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Forest-Associated Fishes of the Conterminous United States

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Abstract: Freshwaters are important, interconnected, and imperiled. Aquatic ecosystems, including freshwater fishes, are closely tied to the terrestrial ecosystems they are embedded within, yet available spatially explicit datasets have been underutilized to determine associations between freshwater fishes and forested areas. Here, we determined the spatial co-occurrence between freshwater fish distributions and forests within 2129 watersheds of the conterminous United States. We identified 21% of freshwater fishes as associated with forested areas, and 2% as strictly present only in highly forested areas (75–100% forested). The northern coasts and southeast regions, both heavily forested, showed the largest numbers of forest-associated fishes in highly forested areas and fish species richness. Fish associated with low-forested areas occurred in the southwest and central plains. Imperiled fishes were relatively evenly distributed among percent forest categories, which was distinctly different from patterns for all fishes. The identification of forest-associated fishes provides insights regarding species-specific landscape contexts. Determining these large-scale patterns of freshwater biodiversity is necessary for conservation planning at regional levels, especially in highly impacted freshwater ecosystems.

Keywords: freshwater fish; fish biodiversity; forests; fish distribution

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1. Introduction

Globally, freshwater aquatic biodiversity is declining at rates that exceed either marine or terrestrial ecosystems, and freshwater fish experienced the highest extinction rate of the 20th century [1–3]. Declines reflect a nexus of threats to freshwater ecosystems including human consumption of water for municipal uses and agriculture, contamination of water sources, hydroelectricity development, and altered precipitation patterns reflecting more extreme events linked to climate change [2,4–6]. Recognition of the vulnerability and losses experienced in both freshwater and inland waters has led to global calls for their protection (e.g., Target 11—Convention on Biological Diversity, Strategic Plan for Biodiversity (2011–2020) [7]). However, the implementation of science-driven freshwater protections are inconsistent at best, often reflecting a lack of comprehensive understanding of longitudinal and lateral connectivity inherent in freshwater systems, species-specific needs of resident or mobile aquatic biota, as well as uneven political implementation and conservation prioritization [4,8,9].

In the United States, freshwater protections are often associated with land ownership, which is linked to land management rather than to multi-ownership watershed-scale management. For example, watershed-scale management implies coordination in applications and protections throughout a system. In practice, freshwater protections are pragmatic, reflecting, for example, the application of different standards applied to commercially owned and managed forested lands compared with agricultural and residential areas that may all occur in the same watershed [10,11]. At regional or local scales, a mosaic of riparian protections is present, reflecting differing local, state, and federal policies for different land uses and ownerships that follow the ribbon of the river network [10,11]. These efforts can overlap, or they can leave gaps leading to a lack of coordinated work in the protection of continuous stretches of freshwater for aquatic ecosystems [12].

Targeted national-scale protections in the U.S. that focus on freshwater are usually designed for a specific issue and may not provide coordinated protection when implemented (examples of relevant federal laws in United States include the Clean Water Act, Weeks Act, Safe Drinking Water Act, Forest Practices Act, National Environmental Policy, Wild and Scenic Rivers Act, and the Endangered Species Act) [13]. However, some regional land management plans by federal agencies, such as the USDA Forest Service in the Pacific Northwest, have shifted to focus on restoration of freshwater areas through deliberate consideration of watershed processes, resulting in established riparian protections and a more holistic approach to management [14]. One missing element that could contribute to more comprehensive and consistent freshwater protections at the federal scale is a consistent framework from which to represent aquatic biodiversity generally, and fishes in particular.

In order to develop well-informed decisions for biodiversity conservation, it is essential to use detailed and scale-specific datasets that inform our understanding of how distribution patterns of species interact with one another [15–17]. Here, we focused on native freshwater fishes in the conterminous U.S., exploring their patterns of biodiversity with respect to forested watersheds. Our focus on fishes and forests reflects strong management interest at state, regional, and national levels in their recovery and conservation as demonstrated by the listing of many fish as imperiled under the Endangered Species Act. Associating fish with forested ecosystems at a watershed-scale is important to inform current resource use, make restoration decisions, and for future forecasting [18,19].

Methods for establishing habitat associations (in this case between forests and fish) vary widely across taxa. For fishes, primary habitat estimates have been made via field expertise or extensive physiological research [20–22]. Habitat associations are often established at the stream reach level in the field (e.g., [23,24]). At larger geographic extents, expert opinion and models based on physiological limits or habitat preferences are common approaches [25,26].

There are few large-scale, multi-species analyses of North American fish-habitat associations. The objective of this paper was to fill that gap by finding associations between fish species and forested areas. Therefore, we analyzed the overlap of fish distribution and the amount of forest in watershed units in the conterminous United States. This approach allowed us to determine which fish species are associated with one of four categories of forested area: least forested (0–25% forested), low forested (26–50% forested), moderately forested (51–75% forested), and highly forested (76–100% forested). We were able to look at how many species had less than 25% of the spatial extent of their distribution in each of the above categories, and how many species had more than 25%, 50%, and 75% of their distribution in each forested category.

