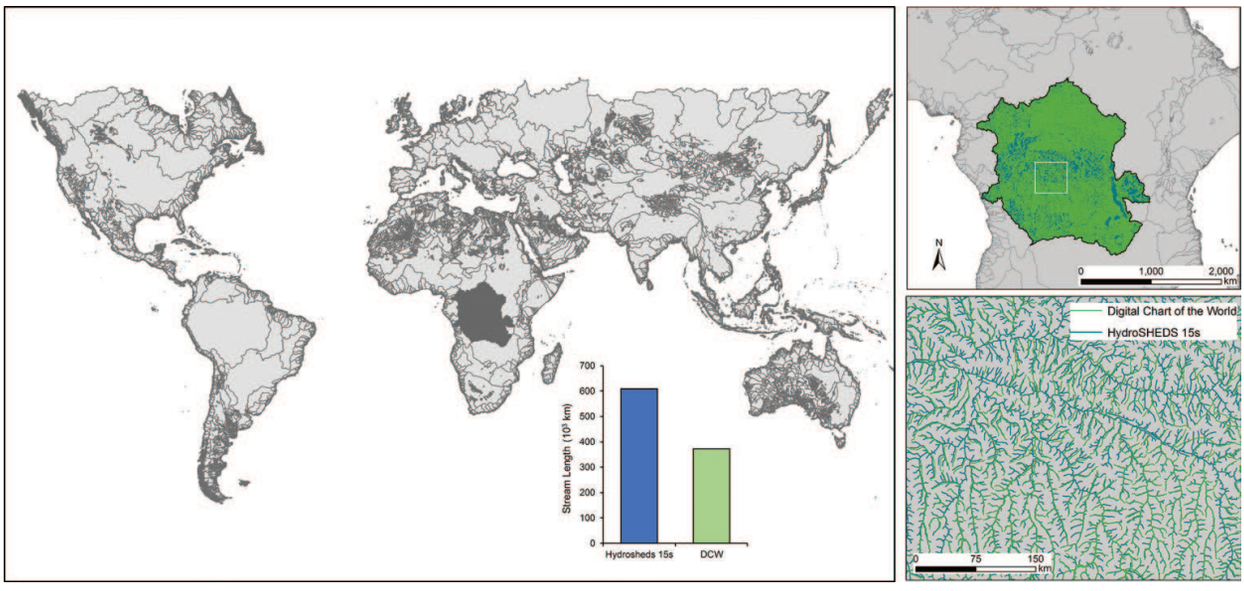


Figure 1. HydroSHED 15s basin boundaries (left). Example of improved accuracy of rivers mapped in HydroSHEDs 15s versus the Digital Chart of the World in the Congo River Basin, Africa.

Study or database	Length (km)	Area (km^2)
Theoretical		
Downing et al. [20]: A	88,325,340	662,100
Downing et al. [20]: B		640,400
Downing et al. [20]: C		485,000
Aufdenkampe et al. [29]		510,000
Downing [30]		508,000
Empirical		
HydroSheds [9]	27,300,269	
Global Wetlands and Lakes Database [21]		360,000
Digital Chart of the World [26, 27]	16,610,004	
Hydro1K [28]	46,900,425	

Downing et al. [20] use three different approaches to estimating stream and river area as denoted by A, B, and C (see text).

Table 1 Theoretical and empirical estimates of global stream and river length and area provided by different studies and datasets**.**

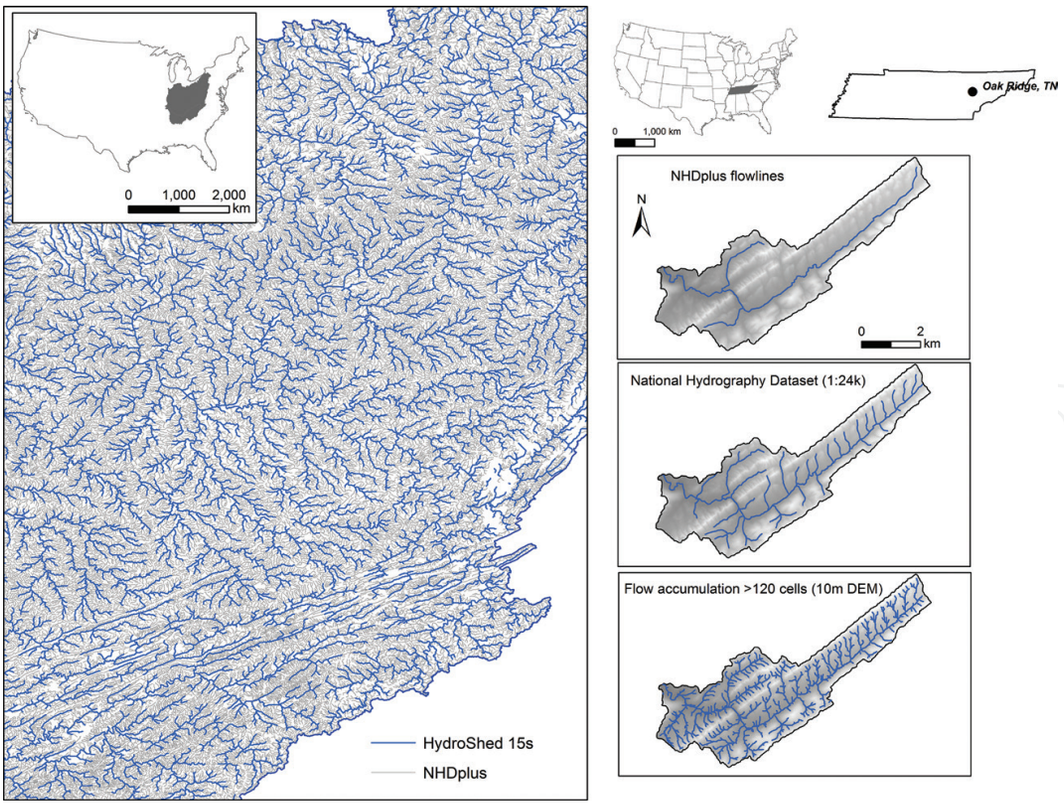


Figure 2. Comparison of HydroSHEDs to NHDPlus (1:100k) flowlines in the Ohio and Tennessee River Basins of the US (left). Example of the increased spatial resolution provided by the National Hydrography Dataset (High-resolution, 1:24k) over that of NHDPlus in Bear Creek, near Oak Ridge, Tennessee, USA. However, ephemeral channels are likely even underestimated by the NHD High-resolution dataset.

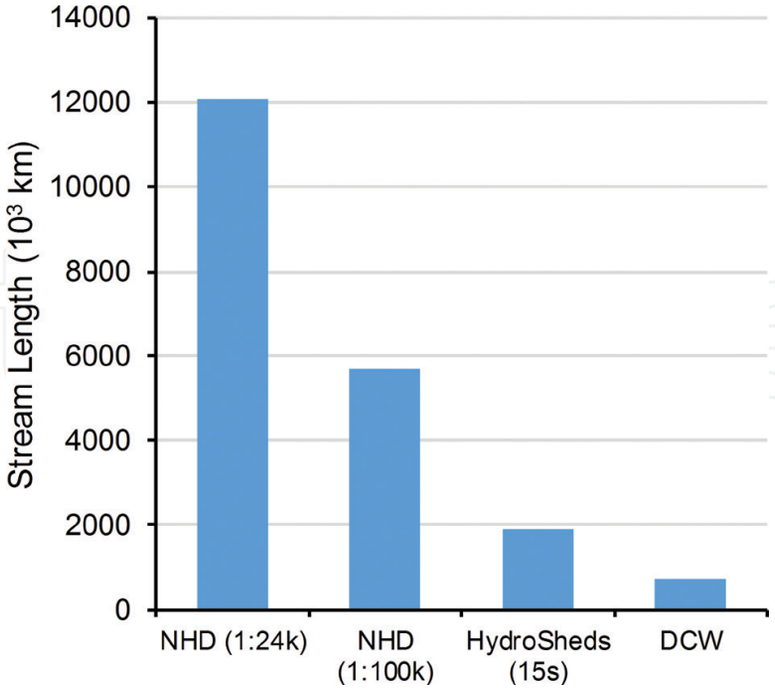


Figure 3. Total continental US stream distance represented by four spatial datasets depicting river networks.

