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Assessing threats of non-native species to native freshwater biodiversity: Conservation priorities for the United States

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Abstract

Non-native species pose one of the greatest threats to native biodiversity, and can have severe negative impacts in freshwater ecosystems. Identifying regions of spatial overlap between high freshwater biodiversity and high invasion pressure may thus better inform the prioritization of freshwater conservation efforts. We employ geospatial analysis of species distribution data to investigate the potential threat of non-native species to aquatic animal taxa across the continental United States. We mapped non-native aquatic plant and animal species richness and cumulative invasion pressure to estimate overall negative impact associated with species introductions. These distributions were compared to distributions of native aquatic animal taxa derived from the International Union for the Conservation of Nature (IUCN) database. To identify hotspots of native biodiversity we mapped total species richness, number of threatened and endangered species, and a community index of species rarity calculated at the watershed scale. An overall priority index allowed identification of watersheds experiencing high pressure from non-native species and also exhibiting high native biodiversity conservation value. While priority regions are roughly consistent with previously reported prioritization maps for the US, we also recognize novel priority areas characterized by moderate-to-high native diversity but extremely high invasion pressure. We further compared priority areas with existing conservation protections as well as projected future threats associated with land use change. Our findings suggest that many regions of elevated freshwater biodiversity value are compromised by high invasion pressure, and are poorly safeguarded by existing conservation mechanisms and are likely to experience significant additional stresses in the future.

Keywords

Freshwater biodiversity; Priority mapping; Threatened and endangered species; Invasive species; Non-native species

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1. Introduction

Biodiversity is in decline globally, with little indication of improving trends despite broad international consensus on conservation needs (Ceballos et al., 2015; Pimm et al., 2014; Tittensor et al., 2014). This decline is associated with a variety of human drivers ranging from habitat fragmentation and degradation to overexploitation (Murphy and Romanuk, 2014; Tilman et al., 2017). With limited resources available, prioritization of conservation action has become a necessary component of biodiversity science (Tulloch et al., 2015). Due to the uneven spatial distribution of diversity and the drivers of decline, many researchers have focused efforts to map locations that may be especially vulnerable to diversity loss, at multiple spatial scales, across taxonomic groups, and over terrestrial, freshwater, and marine ecosystems (Brum et al., 2017; Collen et al., 2014; Dobson et al., 1997; Jenkins et al., 2013; Mokany et al., 2014; Selig et al., 2014). They have also adopted a variety of diversity metrics to assess vulnerability and determine conservation priority, including species range size and protection coverage (Jenkins et al., 2015a), threatened status (Wickham et al., 2013), and phylogenetic, taxonomic, and trait diversity (Brum et al., 2017; Moorhouse and Macdonald, 2015).

Such prioritization of conservation needs is acutely important for freshwater systems. These systems support a disproportionate share of global diversity; at the same time, the insular nature of freshwater habitat and growing demands by human populations for services derived from freshwater ecosystems suggest that concerted action will be required to prevent considerable future losses of freshwater biodiversity (Chester and Robson, 2013; Collen et al., 2014; Dudgeon, 2014; Garcia-Moreno et al., 2014). Freshwater diversity has generally been under-represented in efforts to map conservation priorities at broad spatial scales (Abell et al., 2011). A number of studies have identified priority regions for freshwater biodiversity conservation with particular emphasis on amphibian and fish taxa (Abell et al., 2011; Grenyer et al., 2006; Jenkins et al., 2015b; Wake and Vredenburg, 2008), but relatively few prioritization studies examine freshwater invertebrate or microbial diversity (Collen et al., 2014; Stomp et al., 2011).

Biological invasions have been implicated in the decline of biodiversity across virtually all ecological systems and taxonomic groups (Doherty et al., 2016; Galiana et al., 2014; Vila et al., 2011), and remain the most common threat associated with the extinction of vertebrate species worldwide (Bellard et al., 2016a). But freshwater systems may, in fact, be especially susceptible to the negative impacts of species introductions (Moorhouse and Macdonald, 2015). Indeed, invasive species have been associated with decline in diversity of freshwater shrimps (De Grave et al., 2015), crayfish (Richman et al., 2015), mussels (Haag and Williams, 2013), and fish (Liu et al., 2017) at both national and global scales. The importance of non-native species as a driver of native diversity loss has led to an increased interest in mapping non-native diversity. The availability of data on the distribution of non-native species provides opportunity to ascertain spatially explicit areas of high native biodiversity experiencing anthropogenic stress of known relevance to diversity decline. Such overlay analysis has been employed to inform conservation prioritization based on broad suites of factors associated with human impact (Selig et al., 2014); only few studies, however, have explored this approach to specifically identify potential conflict

areas between native and non-native biodiversity (Carpio et al., 2017; Padalia and Bahuguna, 2017; Thalmann et al., 2015), and these mapping efforts have rarely targeted freshwater systems (Dawson et al., 2017; Dyer et al., 2017; Stohlgren et al., 2006).