2. Materials and Methods

2.1. Datasets

Hydrologic units. The overall extent of our study is the watersheds of the conterminous United States. Fish distributions and forested areas datasets were attributed to watersheds at the 8th field hydrologic unit scale defined by the U.S. Geological Survey (HUC8; https://water.usgs.gov/GIS/huc.html, accessed on 3 September 2020). We identified 2129 HUC8s within the conterminous United States, which ranged between 184 and 84,708 km^2 with a median size of 3361 km^2. The smallest HUC8s were generally associated with underlying terrain rather than partial HUC8s bisected by national borders. We chose this scale partly because of data availability, but also because evaluating fish-habitat associations at the HUC8 scale has been completed in a variety of other studies and applications (i.e., [27–29]). Further, HUC8s are designed to be relatively uniform in discharge area, although the spatial context of where a watershed is located (i.e., in the larger Mississippi River Watershed compared with an isolated HUC8 unit in the Oregon Great Basin) likely influences biodiversity [30,31].

Freshwater fish biodiversity. We classified fish species richness as the number of native fish species documented in each HUC8. Fish distributions were developed by NatureServe from an extensive review that included published literature, museum records, and collections archives [32]. To consistently identify fish species and calculate species richness, we merged all subspecies and populations into species-specific designations. When merged, the dataset contained 905 species of native freshwater fishes for the conterminous United States (Figure 1). NatureServe mapped distributions to HUC8 units, with 38 HUC8 units not containing documented freshwater fishes. These fishless units are primarily located in the desert southwest, and many have intermittent water flow. Of the remaining 2091 HUC8 units, the median number of freshwater fish species present was 27, with 166 as the largest number found at Pickwick Lake, in Mississippi, Alabama, and Tennessee.

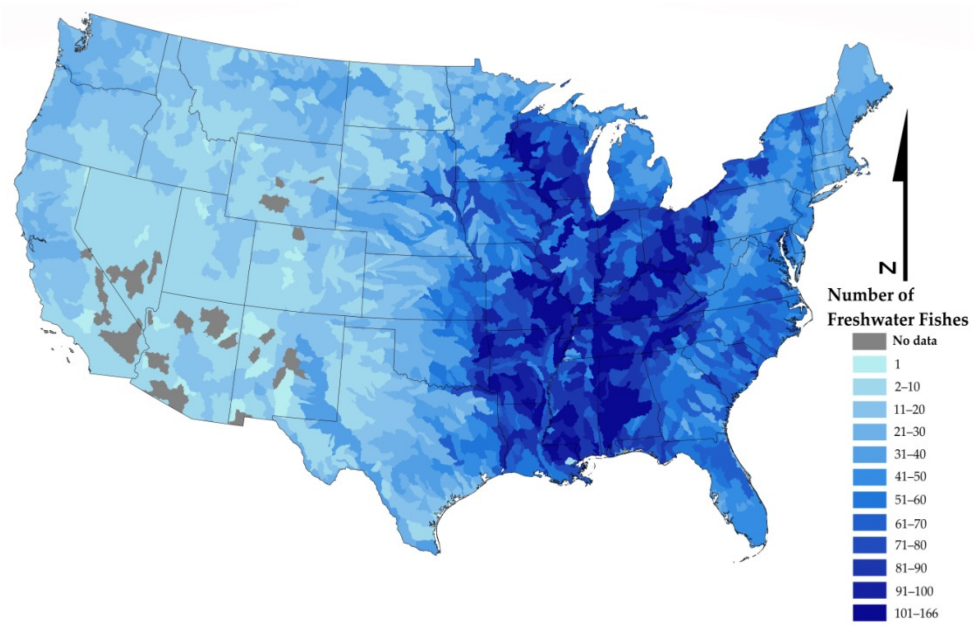

Figure 1. Number of freshwater fish in each HUC8 of the conterminous United States, including watersheds that did not contain information about the presence of freshwater fishes (grey).

Federally listed freshwater fishes. Federally listed freshwater fishes were identified by NatureServe through literature review and mapped to HUC8 units. This dataset included species that are federally listed under the Endangered Species Act as endangered or threatened, proposed endangered or threatened, candidate, species of concern, and listed threatened because of similarity of appearance to another species. For this analysis, we used the data at the level of species, populations, and subspecies listed in any of the federal designations above because this accurately represents the spatial extent of listed populations and subspecies. We analyzed 167 at-risk taxa (Figure 2), with imperiled fish ranging up to 9 per HUC8 unit.