Interestingly, global length-stream order relationships do not follow global area-stream order relationships. For example, the number and length of 1st order systems in the world are, by far, numerically dominant constituting 52% of global river length (28.5 million and 45.7 million km^2, respectively) [20]. However, global river area is dominated by larger order systems (≥6th order), which represent 65% of total river area. Size-specific stream distribution estimates are extremely important for accurately portraying or modeling the distribution of aquatic organisms.

2.2. Lakes, reservoirs, and farm ponds

Studies estimating the global extent of lakes and reservoirs were more numerous than those estimating river and stream distributions. Global numbers of lakes range from 800,000 to 304 million whereas cumulative area of world lakes ranges from 2.3 to 5 million km^2 (**Table 2**, **Figure 4**). Human construction of reservoirs has been extensive, the most current estimate at 16.7 million waterbodies with a cumulative surface of 305,723 km^2, an area equivalent to increasing the world's naturally occurring terrestrial water surface by 7.3% [11]. Other estimates of global reservoir surface area range from 150,000 to 600,000 km^2, depending on the source and whether regulated natural lakes are included (**Table 2**). Only one study provided an estimate of global farm pond coverage (77,000 km^2) using relationships between the fraction of farm pond area within farm land and annual precipitation [22].

Similar to rivers and streams, lakes and reservoirs have been estimated using both empirical observation of available geospatial datasets or via extrapolation of observed data to unobserved features. Until recently, theoretical estimates of lakes exceeded that of empirically derived estimates. New high-resolution satellite imagery provided means to observe lakes

Area	Lakes	Reservoirs	Farm ponds
	10^3 km^2	10^3 km^2	10^3 km^2
Kelly et al. (1994) [37]		500	
Pearce (1996) [38]		600	
Meybeck (1995) [39]	2300–2600		
Lehner and Doll (2004) [21]*	2428	251	
Lehner and Doll (2004) [21]*	3200		
McDonald (2012) [40]	3800		
Downing et al. [22]	4200	260	77
St. Louis et al. (2000) [41]		150	
Lehner et al. (2011) [11]*		305	
Messager et al. (2016) [42]*	2677	250	
Verpoorter et al. (2014) [13]*	5000		
Number	10^3	10^3	10^3
Meybeck (1995) [39]	800–1300		
Lehner and Doll (2004) [21]*	246	0.822	
Lehner and Doll (2004) [21]*	15100		
McDonald et al. (2012) [40]	64000		
Downing et al. [22]	304000		
Lehner et al. [11]*		16700	
Messager et al. [42]*	1421	7	

*Empirical estimates.

Table 2 Global estimates of the area and number of lakes, reservoirs, and farm ponds according to different studies**.**

>0.002 km^2 [13]. Using this technology, the GLObal WAter BOdies database (GLOWABO) was developed for 117 million lakes with a total surface area of 5 million km^2 [13]. This surface area estimate exceeds that of the highest theoretical estimate [20], but is still smaller in total lake abundance (**Figure 4**).

The development of reservoir mapping datasets has provided valuable spatial representations of waterbodies in recent years. For example, the GLWD dataset consists of polygon shapefiles of approximately 250,000 lakes and reservoirs >0.1 km^2 and raster datasets of other lakes, reservoirs, and wetland coverages [21]. The GLWD included only information for the world's largest reservoirs (storage >0.5 km^3) either because spatial information was limiting or existing lake datasets did not explicitly clarify whether a given waterbody was manmade. Because of the incomplete nature of global datasets on impoundments, the Global Reservoir and Dam database (GranD) was developed as a compilation of spatial coverages of 6862 reservoir polygons and associated dams and attributes [11]. More recently, a new geospatial coverage of

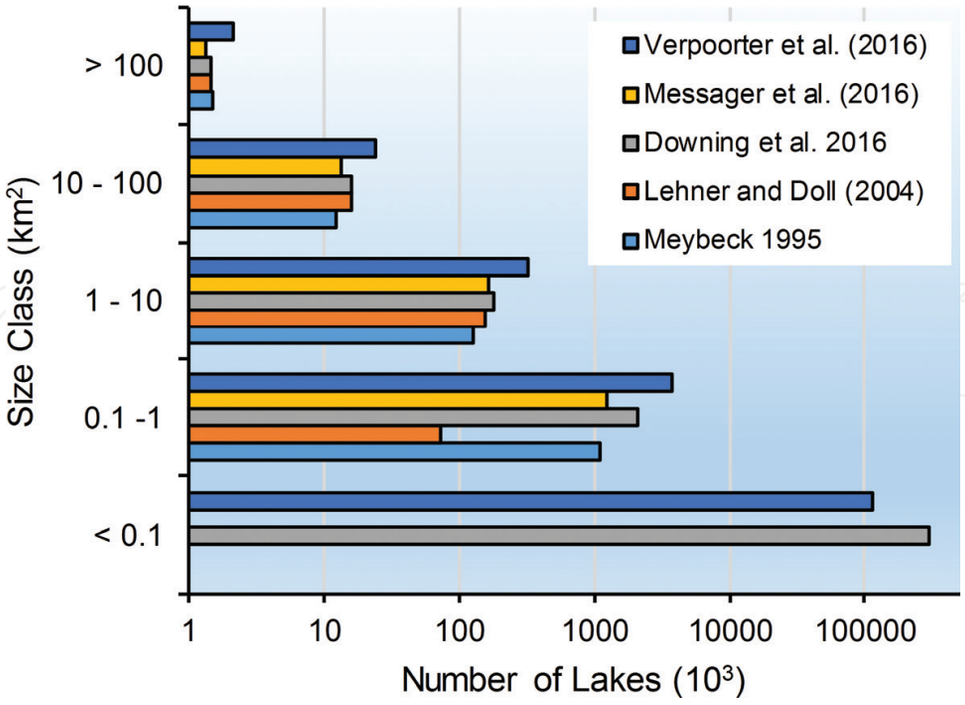


Figure 4. Global lake abundance estimated by several different studies.

global lakes and reservoirs, HydroLakes, was developed and includes hydrologic attributes, such as volume and residence time, using a geo-statistical model [42] (**Figure 5**). Within the US, the NHDplus (1:100k) dataset provides coverage of lakes and areas as polygons, an area estimated at almost 250,000 km^2; however, this dataset misses small waterbodies, especially farm ponds. The NHD high-resolution (1:24k) dataset estimates lake and reservoir area coverage as approximately 890,000 km^2, almost 3.5 times higher than that of NHDplus.

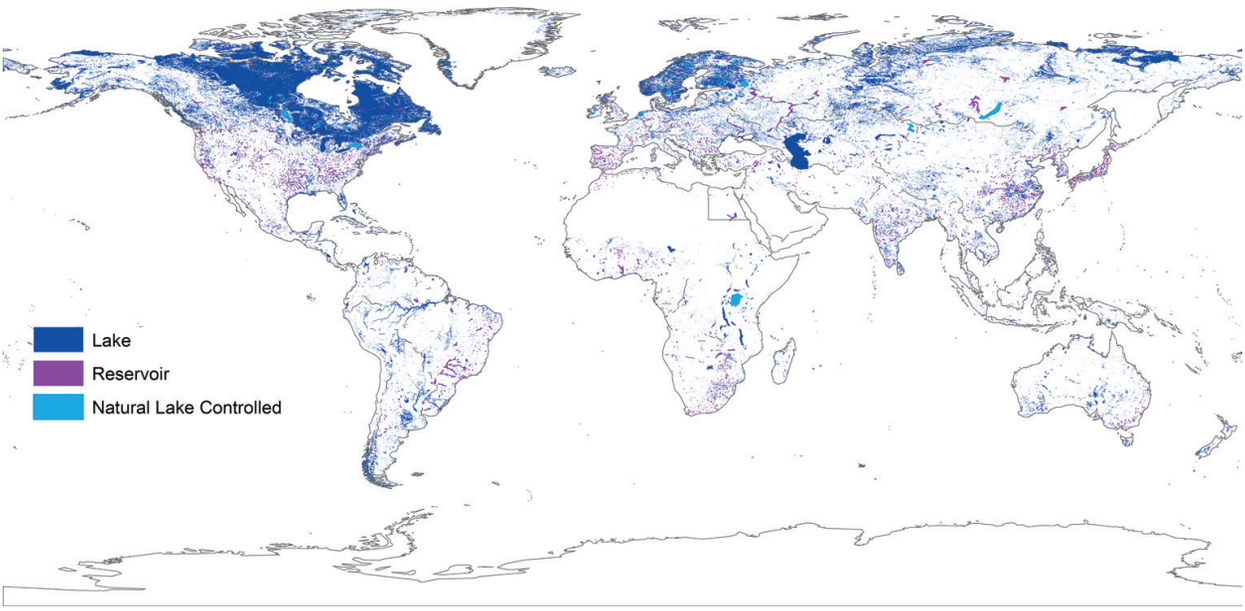


Figure 5. HydroLakes database depiction of global lakes and reservoirs.