Here we employ geospatial analyses to determine conservation priorities for native freshwater biodiversity across five taxonomic groups, by better understanding the distribution of pressures from non-native aquatic species (NAS) on rare and imperiled native species across the continental US (CONUS). We describe the spatial distributions of both native and non-native diversity across the CONUS using distribution information drawn from multiple publicly available databases and develop a prioritization metric based on native species richness, threatened and endangered status, and rarity, as well an index designed to estimate cumulative stress associated with NAS at the watershed scale. We used prioritization scores to identify regions exhibiting overlap of elevated native biodiversity value and high levels of NAS colonization. In keeping with a number of recent studies highlighting the inadequacy of existing protected lands to preserve vulnerable bio-diversity (Brum et al., 2017; Jenkins et al., 2015b; Quan et al., 2017), we also explored the degree to which our priority regions overlapped known conservation areas in the US. To assess potential for multiple and cumulative future threats to biodiversity in these priority areas we further investigated trends in projected land use change, as increases in urbanization are likely to bring not only increased pressure from non-native species but also additional anthropogenic stressors to freshwater systems (Martinuzzi et al., 2014). Our results recognize regions of conservation need that may be ignored by other prioritization methods focused exclusively on the distribution of native species.

2. Materials and methods

2.1. Data acquisition and database development

We compiled a database of native aquatic species distributions across the CONUS by reallocating ranges from the International Union for Conservation of Nature (IUCN) Red List spatial database (IUCN, 2014) to watersheds using ArcGIS (v. 10.3.1) and R (v. 3.3.3). We selected the US Geological Survey (USGS) eight-digit hydrologic unit code (HUC8), which represent surface drainage basins, as the unit of spatial analysis. The hydrologic unit code system is a system of hierarchically nested watersheds delineated by topographic and hydrological features. There were a total of 2106 HUC 8 watersheds in our study extent, with an average size of 1821 km². Our native biodiversity database contains 1510 species, including fish, mollusks, amphibians, turtles, and crustaceans (shrimps and crayfish).

To generate non-native richness estimates, we curated a list of non-native freshwater aquatic species (192 plant species and 287 animal species), where “non-native” was defined as introduced to the continental US during or after European settlement (~1500 CE). The plants list was compiled initially using the USDA Natural Resources Conservation Service’s (NRCS) plants database (<https://plants.usda.gov>). Candidate species were identified by searching for species non-native to the lower 48 states and listed with a National Wetland Indicator Status of “obligate wetland” in at least some part of that range. This list was later extended to include several species (e.g. *Lythrum salicaria* and others) that are widely considered to be “aquatic” invasive species by management groups throughout the US

despite not being listed as obligate wetland species by the NRCS. These additional species were identified based on existing lists of invasive aquatic plants maintained by the USDA's National Invasive Species Information Center (<https://www.invasivespeciesinfo.gov>), the University of Georgia's Center for Invasive Species and Ecosystem Health (<https://www.invasive.org>), and regional databases such as the Great Lakes Non-indigenous Species Information System (GLANSIS, <https://www.glerl.noaa.gov/glansis>) and the University of Florida Center for Aquatic and Invasive Plants (<https://plants.ifas.ufl.edu>). The plant data analyzed here expand considerably on those utilized in previous studies (Davis et al., 2017). Species included in the NAS animal list were obtained from the USGS Non-Indigenous Aquatic Species program (USGS-NAS; <https://nas.er.usgs.gov/>). While we recognize that species translocated within the continental US ("native transplants") can also have considerable negative impacts in freshwater systems, we have excluded them from the current analysis. The difficulty of defining precisely the non-native range of native transplants can lead to uncertain ascription of non-native occurrences nearby, bordering, or even sometimes within the described native range of these species. This, in turn, raises the possibility of overestimating non-native richness. Excluding these species avoids such overestimation, resulting in what we consider to be justifiably conservative estimate of that richness.

Using these lists, we assembled species occurrence data from USGSNAS, the Early Detection and Distribution Mapping System (EDDMaps), and the USGS Biodiversity Serving Our Nation (BISON) databases, which is a curated US data repository for the Global Biodiversity Information Facility (GBIF). We used the Integrated Taxonomic Information System (ITIS) to ensure that species were not double counted, or that synonymous taxa were accidentally excluded. Duplicate occurrence records, centroids, records with missing spatial coordinates, and occurrence data outside of the conterminous US were removed. Despite the fact that our native biodiversity data is exclusive to animal species, we included plants and animals in our analysis of non-native species because they are both important indicators of overall invasion pressure and significant drivers of general ecological impairment, including native animal species decline (Vilà et al., 2011).