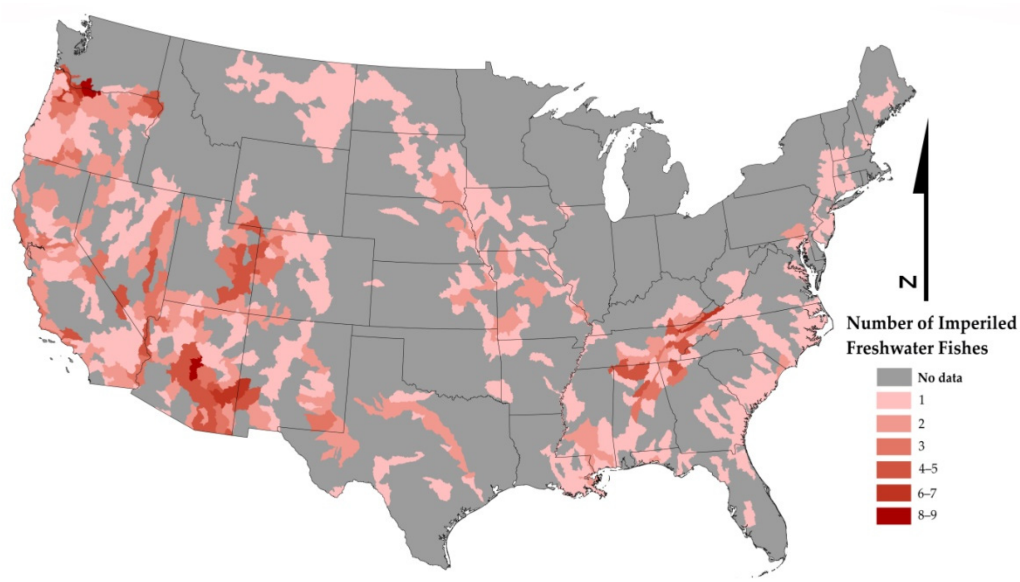

Figure 2. Number of endangered fishes per HUC8 of the conterminous United States, based on the NatureServe dataset. This dataset only includes HUC8s where endangered fish are recorded, and HUC8s with no records of imperiled fish are displayed as "no data".

Forested land. The area of each HUC8 categorized with forested land was calculated from a baseline forest raster for the conterminous U.S. This raster was generated by harmonizing a map of the land base [33] with land use maps from the National Land Cover Dataset series [34–37] according to the methods of Brooks et al. [38]. We constrained statewide forest areas to match tabulated 2016–2017 statewide total forest areas (Figure 3) as defined by the Resource Planning Act [39]. The area of each HUC8 categorized as forested was converted into a percent of the watershed area to standardize analysis across watersheds of varying sizes. For each HUC8, we assigned categories of percent forested area. Each HUC8 was classed as least forested (0–25%), low forested (26–50%), moderately forested (51–75%), or highly forested (76–100%) (Figure 3, Appendix A).

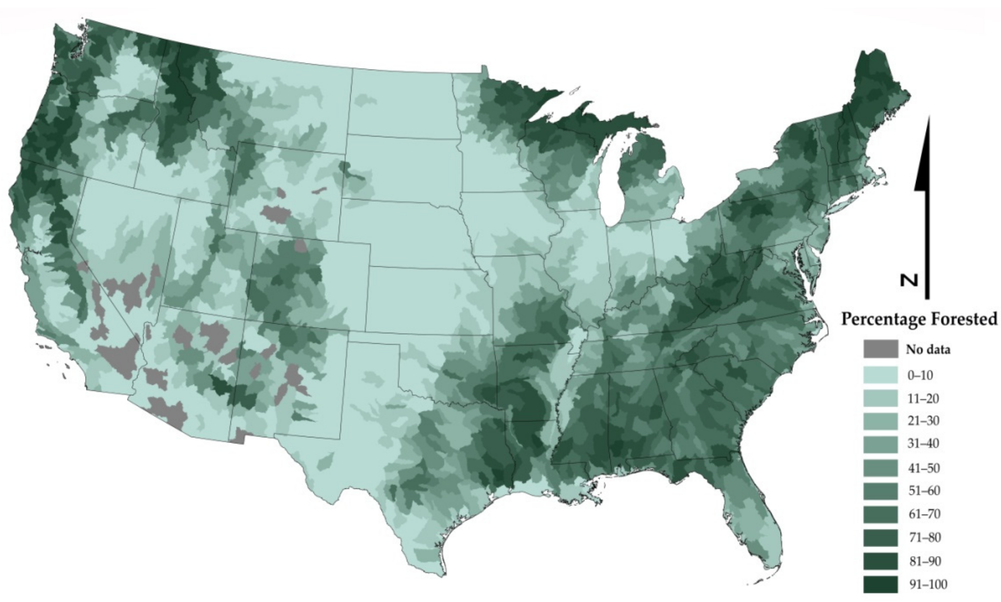

Figure 3. Percentage forested of each HUC8 unit in the conterminous United States.

2.2. Analysis

We assessed the degree of overlap between forested area data, the USDA Forest Service, and NatureServe fish distributions (all fish, and federally listed taxa). NatureServe provided us with a list of HUC8 units where each fish species lives, and USDA Forest Service a percent of the HUC8 unit that is classed as forested. For these HUC8 units, the number of HUC8s in each forested category was summed. The proportion of HUC8s in each forested category was calculated, then scaled to the percent of HUCs in each category (for a species-specific example, see Appendix B). We summarized fish species counts at different forested levels based on 25% increments. This selection of increments is pragmatic and reflects the complexity of both the fish and forest datasets across the large and varied landscape of the conterminous United States. Thus, we were able to meaningfully differentiate between watershed-scale combinations of forest and fish biodiversity at a large spatial extent. For example, all fishes whose distribution includes at least 25% of HUC8s with more than 25% forested area (summing forest category 25–50%, 51–75%, and 76–100% were identified. Similarly, all fishes whose distribution included at least 50% of HUC8s with more than 50% forested area (now summing forest category 51–75% and 76–100%) were identified. Likewise, those fishes whose distribution included at least 75% of HUC8′s with more than 75% forested area were identified.

3. Results

3.1. All Freshwater Fishes

Fish spatial distribution sizes varied from a single HUC8 (71 species) to 1125 HUC8s (1 species), with a median of 17 HUCS (11 species (see Supplementary Materials)). Many species (n = 282) had distributions between two and ten HUC8s, but most (82%) included fewer than 150 HUC8s. The ten fish species with the widest distributions encompassed between 782 and 1125 HUC8s (Table 1).