http://dx.doi.org/10.5772/intechopen.70296

The most numerous lake and reservoir waterbodies are very small (<0.1 km^2) (**Figure 4**), yet these are typically omitted from most maps (with recent exceptions, [13]). To estimate the size and distribution of these smaller waterbodies, Pareto distributions of log-abundance versus log-size are fit to observed larger lakes and then those coefficients are used to extrapolate the abundance of smaller, unobserved lakes [43] or reservoirs [11]. Obviously, these estimates do not come without error, with some suggesting that numbers of small lakes and any related scaling estimates (e.g., carbon fluxes) are unreliable [44].

2.3. Wetlands

Wetlands are transitional systems by nature, making them difficult to distinguish from other waterbodies. A distinction is provided by the U.S. Fish and Wildlife Service (USFWS) [45], which defines wetlands as "lands transitional between terrestrial and aquatic systems where the water table is usually at or near the surface or the land is covered by shallow water". USFWS [45] goes on to list three main attributes of wetlands: "(1) at least periodically, the land supports predominantly hydrophytes, (2) the substrate is predominantly undrained hydric soil, and (3) the substrate is non soil and is saturated with water or covered by shallow water at some time during the growing season of each year." In contrast, the International Union for the Conservation of Nature (IUCN) broadens the definition of wetlands to be all-inclusive of "areas of marsh, fen, peatland or water, whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed 6 m" [46]. For our purposes, we include wetlands as any waterbody or part of the landscape that falls within the definitions above, but cannot be distinguished as a lake, reservoir, pond, river or stream.

Unfortunately, there is little consistency in the nomenclature distinguishing among various waterbodies in the spatial datasets used to estimate global coverage of wetlands. The GLWD is commonly used in representations of wetlands across the globe (**Figure 6**). Many of the spatial datasets contributing to the GLWD, however, have contrasting naming conventions for waterbodies [21]. In particular, the DCW does not distinguish between vectors portraying lakes, reservoirs, larger rivers, and wetlands [26]. In comparison, the Wetlands Map of the World Conservation Monitoring Center (WCMC) includes 20,000 wetland and lake polygons classified into 21 types and represents the most comprehensive and accurate vector map of the world's wetlands [47]. As opposed to representing wetlands as vectors or polygons, other mapping efforts display wetlands as raster maps. For example, the US Geological Survey Global Land Cover Characteristics (GLCC) database [48] and MODerate resolution imaging spectroradiometer (MODIS) data [49] provides classification of global landcover, including wetlands, as 30 second grids (MODIS). Others have developed global wetland land cover maps at coarser resolutions using varied methodologies [50–52]. Because of the uncertainties on global wetland extents and inventories, the Ramsar Convention on Wetlands has promoted new efforts and advanced remote sensing technologies to provide new and improved global wetland inventories [53, 54].

Similar to other freshwater systems, estimates of the global coverage of wetlands have increased over time with advances in higher-resolution spatially comprehensive datasets.

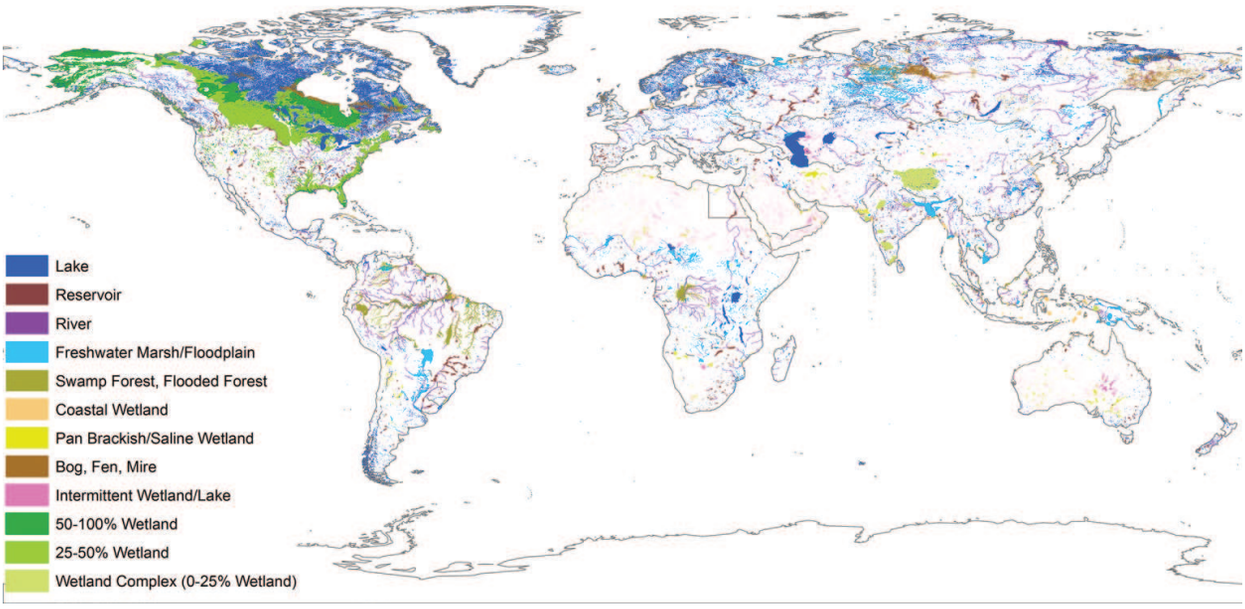


Figure 6. Map of global waterbodies based on the Global Lakes and wetlands database (GLWD).

Early estimates (pre-2000) ranged from 4.3 to 5.3 million km^2 whereas current estimates approach almost 13 million km^2 (**Table 3**). However, the highest estimate may be an overestimate inclusive of lake and reservoir waterbodies [57] relative to the reference [21] estimate of 9.2 million km^2. Within the US, wetlands are depicted by a few vector and raster datasets. For the conterminous US, the Multi-Resolution Land Characteristics Consortium (MRLC) provides National Land Cover Databases (NLCD) as raster images [58]. According to the 2011 NLCD data, the area classified as woody or herbaceous wetlands sums to 417,442 km^2. Open water constitutes almost the same spatial area, 422,111 km^2. The USFWS maintains the

Study	Wetlands (10^3 km^2)
Lehner and Doll [21]	9167
Williams [55]	8558
Mitch and Gosselink [56]	7000 - 9000
Mathews and Fung [50]	5260
Cogley [51]	4340
Sillwell-Soller et al. [52]	4795
GLCC [48]	1093
MODIS [49]	1291
Gross Wetlands Map [21]	11711
Finlayson et al. [57]	12800

Numbers provided by Lehner and Doll [21].

Table 3 Global areal estimates of wetland coverages according to different studies.