Table 1. The ten species of freshwater fish of the conterminous United States with the largest geographic distributions.

Scientific Name	Common Name	Number of HUC8s in the Fishes′ Distribution	% of Fishes′ Distribution in HUCs 25–50% Forested	% of Fishes′ Distribution in HUCs 25–75% Forested	% of Fishes′ Distribution in HUCs 25–100% Forested
Lepomis cyanellus	Green Sunfish	782	52	33	12
Catostomus commersonii	White Sucker	805	53	35	14
Semotilus atromaculatus	Creek Chub	824	61	44	17
Notemigonus crysoleucas	Golden Shiner	864	68	47	15
Lepomis macrochirus	Bluegill	879	62	41	14
Micropterus salmoides	Largemouth Bass	907	65	42	14
Ameiurus melas	Black Bullhead	999	43	25	9
Dorosoma cepedianum	American Gizzard Shad	1023	55	33	9
Ameiurus natalis	Yellow Bullhead	1054	58	38	12
Ictalurus punctatus	Channel Catfish	1125	45	28	10

For the forest-associated fish species, we are primarily presenting three combinations: the species that have more than 25% (26–100%) of their distribution in the low forested category (26–50% forested), the species that have more than 50% (51–100%) of their distribution in the moderately forested category (51–75% forested), and the group of species that have more than 75% (75–100%) of their distribution in the highly forested category (76–100% forested). Results in these three categories are highlighted in bold in Table 2.

Of the 905 species of freshwater fish in the conterminous United States, 9% (78 species) of fish have at least 25% of their distribution that is 26–50% forested; 21% (193 species) of fish have more than half their total distribution in HUC8s classified as 51–75% forested, and; 2% (17 species) of fish species have 75 percent or more of their distribution in HUC8s over 75% forested (Table 2). The largest number of forest-associated fish species were found when 0–25% of the fish species' distribution occurred in watersheds that are more than 75% forested (Table 2). The average number of species per HUC8 unit was six, where more than 25% (26–100%) of each fishes' distribution was in HUC8s 26–50% forested. The average number of species per HUC8 when more than 75% of the fishes' distribution was more than 75% forested was 0.02 (see Supplementary Materials).

Table 2. Number of native freshwater fish summed across different categories of forested area found in different percentages of fish distribution. The three categories of forest-associated fish highlighted in the rest of the paper are indicated in bold.

Percent Forested/Forested Area Category	Percent of Fishes' Distribution			
	0–25%	**26–100%**	**50–100%**	**75–100%**
0–25%/Least	583	91	198	679
26–50%/Low	171	**78**	201	175
51–75%/Moderately	63	166	**193**	34
76–100%/Highly	88	570	313	**17**
TOTAL # FISH SPECIES	905	905	905	905

Freshwater fishes with >25% of their distribution associated with low forested HUC8s (26–50% forested) tended to be found in the upper Mississippi River drainage (Figure 4). HUC8s with many forest-associated species were concentrated in the south-eastern United States, especially in the Lower Mississippi basin (Figure 4). There was an additional group of forest-associated fish along the Pacific coast (Figure 4). Fishes with a strict association of >75% of their distribution in highly forested HUCs (>75% forested) were uncommon and not associated with a specific region of the United States (Figure 4, Table 1).

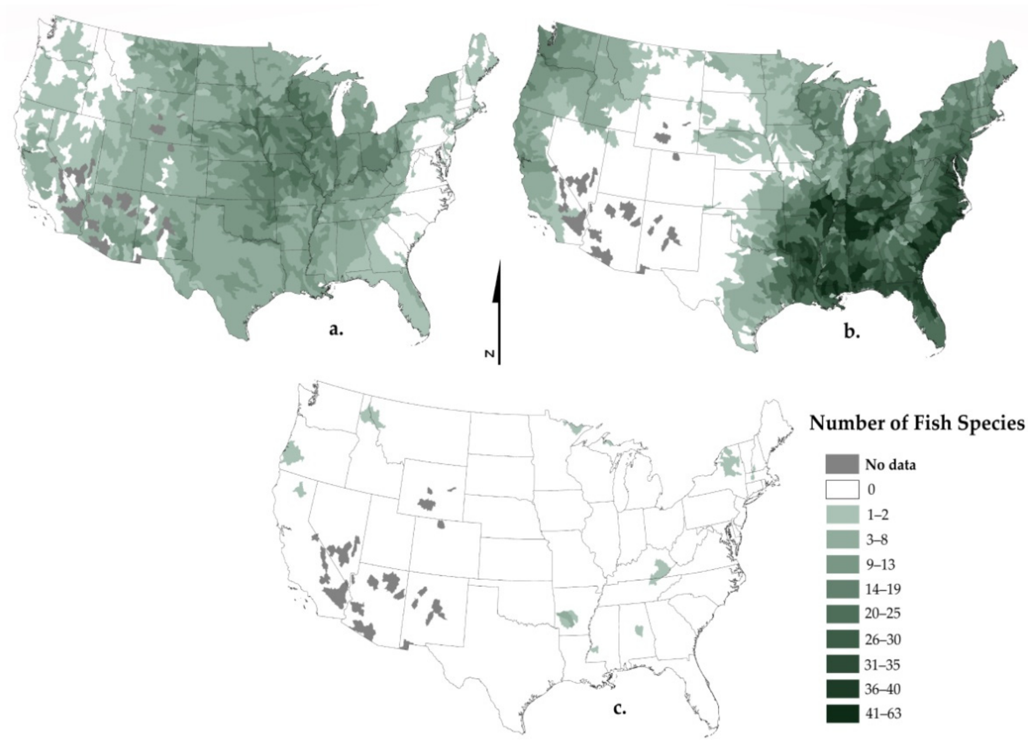

Figure 4. (**a**) Fish species richness associated with low-forested areas (HUC8s for whom more than one quarter of their distribution is associated with 26–50% forested area). (**b**) Fish species richness associated with forested areas (HUC8s for whom more than half of their distribution occurs in HUCs with 51–75% forested area). (**c**). Fish species richness associated with highly forested areas (HUC8s that have more than three quarters of their distribution in HUC8s with 76–100% forested area).

The fishes with the strictest forest-association (75% of the fishes' distribution is more than 75% forested) were scattered across the United States, and there were only 17 species in this category (Table 3). Fishes associated with more forested habitat (over 50% forested) mostly had a wide range of amount of forest in their distribution (Table 3). Only 17 species of fishes were identified with over 75% of their distribution being more than 75% forested (Table 3).

Table 3. List of freshwater fishes of the conterminous United States with more than 75% of their distribution categorized as more than 75% (highly) forested.

Scientific Name	Common Name
Etheostoma spilotum	Kentucky arrow darter
Catostomus utawana	Summer Sucker
Cottus schitsuumsh	Cedar Sculpin
Ptychocheilus umpquae	Umpqua Pikeminnow
Rhinichthys evermanni	Umpqua Dace
Coregonus hubbsi	Ives Lake Cisco
Coregonus nipigon	Nipigon Cisco
Cottus asperrimus	Rough Sculpin
Etheostoma clinton	Beaded Darter
Etheostoma lemniscatum	Tuxedo Darter
Etheostoma pallididorsum	Paleback Darter
Etheostoma rubrum	Bayou Darter
Etheostoma sp. 3	Darter #3
Noturus lachneri	Ouachita Madtom
Noturus taylori	Caddo Madtom
Percina brucethompsoni	Madtom
Salvelinus agassizii	Silver Trout

3.2. Imperiled Freshwater Fishes

Of the 118 species of federally imperiled freshwater fishes in the conterminous United States, 14% (16 species) of imperiled fish had more than 26% of their distribution that is 26–50% forested; 8% (10 species) had more than half their total distribution that is 51–75% forested and 3% (4 species) had 75 percent or more of their distribution that is over 76% forested (Table 4). Imperiled freshwater fishes with 25–50% of their distribution associated with low forested HUC8s (26–50% forested) are clustered in the Southwestern United States (Figure 5). Of the fish that are associated with 25–50% forested, 16 species have 25–100% of their distribution in that category, and 11 each have over 50% and over 75% of their distribution in this category (Tables 4 and 5). HUC8 units with many imperiled forest-associated species are concentrated in the Southeastern United States and along the Pacific coast (Figure 5). Imperiled fish with >75% of their distribution found in highly forested HUCs (>75% forested) were often found in the Ohio River subbasin of the Mississippi River (Figure 5).

Table 4. Number of imperiled freshwater fishes in each combination of: (a) percent of the distribution of each fish species and; (b) how much of that distribution was classified as forested. Bolded numbers are relationships discussed in the text.

	Percent of Fishes' Distribution			
Percent Forested	**0–25%**	**25–100%**	**50–100%**	**75–100%**
0–25%-Least	60	34	63	99
25–50%-Low	15	**16**	11	11
50–75%-Moderately	10	9	**10**	4
75–100%-Highly forested	33	59	34	**4**
Total number of fishes	118	118	118	118

Figure 5. (**a**) Imperiled fishes associated with low-forested areas (number of endangered freshwater fishes in each HUC8 that have more than one quarter of their distribution is in watersheds with 26–50% forested area). (**b**) Imperiled fishes associated with forested areas (number of endangered freshwater fishes in each HUC8 that have more than half of their distribution in watersheds with 51–75% forested area). (**c**) Imperiled fishes strictly associated with highly forested conditions (number of endangered freshwater fishes in HUC8s that have more than three quarters of their distribution in HUC8s with 76–100% forested area). This dataset only includes HUC8s where endangered fish are recorded, and HUC8s without imperiled fish are recorded as "no data".

Table 5. Species list of imperiled fishes in three different forested conditions. Seventeen fish species have more than 25% of their distribution in low-forested areas (26–50% forested); ten fish species have more than 50% of their distribution in moderately forested areas (51–75%); and four fish species have more than 75% of their distribution in highly forested areas (76–100%).