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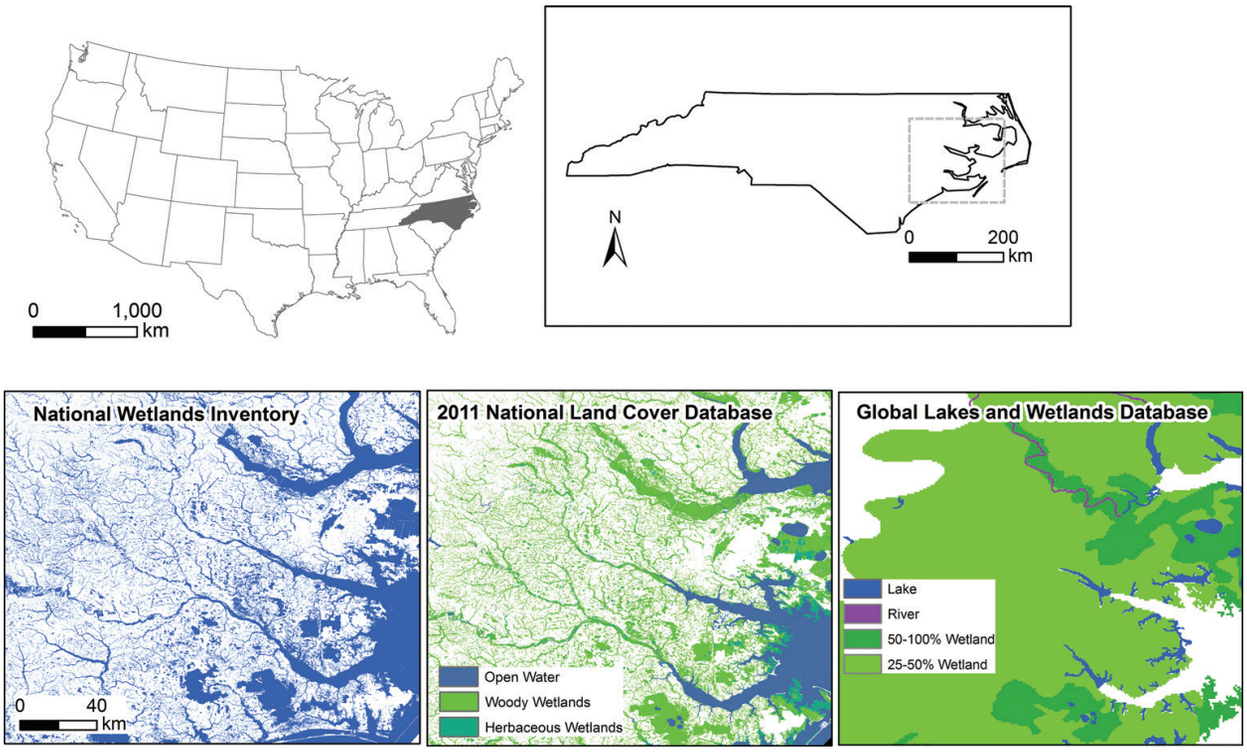


Figure 7. Comparison of wetland maps derived from the National Wetlands Inventory (NWI), the National Land Cover Database (NLCD), and the Global Lakes and Wetlands Database (GLWD) for a coastal portion of the State of North Carolina located in the eastern United States. Examples of types of wetland databases available in the conterminous US.

National Wetland Inventory (NWI), a database of polygons and associated very detailed classification framework for the conterminous US [59] (**Figure 7**). The NWI provides a status update of the nation's wetlands every five years with the latest 2009 report indicating there were 445,559 km^2 of wetlands, 95% of which are freshwater systems [60]. The difference of 28,118 km^2 between NWI and NLCD estimates of wetland area for the entire conterminous US suggests differences in the approaches taken to classify wetlands (**Figure 7**). Both of these datasets, however, far exceed the spatial granularity of wetlands depicted by the GLWD (**Figure 7**).

3. Global biodiversity mapping efforts

Global and continental-scale mapping of freshwater species distributions has lagged freshwater habitat mapping efforts in terms of finer spatial granularity. More specifically, there are mismatches between the resolution of current global biogeography efforts and the spatial fidelity of waterbodies in the landscape. This makes intuitive sense for two main reasons: (1) The presence of a species within a given area typically requires in situ observation, as opposed to detection via remote sensing technologies, such as in the case of waterbodies and other landscape features. That being said, remote sensing of biodiversity is a rapidly growing area of research [61], with potential new capabilities for direct aerial observation of biota [62]. (2) Most observations of species are discrete points in space and time, are influenced by

methods of detection, and are not spatially comprehensive. Hence, extending species presences into unsampled areas requires various levels of inference ranging from summarization into regions or watersheds to sophistical statistical models predicting probability of presence using a suite of predictor variables characterizing habitat. Obviously, the first approach requires less resources and information, whereas the latter approach requires rich information on descriptions of habitat, not just the features themselves.

3.1. A synopsis of published global biodiversity mapping

Generally, we found little congruence between global mapping of biodiversity and global mapping of freshwater habitats (**Table 4**). Only two studies in **Table 4** used spatial products from recent global habitat mapping efforts [19, 72]. Richman et al. [19] summarized crayfish range maps from IUCN and georeferenced occurrences (from experts) in Hydro1K basins [28] to examine factors responsible for their decline. All but one of the studies outlined in **Table 4** have been published within the last 15 years, and opposite as expected, species mapping efforts do not display a clear trend of increasing spatial granularity over time. In contrast, studies seem to summarize biogeographical information at the coarsest scales sufficient to achieving their purpose, which in most cases, was related to examining declines in species and threats to their existence. Spatial resolutions of freshwater species mapping ranged from biogeographic regions and range estimates (polygons) to 96-km^2 gridded cells and small watersheds (e.g., Hydro1K).

Source	Description	Spatial resolution	Source
Fish			
Oberdorff et al. [63]	Analyze fish species richness patterns across continents and show that species-area and species-energy relationships explain most of the variation	Major drainage basins (n = 292)	Multiple published sources
Amarasinghe & Welcome [64]	Developed models of fish species richness from natural lake characteristics	Nature lake features	Multiple published sources; International Lake Environment Committee Foundation (ILEC) global lake database [65]
Xenopoulos et al. [66]	Use global hydrologic model to simulate scenarios of future fish species loss with losses in river discharge from climate change and withdrawal	Major drainage basins (n = 325)	Oberdorff et al. 1995 [63]; FishBase [67]
Abell et al. [10]	Developed first global biogeographic regionalization of Earth's freshwater systems based on composition of freshwater fish species	Freshwater ecoregions (n = 397)	Multiple

Source	Description	Spatial resolution	Source
Oberdorff et al. [68]	Developed a framework of mechanisms and processes driving global and regional patterns in fish richness	Major drainage basins	Multiple published sources
Liermann et al. [69]	Use spatial distribution of fish, their traits, and current dam development to examine risks of fish species loss	Freshwater ecoregions (n = 397)	Abell et al. 2008 [10]
Bross et al. [70]	Developed a database of native, endemic and non-native fish species richness in major basins of the world	Major drainage basins (n >1000)	Multiple published sources
Toussaint et al. [71]	Examine world patterns in functional diversity of fish relative to species diversity	Biogeographic regions (n = 6)	Bross et al. 2013 [70]
Winemiller et al. [72]	Examined patterns in fish biodiversity and endemic species overlapping with current and proposed dam construction in the Amazon, Congo, and Mekong River basins	Freshwater ecoregions; hydroBasins	Abell et al. 2008 [10]; IUCN [73]
Amphibians			
Stuart et al. [74]	Status and trends of worldwide amphibian declines and extinctions. Mapped species distributions by reason for decline	1^0 Cell	Global Amphibian Assessment (IUCN) [75]
Gallant et al. [76]	Global assessment of land use dynamics in the context of amphibian distributions	Global ecoregions (n = 21)	Global Amphibian Assessment (IUCN) [75]
Sodhi et al. [77]	Global analysis to quantify the influences of life history, climate, human density, and habitat loss on declines and extinction of 45% of known amphibians	Range maps	Global Amphibian Assessment (IUCN) [75]
Wake and Vredenburg [3]	Global assessment of the decline and extinction of amphibians	Country	Multiple
Rödder et al. [78]	Global risk assessment for amphibian extinction for the Panzootic Chytrid Fungus	0.5^0 Cell	Global Amphibian Assessment (IUCN) [75]

Source	Description	Spatial resolution	Source
Hof et al. [79]	Assess the current and future interactions of climate change, land-use change, and spread of the pathogenic fungal disease chytridiomycosis on amphibian species declines	2^0 Cell	Multiple
Ficetola et al. [80]	Assessment of error in global range maps for amphibians	Range maps; point distributions	Global Amphibian Assessment (IUCN) [75]; GBIF [81]; Check List Online Journal [82]
Mussels			
Graf and Cummings [83]	Review of systematics and global diversity of freshwater mussel species	Geographic regions (n = 32)	MUSSEL Project [84]
Nobles and Zhang [85]	Assessment of global biodiversity loss in mussels including threats and solutions	Biogeographic regions (n = 6)	Multiple published sources
Crayfish			
Crandall and Buhay [86]	Description of global diversity in crayfish	Continents	Multiple
Richman et al. [19]	Evaluation of factors responsible for global declines in crayfish	HydroIK river basins	IUCN; expert georeference collection efforts
Multiple taxa			
Rodrigues et al. [87]	Examination of global protected areas in representing species diversity (includes amphibians, mammals, birds, turtles).	0.5^0 Cell	IUCN [73]
Rodrigues et al. [88]	Global gap analysis assessing the extent of protected land coverage for representation of biodiversity including amphibians, mammals, freshwater turtles and tortoises, and globally threatened birds	0.25^0 Cell	IUCN [73]
Grenyer et al. [89]	Examine congruence and commonalities in biodiversity and rare and threatened species among amphibians, mammals, and birds	96.3 km^2 grids	Multiple

Source	Description	Spatial resolution	Source
McGeoch et al. [90]	Development of indicators describing relationships between the extent of biological invasion by alien species, its impact on biodiversity and policy response. Species included mammals, birds, amphibians, freshwater fish, vascular plants and marine organisms (including algae, corals, invertebrates and fish)	Countries	Convention on Biological Diversity [117]
Collen et al. [18]	Examined geographical ranges of 7083 freshwater species of mammals, amphibians, reptiles, fishes, crabs and crayfish to examine commonalities in distribution of richness, threatened species, endemism, and congruence in diversity measures among taxa	1^0 Cell	IUCN [73]
Prim et al. [91]	Review of global species biodiversity, their rates of extinction, distribution, and protection (includes amphibians, fish, terrestrial birds, terrestrial mammals, and plants)	Varied (amphibians, 0.5^0 cell; fish, Freshwater Ecoregions, n = 397)	IUCN [73]; Abell et al. 2008 [10]
Jenkins et al. [92]	Assessed the US protected areas with respect to biodiversity of freshwater fish, terrestrial vertebrates, and trees	Varied	Nature Serve [93]; BirdLife International [94]; IUCN [73]; US Geological Survey Tree Database [95]

Table 4. Examples of studies developing or utilizing global freshwater biogeography databases.

In most cases, global mapping of biodiversity has been achieved by summarizing occurrence or estimated range information into spatial units as opposed to developing predictive species distribution models (SDMs) (**Table 4**). There are, however, several global-scale species modeling efforts, many of which are provided as interactive online resources (see following sections). Of freshwater taxa, amphibians and fish mapping efforts have been documented more than crayfish and mussels (**Table 4**), possibly because more vertebrate species have been described and more is known about the details of their life histories, habitat requirements, and conservation status. Additionally, global mapping efforts for amphibians are more common because of the

wealth of data for that taxa. In particular, the Global Amphibian Assessment conducted by the International Union for the Conservation of Nature (IUCN) produced polygon range maps for >6000 known amphibian species [75] (**Figure 8**) and was used in six different studies (**Table 4**). The IUCN provides similar spatial data for mammals, reptiles, and marine and freshwater taxa [73]. The range maps are many times converted to gridded raster datasets [74] (**Figure 8**) or overlapped with region polygons to provide summaries of species within those areas (e.g., [76]).

The IUCN recently produced a set of higher-resolution global maps of ranges of freshwater taxa (IUCN) within HydroBasins (240,000 basins globally) [12] (**Figure 9**). One study relied on this resource to examine spatial relationships between fish biodiversity and planned hydropower dam construction in three large basins of the world [72]. The authors suggested that site selection for dams not be conducted purely on the grounds of energy, but should be conducted strategically through tradeoff analyses to conserve the most biodiversity while financing new dams. The IUCN data is currently the best openly available global information on freshwater species occurrences, but has many gaps in spatial coverage (e.g., **Figure 9**). While the Congo and Mekong River (China) basins had sufficient information at the resolution of HydroBasins, the Amazon Basin did not have comprehensive biodiversity mapping at that resolution; hence, reference [72] relied on biodiversity estimates in Freshwater Ecoregions [10], a far coarser alternative. The Amazon basin is over 7 million km^2 yet only contains 13 Freshwater Ecoregions. Obviously, for conservation purposes, higher-resolution granularity is required to inform dam site selection in many areas of the globe. To compensate for lack of knowledge in many areas of the world, other mapping efforts have relied on published resources to compile freshwater species lists within regions or basins [63, 70]. While these resources can fill in important knowledge gaps, they are coarse (presented at the resolution of large basins) and leave large regions of the globe vacant of information (**Figure 9**).

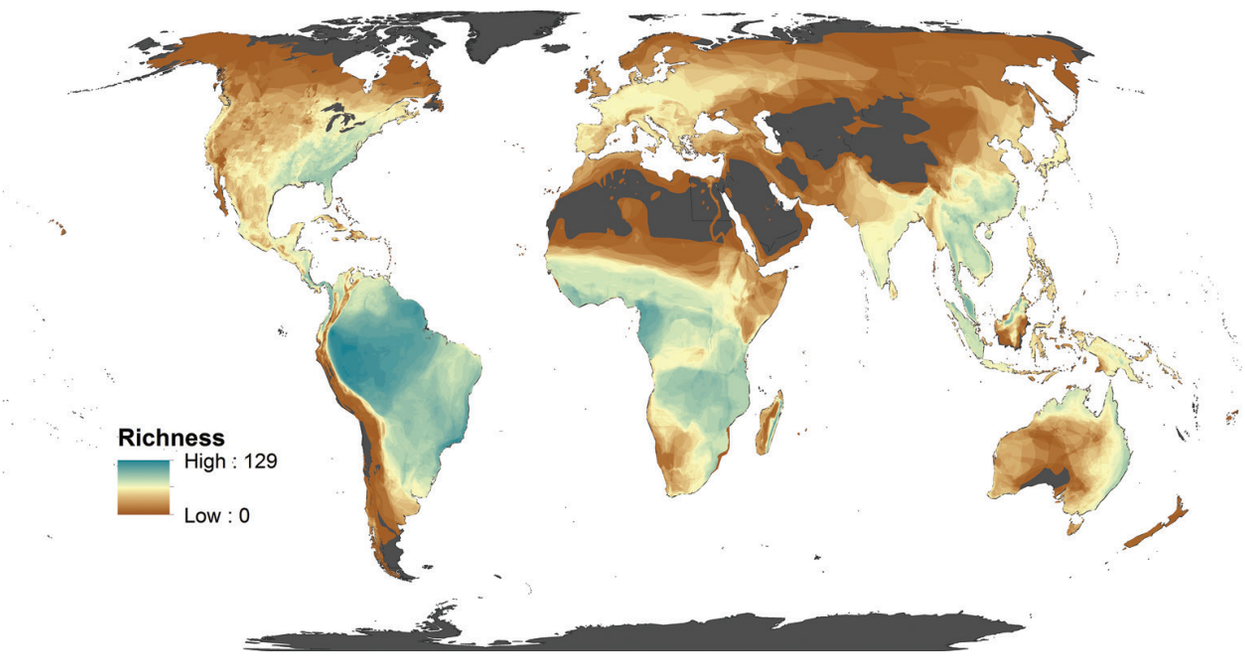


Figure 8. Global amphibian richness from the International Union for the Conservation of Nature (IUCN) Global Amphibian Assessment.