Scientific Name	Common Name	Proportion of Distribution by Percentage of Forested Area		
		26–50%	51–75%	76–100%
Scaphirhynchus albus	Pallid Sturgeon	X		
Gila elegans	Bonytail	X		
Gila intermedia	Gila Chub	X		
Gila cypha	Humpback Chub	X		
Gila nigrescens	Chihuahua Chub	X		
Gila seminuda	Virgin River Chub	X		
Meda fulgida	Spikedace	X		
Moapa coriacea	Moapa Dace	X		
Notropis oxyrhynchus	Sharpnose Shiner	X		
Notropis simus	Bluntnose Shiner	X		
Hybognathus amarus	Rio Grande Silvery Minnow	X		
Chasmistes cujus	Cui-ui	X		
Xyrauchen texanus	Razorback Sucker	X		
Oncorhynchus apache	Apache Trout	X		
Oncorhynchus gilae	Gila Trout	X		
Empetrichthys latos	Pahrump Poolfish	X		
Acipenser brevirostrum	Shortnose Sturgeon		X	
Acipenser oxyrinchus	Gulf Sturgeon		X	

Table 5. *Cont.*

Scientific Name	Common Name	Proportion of Distribution by Percentage of Forested Area		
		26–50%	51–75%	76–100%
Chrosomus saylori	Laurel Dace		X	
Erimonax monachus	Spotfin Chub		X	
Erimystax cahni	Slender Chub		X	
Noturus flavipinnis	Yellowfin Madtom		X	
Oncorhynchus keta	Chum Salmon		X	
Oncorhynchus tshawytscha	King Salmon		X	
Salvelinus confluentus	Bull Trout		X	
Percina tanasi	Snail Darter		X	
Crystallaria cincotta	Diamond Darter			X
Etheostoma lemniscatum	Tuxedo Darter			X
Etheostoma rubrum	Bayou Darter			X
Etheostoma susanae	Cumberland Darter			X

4. Discussion

The primary objective of our work was to understand linkages between fish species and different levels of forested area. Further, we were interested in where assemblages of these fish species are located, providing novel information to develop tools needed for the management of freshwater systems in a complex future [40,41]. Ideally, dependence of fish upon forested areas would be assessed by analyzing long time series of fish species richness and forested area data at fine spatial scales, while controlling for other potential agents of change. However, paired datasets of forested area and richness are rarely available for large geographic extents, particularly for sub-continental scales as were assessed in this study. Instead, most previous studies are constrained to either smaller geographic extents, to single species, or both (e.g., [27,30,42,43]). Given these constraints, we presented the most spatially resolute and coincident datasets of fish species richness and forested area available across the conterminous United States to assess forest association among fishes.

Given the strong linkages between terrestrial and freshwater ecosystems, understanding the association of fish with the amount of forested area in a watershed feeds directly into the ability to maintain functional systems [44,45]. Forested lowland and mountain ecosystems are the highest source area of renewable freshwater, providing 57% and 28% of total global runoff respectively as well as renewable water supplies to two-thirds of the world's population [5]. Forested areas contribute disproportionately to surface water yield within the conterminous United States [46]. Areas with higher forested area have been linked to higher fish biodiversity in neotropical environments, likely due to the diversity of habitats that can be developed and supported by forests [47]. The broad extent of our analysis across diverse ecoregions highlights the variation in patterns of association between forested area and freshwater fishes in the Unites States.

The conterminous United States has many ecoregions, and within each, disturbance has created a mosaic of forested area [48,49]. Because the maintenance of functional freshwaters is dependent on managing both the water and the surrounding terrestrial ecosystems, we documented the associations between fish species and amount of forested area [40,50]. Of the fish species that are associated with forests, most have a distribution primarily in the moderately forested watersheds. Intuitively, fish associated with moderate-to-high levels of forests are located in areas with large amounts of forest, and the reverse is also true. Imperiled fish are located mostly in biodiversity hotspots that are also areas with large amounts of land-use change [35,51]. The two fish datasets we analyzed here (all freshwater fishes and only imperiled freshwater fishes) demonstrated varying patterns of forest associations. Below, we discuss our findings separately because imperiled fishes are of particular interest to managers and the public.

4.1. All Freshwater Fishes

The overall patterns we observed in freshwater fishes of the United States were different for each forested category and fit with the conterminous biogeographic patterns of the United States. The arid southwest contained species associated with low-forested areas, whereas the coasts and southeast, heavily forested, contained many fishes associated with high levels of forested areas. Fishes associated with moderate levels of forested watersheds had most of their distribution in that category, whereas fishes inhabiting areas with either very high or very low-forested areas had varying associations.

The patterns we observed in the low forest-associated fishes are congruent with known patterns of specialization in desert fishes [52–54]. Low forest-associated fish had either very little (less than 25% of their distribution) or more than half of their distribution in areas with little forested area (see Figure 4). There were fewer fish species between these two extremes (Table 4). Spatially, there was a cluster of fishes associated with low-forested areas in the Upper Mississippi Basin, and few fishes on the coasts (Figure 4). This can be explained by observing the overlap between the large number of fishes in the watershed and the areas with little forested areas in the middle of the United States (see Figure 3).

Fishes with very large ranges were associated with low-forested areas. The ten species of freshwater fishes with the highest number of HUC8s units in their distributions were mostly catfishes and centrarchid fishes native to basins east of the Rocky Mountains (Table 1). These widespread fishes are economically and culturally important [55–58]. None of the fishes with large distributions had over 50% of their distribution in 25–75% forested or 25–100% forested HUCs. Of the ten species, all had over 25% of their distribution (mean 56% of distribution) in HUC8s classified as 25–50% forested, the lowest category of forest association.

The more forested-associated fishes were concentrated in the southeastern United States, a biodiversity hotspot, and along the coasts where there are many highly forested areas (Figure 4) [59,60]. There are fewer forest-associated fishes in the parts of the United States without extensive forested area (Figure 3).