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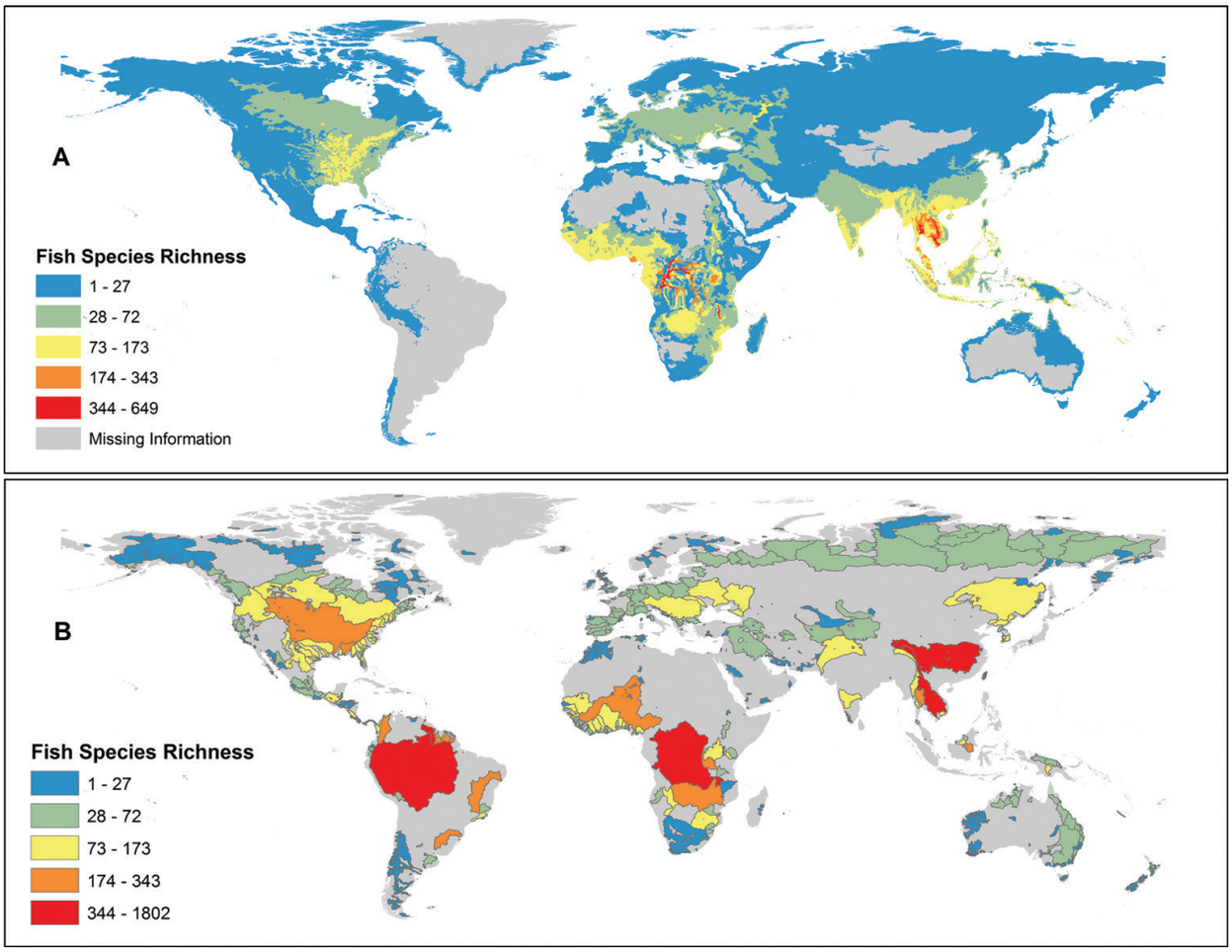


Figure 9. Global maps of fish richness provided by the IUCN [73] and Bross [70].

3.2. What is limiting global high-resolution freshwater species distribution models (SDMs)?

Although many of the world's freshwater species lack formal description, are prone to misidentification, and have few georeferenced occurrences, databases of species observations and species characteristics are growing rapidly. For example, the Global Biodiversity Information Facility (GBIF) currently has over 730 million occurrences for over 1.64 million species and harnesses global community participation [81]. GBIF operates through more formal data publishing, whereas other databases, such as iSPOT [96] provides a platform for crowd-sourced species observations. Additionally, rich databases on species ecology and conservation status have emerged to assist with linking biodiversity with their global freshwater habitat requirements [67, 93]. The wealth of information from georeferenced occurrence databases and descriptive databases suggests that global freshwater biodiversity SDM efforts are not limited by observations, but the inability to extrapolate occurrences to fine-grain freshwater habitats via distribution modeling. This is not to suggest that global freshwater biodiversity SDM efforts are completely absent. Indeed, novel web tools are available to enable users to perform their own SDM projections, both current and future. The Life Mapper project is an online resource that utilizes GBIF observations and global climate, terrain and land cover

information to model the current and future distributions of species (including freshwater) [97]. Models of current ranges of species and habitat specifications are calibrated based on existing observations and climate information and used to model future potential ranges based on four climate scenarios spanning 2050 and 2070, according to the International Panel on Climate Change (**Figure 10**). As another example, AquaMaps uses a simplistic "environmental-envelope" method to develop large-scale predictions of marine and freshwater species occurrences [98, 99]. Occurrence data are obtained from GBIF and literature available through FishBase and summarized within bounding basins to constrain subsequent projections of distribution to only natural ranges. Occurrence data are overlain with eight environmental parameters to create an envelope of environmental suitability, which is essentially using the percent of observations (percentiles) in conjunction with local habitat conditions to estimate probability of occurrence [98]. Environmental envelopes are then used to model probabilities of species occurrence based on local conditions. Both the Life Mapper project and Aquamaps are freely available and are a quick approach to developing distribution maps; however, they are still relatively coarse projections, currently set at 10 arc-minutes and 0.5° (30 arc-second) cells, respectively, and do not approximate freshwater habitat features.

We suggest that the current leading limitation of achieving high-resolution global freshwater biodiversity mapping efforts has been a matter of limiting global habitat characteristic data, as opposed to limitations in occurrence data. Even if occurrences for a species are limited, current modeling approaches (e.g., Maxent) are capable of developing SDMs with low sample sizes [100]. By high-resolution, we are referring to the spatial granularity that approximates that of global freshwater habitat features. Recent developments have produced high-resolution depictions of freshwater features in the landscape, but much of these features have little accompanying information on habitat requirements for species (e.g., temperature, hydrology, depth, etc). One exception is a database on world lakes (n = 217) provided by the International Lake Environment Committee Foundation (ILEC), which includes location, morphometric features, climate, water quality, and edaphic variables [65]. This provided an opportunity to model fish species richness in selected natural lakes across the globe [64].

In comparison to terrestrial ecosystems, habitats within freshwater systems are shaped by upstream hydrologic processes, which require sophisticated geospatial summarization methods for appropriate characterization. For example, suppose air temperature is being used as a surrogate of water temperature in a fish species distribution model at the resolution of stream reaches or small watersheds. In this case, air temperature summarized at the location of the individual stream reach is unlikely to be representative of actual water temperature conditions. In contrast, using stream network routing to accumulate air temperature values for the entire upstream drainage network of each reach would be more representative [35]. Until recently, this type of habitat characterization was globally unavailable to support high-resolution freshwater species distributions. A near-global dataset summarizing 324 layers describing climate, land cover, topography, geology, and soils was recently developed for upstream drainage network of HydroSHEDs river reaches [101]. For the US, a comparable dataset is the NHD plus system (1:24K scale), which provides climate, hydrology, and land-use information summarized within the entire upstream network above each stream reach. Many freshwater species distribution modeling efforts have utilized the NHDplus data (1:24k) and architecture