Of the fish species identified as having more than 75% of their distribution in highly forested areas, most were small body fishes. Six of these species were darters living in the southeastern United States. There were three madtoms and two ciscos, with the rest scattered not only spatially but also across phylogenies. Generally, these species have small ranges (Appendix B), and they varied from newly named species to having been described over 100 years ago (e.g., *Salvelinus agassizii*, Garman, 1885).

4.2. Imperiled Freshwater Fishes

The ecology of the imperiled fishes explains many of the patterns we observed. For the fishes associated with low-forested areas, almost all of them were located in areas with dry conditions and little forested areas in the southwestern part of the United States (e.g., Gila Chub, Apache Trout). One species, the Pallid Sturgeon, lives in the Missouri and Mississippi River Basin, in areas that are primarily plains with little forested area. Percent of distribution for imperiled fishes was relatively evenly distributed among percent forest categories, whereas for all fishes in the conterminous United States there were distinct differences (Figures 4 and 5).

Imperiled fishes that are associated with both moderately and highly forested areas were primarily on the coasts and in the Southeastern United States (Figure 5). The imperiled fishes which were associated with highly forested conditions had a similar pattern to what is seen in all freshwater fishes. There were many imperiled species that have 25% of their distribution in highly forested areas, and very few species had the strictest classification (over 75% of their distribution being 75–100% forested). Imperiled fishes associated with forests (50–75% forested, with more than 50% of the fishes' distribution in that category) were concentrated on the coasts and in small rivers of the southeastern United States. Salmonid fishes dominated the forest-associated imperiled fishes in the Western states, whereas imperiled sturgeon species drove the patterns observed on the East coast. Many sturgeons are classified as megafauna, a group which is globally imperiled and declining [61–63]. The fishes distributed solely in freshwaters in the Eastern states are primarily chub, darters, and dace. Four species of fish were strictly associated with highly forested conditions. All these fishes are darters with restricted ranges in the eastern part of the United States. For example, only a single HUC8 had more than one species of fish for whom 75% of their distribution occurred in watersheds that were more than 75% forested.

Areas with low fish species richness can still be important in many ways, including their contributions to gamma diversity across geographic extents of different scales. For example, species in HUC8 units of low local richness can still contribute to overall richness if local richness includes endemic species not found elsewhere within conterminous United States.

Freshwater fishes are culturally, economically, and ecologically important parts of the systems within which they are embedded [64]. For example, a single fish species may be a keystone species [65,66], essential to energy transfer with a terrestrial system [67–69], or determine local economic success [9,56,70]. Recreational fishing is a multi-billion dollar industry in the conterminous United States [58,71–73], and fish caught by anglers are consumed regularly in many households [74,75]. Fishing is central to a variety of the cultures within the United States [76,77] and is an important part of individuals' identities [78,79]. This has been most studied in Indigenous people, for whom fish, fishing, and aquatic ecosystems provide a plethora of important features such as cultural connectivity, ceremonial uses, subsistence, education, and income [80–83].

Freshwater ecosystems are some of the most changed and exploited on earth [40,84]. Throughout the world, freshwaters provide critical ecosystem services including water for municipal and agricultural uses, flood control, toxin filtration, and groundwater recharge, among others [85–87]. Freshwater, and the biodiversity it supports, is a limited resource, constrained by the inter-annual patterns of the global water cycle, making freshwater ecosystems vulnerable to disturbance [6,88]. The interacting pressures of climate change, urbanization and other land use changes, introduction of species, and resource extraction are all forecast to increase in the future [4,89–92]. Given these pressures on freshwater ecosystems, managers need comprehensive and consistently derived data and tools to respond to often competing priorities and needs to identify areas that are important for maintaining fish biodiversity and imperiled species [93,94]. Reserves designed for protection of terrestrial resources sometimes do not fully protect freshwater ecosystems, and management needs to be flexible to human changes [12,50,95].

5. Conclusions

The objective of this paper was to find spatial associations between fish biodiversity and different levels of forested areas. We explored these patterns at a conterminous United States scale, which is unusual in this field. Our approach was to use four categories of forested watersheds: least forested (0–25% forested), low forested (26–50% forested), moderately forested (51–75% forested), and highly forested (76–100% forested), and associate these with the amount of the range of each fish species that fit the above category. We found that many fish species had more than 50% of their range in watersheds that are moderately forested (50–75%), and fewer fish species were associated with highly forested areas (75–100%). In general, we found fish species that are highly associated with forests were found in parts of the country with large amounts of forested areas and biodiversity hotspots. The spatial patterns of imperiled fishes' biodiversity indicate less direct linkages to forest area; rather, their distributions appear likely related to a combination of environmental stressors and habitat requirements.

Though the rich data sets we analyzed allow for many conclusions, there are also limitations related to the spatial grain of our analysis. The dataset from Nature Serve does not indicate how much of a HUC8 is within the fishes' distribution. Therefore, this analysis cannot evaluate how important specific HUCs, or their characteristics, are to freshwater fishes. Within our datasets, we could only determine the association of fish distribution with the total amount of forested area across each entire HUC8. The fish dataset was compiled by NatureServe by drawing from literature reviews, which may not be complete at larger or finer spatial extents [96,97]. Some fish distribution datasets are locally available at finer scales, e.g., HUC10 (watersheds) and HUC12 (subwatersheds), but not for the entire conterminous United States. We recommend further analyses at finer scales where such data exists.

Freshwater aquatic ecosystems are linked to each other and their accompanying terrestrial systems, but our analysis did not account for important flows of energy, populations, or water from one HUC8 to another [12,98,99]. The forested area dataset did not include stand age or reforestation history, which are important for many fish species [100,101]. Additionally, the forest dataset used in this study is based on a combination of modeled and direct estimators, with unknown errors. We recommend further investigation into the sensitivity of analyses results to data errors. Despite these limitations, our approach is valuable and can be applied at many extents and with other scales of data to fill in needed information gaps.

Given the importance of freshwaters, this study contributed needed information for future research and management. We identified patterns at a large spatial scale that are worthy of further study. The framework used here defined associations between fish species and levels of forested area consistently across a broad spatial extent, and it is one of many types of data that managers will need to face the current and future threats to freshwater species.

Supplementary Materials: The following are available at https://www.mdpi.com/article/10.3390/w13182528/s1, Table S1: List of native freshwater fishes of the conterminous United States (n = 906) including the total number of HUC8s in the distribution of the species, and what percentage of the range is (0–25% forested, 25–50% forested, 25–75% forested, and 25–100% forested).

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Data Availability Statement: The HUC8 watershed information is available at https://water.usgs.gov/GIS/huc.html, accessed on 3 September 2020. Please see [38,39] for the forest land use data sets used in this study. The baseline forest raster- and watershed-level maps are available upon request. The fish data was purchased from NatureServe by the Forest Service, and are proprietary data to that company.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

Table A1. Categories of how forested each HUC8 in the data set was sorted into.

Forested Land Percentage	Forested Category
0–25%	Least forested
26–50%	Low forested
51–75%	Moderately forested
76–100%	Highly forested

Table A2. Categories of fish species' distribution. The lowest category is below 25% forested for each forested category above. The other categories are above 25%, above 50%, and above 75% of the HUC8s being forested.

Area of Fish's Distribution within a Specific Forested Category	Category
0–25%	0–25
26–50%	26–100
51–75%	51–100
76–100%	76–100

Appendix B

As an example of how a single species' association with forests was calculated, the following data for White Sturgeon *Acipenser transmontanus* was taken from a NatureServe literature review and combined with Forest Service data on amount of forested land within each HUC8 [32].

Table A3. Single species example of how percent was calculated for different combinations of forested land area in the total distribution of an individual species. The top rows are a count of the number of HUC8s in the distribution of White Sturgeon *Acipenser transmontanus* that fall into the four forested categories. Below are the percent of the distribution in each forested category, and at the bottom, the "over" categories where 25, 50, and 75% distribution in forested was combined to make the "over 25", and the "over 50%" was found by combining 50 and 75%.

Species Name	Total HUC8s in Fish Distribution	# HUCs 0–25% Forested	# HUCs 26–50% Forested	# HUCs 51–75% Forested	# HUCs 76–100% Forested
Acipenser transmontanus	135	39	23	33	40
		% of fish distribution 0–25%	% of fish distribution 26–50%	% of fish distribution 51–75%	% of fish distribution 76–100%
		(100/135) × 39 = 29	(100/135) × 23 = 17	(100/135) × 33 = 24	(100/135) × 40 = 30
		% 0–25	% of fish distribution OVER 26%	% of fish distribution OVER 51%	% of fish distribution OVER 76%
		29	71	54	30
		(29)	(17 + 24 + 30)	(24 + 30)	(30)

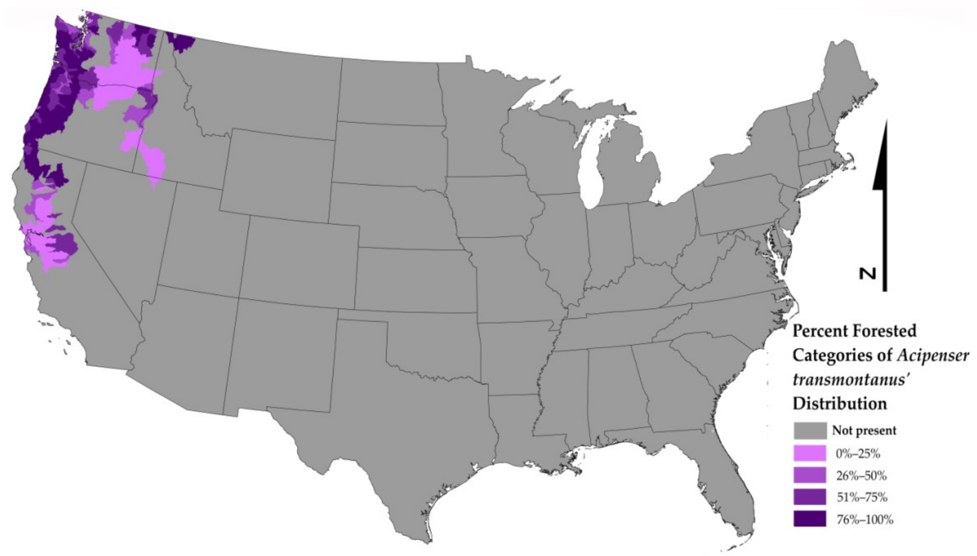

Figure A1. Range of White Sturgeon (*Acipencer transmontanus*) with the four levels of forested area of the HUC8 units. Of the 135 HUCs in the distribution, 39 HUCs are in the least forested category (0–25%), 23 in the low forested category (26–50%), 33 in the moderately forested category (51–75%), and 40 HUCs are in the highly forested category (76–100%).

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