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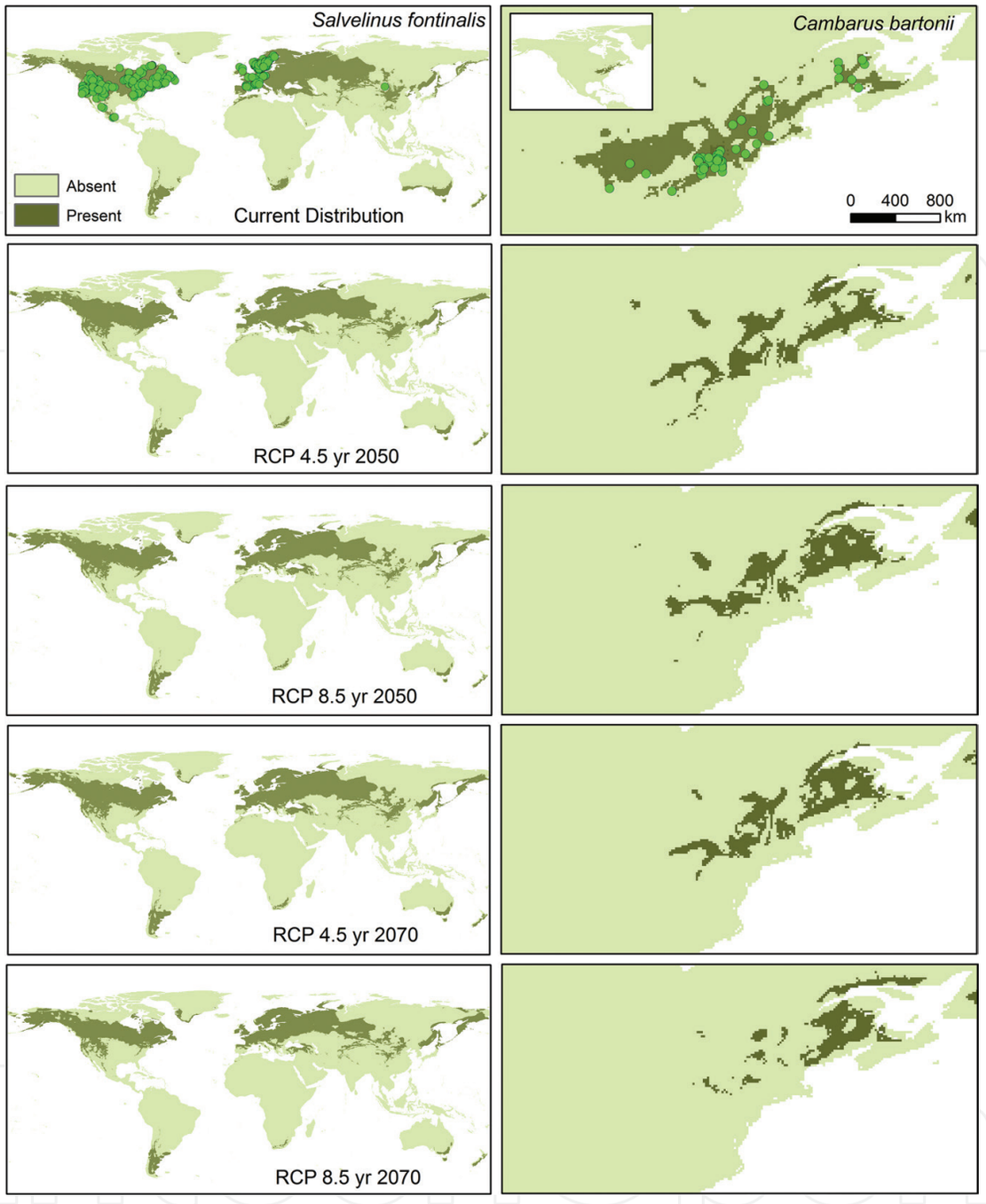


Figure 10. Life map projections of Brook Trout (*Salvelinus fontinalis*) and Appalachian Brook Crayfish (*Cambarus bartonii*) (f-j) distributions for current conditions and future climate projections for 2050 and 2070 under low (4.5 W/m^2) and high (8.5 W/m^2) IPCC representative concentration pathways (RCPs) for radiative forcing levels related to projected greenhouse gas emissions scenarios. Green points represent GBIF occurrences.

because of topological connectivity and habitat predictors offered by the resource [102–107] (**Figure 11**). Although NHDplus is a convenient database to support freshwater species distribution modeling, it does not adequately represent 1st order streams, the majority of which provide habitat for freshwater taxa (**Figure 11**). The NHD High resolution database (1:100k) represents smaller stream systems, but does not provide pre-summarized habitat information.

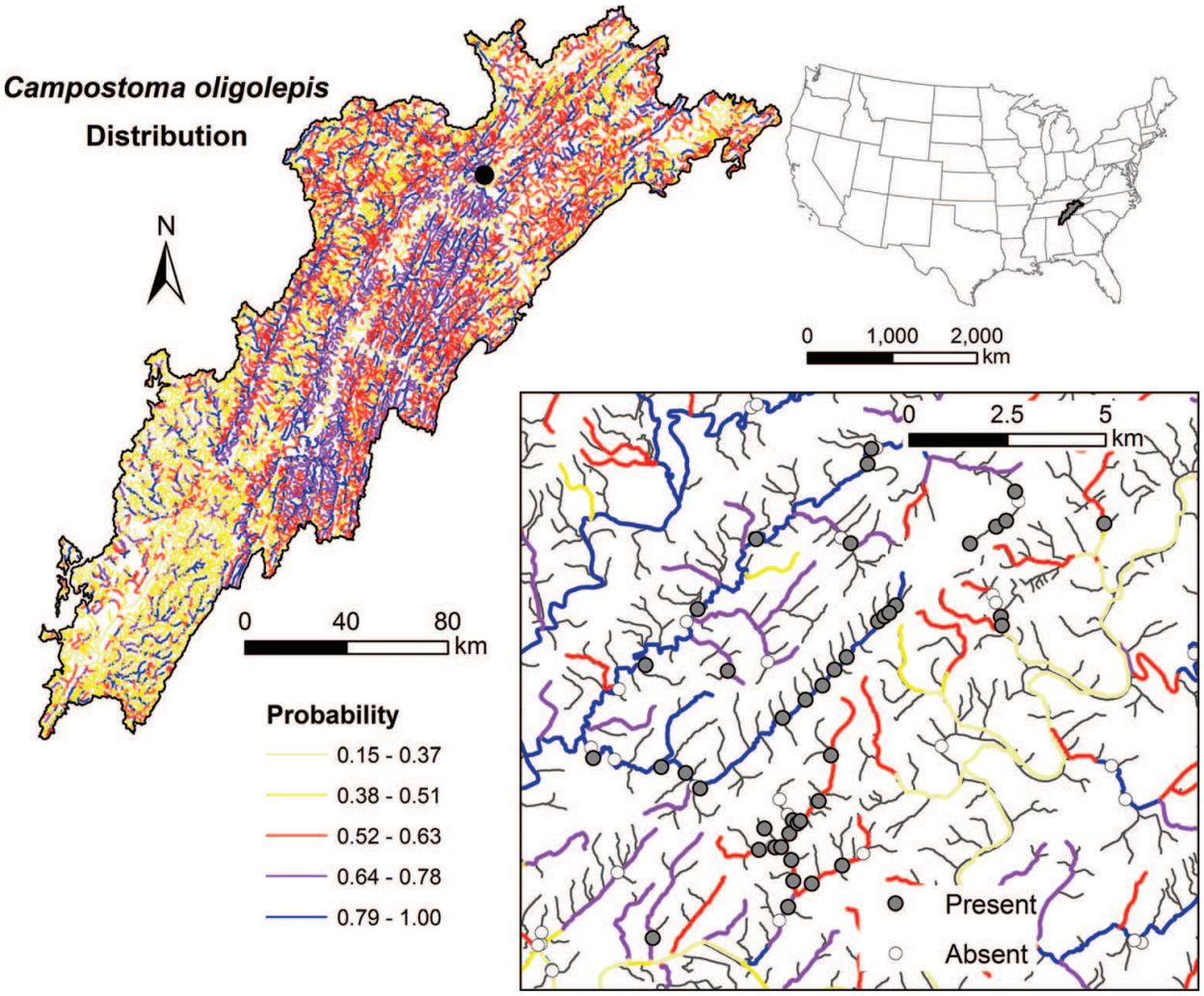


Figure 11. Species distribution model (SDM) developed for Largescale stoneroller (*Campostoma oligolepis*) in the Ridge and Valley and the Southern Appalachian Plateau Ecoregions of the Tennessee River Basin, USA. SDMs are generated for NHDPlus (1:100k) stream reaches and do not account for occurrences in NHD High-resolution stream reaches (smaller gray lines).

For this reason, other studies have developed their own reach datasets with accumulated habitat variables to support freshwater SDMs at resolution comparable to the NHD high-resolution dataset [108].

3.3. Global trends to support freshwater conservation

Mapping species distributions is considered important for conservation efforts because it increases understanding of the spatial patterns of endemism and vulnerability. Species mapping may be conducted along with an inventory of current and future landscape-scale anthropogenic stressors. Understanding the global extent of freshwater habitat alteration is important to prioritize areas for protection and restoration while finding global development pathways that balance human demands (e.g., dam construction) with freshwater ecosystem needs [109]; however, a key challenge to mapping freshwater habitat alteration is lack of

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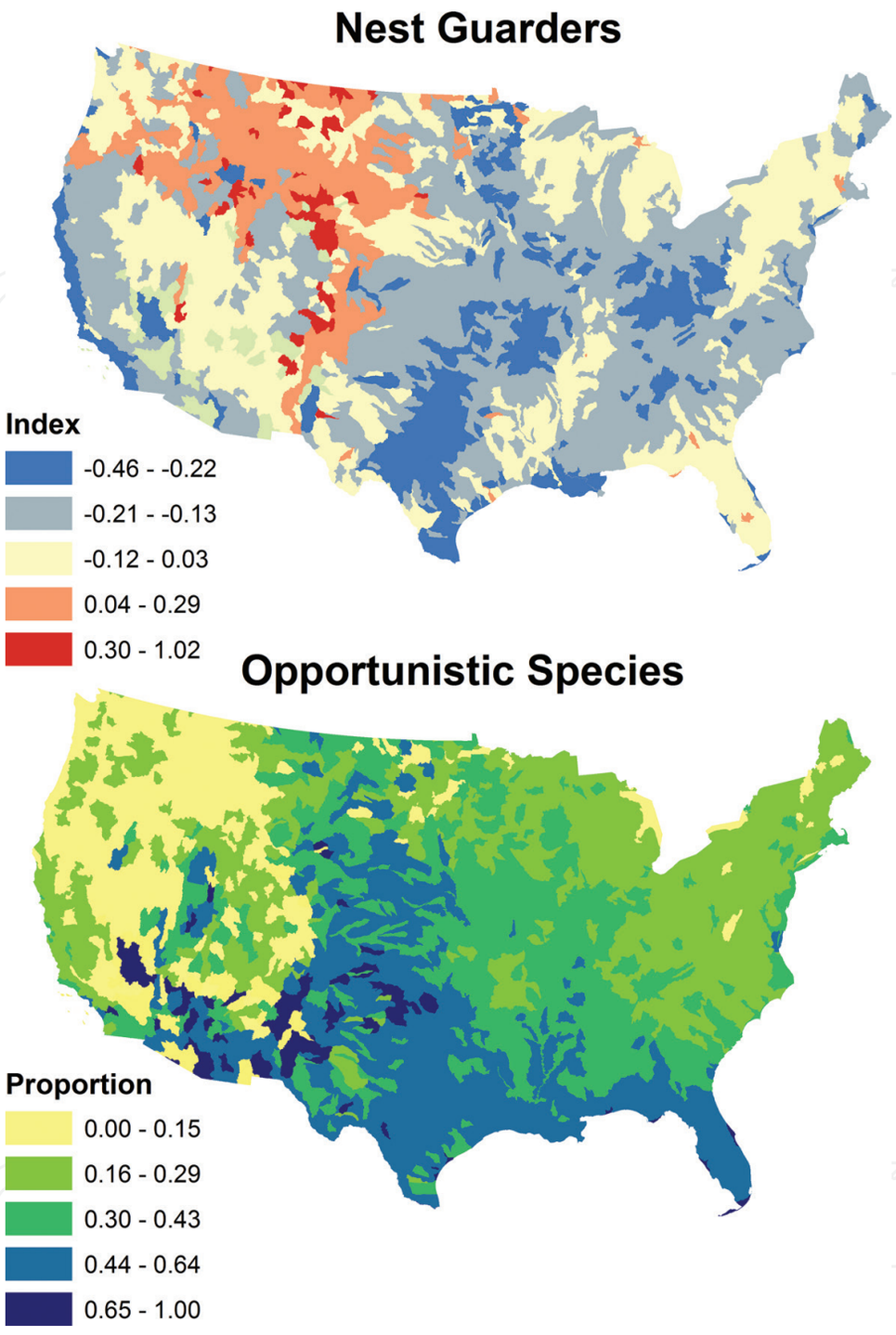


Figure 12. Two examples of species trait biogeography maps for US fish species. Pools of species within watersheds are summarized by their trait values, e.g. averages (nest guarder index) or by proportions of species possessing a trait or having a life history strategy (proportion of opportunistic species). Data from [116].

understanding about how anthropogenic activities propagate impacts in freshwater environments. Freshwaters are influenced by upstream drainage networks, the surrounding landscape, and hence, are recipients of upstream land activities, all of which creates a challenge in modeling, mapping, and understanding conservation challenges [6].

Recently, much progress has been made in understanding the extent and current state of global freshwater habitat alteration due to dam construction and extractive uses of water. Flow regulation and fragmentation were first examined for global large river systems by assessing the percentage of annual runoff captured by reservoirs and the longest mileage of rivers running unobstructed within each basin [110]. The authors found that over half of all large basins in the world are affected by dam fragmentation and/or regulation. Subsequently, reference [111] examined global river flow alterations by using a global water model, WaterGAP, to simulate the effects of reservoirs and withdrawals on river discharges at the 0.5° cell resolution. These were important studies, but properly assessing global impacts of dams and reservoirs required spatially explicit analysis in river networks, which entailed better representation of reservoirs in relation to hydrographic features [11]. The latest estimate suggests that 575,900 river kilometers or 7.6% of the world's rivers have flows regulated by reservoirs [11]. All the above studies provided relatively simplistic indicators of impacts from dams on river environments, which may not translate into predictions of potential biodiversity impacts [109]. In response, Grill et al. [109] developed novel indicators, a river fragmentation index and river regulation index, to examine holistic impacts of dams on major basins of the world currently and planned in the future. Grill et al. [109] concluded that 48% of global river volume is severely impacted by reservoirs and that number would increase to 93% if all dams planned and under construction are completed. Other approaches to quantify widespread anthropogenic alterations to aquatic landscapes also includes historical spatial inventories of waterbodies and habitat loss (e.g., [112])

Examining observed or potential responses of species to environmental change through the lens of species traits provides a mechanism to link species conservation needs to habitat alteration [113, 114]. Species traits are characteristics that describe the life history, ecology, and behavior of organisms. As the name suggests, the field of trait biogeography links species trait values with their spatial distributions [115, 116] (**Figure 12**). This provides a powerful tool to assess or predict individual, community, or regional species pool responses to habitat alterations. For example, by synthesizing global dam occurrences and fish traits in freshwater ecoregions, several fish taxa that were at high risk of species loss could be identified [69]. Several databases are available that provide rich information on species traits. For example, FishBase provides information on taxonomy, conservation status, biology, trophic ecology, and life history for >33,000 freshwater and marine fish species [67]. For North America, the Fish Traits database provides life history information, trophic attributes, reproductive ecology, habitat associations, and salinity/temperature information for >800 native and exotic freshwater fish species [113].

4. Conclusions and implications for biodiversity conservation

Recent developments in global freshwater habitat and biodiversity mapping products (and the rate at which they are updated) is encouraging for future conservation efforts. Assessing the conservation status of species and prioritizing areas of the globe for protection will continue to rely on spatially comprehensive and contiguous inventories of habitats, the biota they support, and evaluation of the degree of alteration at progressively higher spatial resolutions.

Metrics are needed that translate anthropogenic stressors into meaningful measures of global habitat alterations in to freshwater systems. Depicting these relationships is challenging for freshwater ecosystems because they are inherently tied to upstream landscape processes. In turn, the field of trait biogeography shows promise in providing a predictive template to convert habitat alterations into specific biodiversity concerns.

While many nations have their own freshwater mapping initiatives conducted at relatively high resolutions (e.g., the US's NHD and NatureServe projects), many underdeveloped nations experiencing intense pressures from development (e.g., Brazil) are likely to rely on external globally-derived products to inform conservation efforts. Even so, local conservation efforts require more spatial fidelity to guide future development pathways. In particular, the Amazon basin is experiencing rapid hydropower development without proper knowledge of the full diversity and geography of fish, invertebrates, and amphibians, or the strategies needed to prevent extinction of these organisms during energy expansion [72]. The development and justification of global reserves for biodiversity conservation will also be contingent upon the accuracy and resolution of aquatic habitats and the organisms they support. New advances in our observation of earth (e.g. through remote sensing), provide opportunities for filling some of these gaps; however, understanding global biodiversity patterns at high resolutions will require exploring local knowledge bases and building predictive models before they disappear.

Acknowledgements

We thank the countless individuals who have recorded observations of species for hundreds of years and those who make spatial data available to support applications in biogeography. Special thanks to Esther Parish for providing comments on earlier versions of this manuscript. This work was funded by the U.S. Department of Energy, Office of Energy Efficiency & Renewable Energy, Water Power Technologies Office and by program development funds provided by the Climate Change Science Institute at Oak Ridge National Laboratory.

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