For the overlay analyses, we acquired datasets from the USGS Gap Analysis Program's (USGS-GAP) Protected Areas Database of the United States (PAD-US, version 1.4) (DellaSala et al., 2001; USGS, 2016), which includes the boundaries for national parks, national forests, private conservation easements, and other protected areas. We used lands with any level of permanent protection, which are designated with GAP status codes 1, 2, and 3 according to the definitions provided by Scott et al. (1993). GAP status code 1 signifies the strictest protection, with lands maintained in their natural state, while 3 means land is permanently protected but subject to resource extraction. We also acquired 250-meter resolution land cover maps for the years 2000 and projected 2060 from FORE-SCE (Sohl et al., 2014). From the Inter-governmental Panel on Climate Change Special Report on Emissions Scenarios (IPCC-SRES), we used the year 2060 projection of the A2 scenario, which is characterized by moderate economic growth, very high population increase, and a focus on self-reliance and local identity.

2.2. Calculation and mapping of diversity metrics

We employed geospatial analyses to derive metrics associated with both native and non-native diversity across the CONUS, summarizing these metrics at the HUC8 watershed scale. We developed a non-native diversity metric, the Cumulative Invasion Pressure (CIP), which we believe more comprehensively assesses the past stress associated with non-native species in each watershed, relative to non-native richness alone. We calculated CIP as the log of the time-scaled non-native species richness present in the watershed since the first known species introduction. First, each NAS recorded in the watershed was given a value based on the number of years that species was present in the watershed (the year of earliest observation in the watershed subtracted from 2016), and these values were summed across all NAS. Then the sum was log-transformed to account for variation of over 3 orders of magnitude. The CIP metric assumes that once a species is introduced to a watershed it remains present in that watershed. This is consistent with the assumption of other assessments of non-native species richness based on public observation records, which necessarily assume persistence of introduced populations (Seebens et al., 2017; Stohlgren et al., 2006). The CIP metric also assumes that a non-native species that has been present for many years represents greater stress on the community than a species that was introduced one year ago. By combining richness with time since introduction into one index, CIP is meant to provide an estimate of the cumulative impact that non-native species can have on ecosystem health, as opposed to non-native richness alone.

Native species richness was calculated based on IUCN's range maps as the maximum number of potentially present species. These maps were drawn also at the HUC8 watershed scale to display both total richness and richness of each taxonomic group: fish, mollusks, amphibians, turtles, and crustaceans. To identify imperiled native aquatic taxa, we calculated the number of species that are listed as "vulnerable," "endangered", or "critically endangered" according to IUCN Red List (IUCN, 2014); collectively these represent threatened and endangered (T&E) species. We deliberately chose to use the raw count and not the proportion of T&E species based on the assumption that high native richness is in itself worthy of protection, and adoption of raw count would bias our priority index toward recognizing watersheds with high overall richness as well as high counts of T&E species. We also calculated an index of rarity using the "rarity" package in R (Leroy, 2015), which determines rarity based on relative range size (Leroy et al., 2013). For each taxonomic group, the species with range sizes below the lowest quartile are considered rare, while the rest are considered common. Based on this each species is assigned a rarity weight, and finally each watershed receives a rarity score that is the average of the rarity weights of species present in that watershed. These two metrics - the rarity index and the count of threatened and endangered species - were normalized then averaged to generate an overall Native Biodiversity Index (NBI). Finally, the NBI and normalized CIP were averaged to yield an overall priority index (PI). The final equation for PI was thus

$$PI = \left(\left(\frac{RI_N + TE_N}{2} \right) + CIP_N \right) / 2$$

where PI is the priority index, RI_N is the normalized rarity index, TE_N is the normalized count of native T&E species, and CIP_N is the normalized cumulative invasion pressure. Further,

$$NBI = (RI_N + TE_N)/2$$

Spatial distribution of watershed priority scores was visualized by binning scores based on standard deviations from the mean score. As the highest bin contained only two watersheds, we selected watersheds falling into the two highest bins to delineate our priority regions. Thus, watersheds with a priority index greater than or equal to 0.49 (1.5 standard deviations above the mean) were selected as our priority watersheds.

We assessed existing protection coverage by overlaying the priority areas with the boundaries of existing protected areas designated with GAP status codes 1, 2, and 3. We also overlaid priority areas with projected increases in developed land forecast to 2060, in order to assess the potential future threat of increasing development on native biodiversity. Between priority and non-priority watersheds, we compared the amount of protection and amount of increased development using a t-test with Welch's correction, which accounts for the difference in variance as well as the difference in sample size between the two groups. All statistical tests were conducted in R (v. 3.3.1).

3. Results

Native freshwater species richness is concentrated in the eastern half of the country (Fig. 1A–D). Fish and invertebrate species richness follow very similar patterns, with highest richness centered in the eastern Mississippi River drainage (Fig. 1A, C), while amphibian bio-diversity is highest in the South Atlantic-Gulf region (Fig. 1B). T&E species are similarly concentrated in eastern watersheds, with particularly high overall counts of T&E species in the Tennessee River watersheds in Southern Appalachia (Fig. 1H), although regions of high freshwater species vulnerability also appear in the southwestern US. While T&E invertebrates again cluster within the eastern Mississippi River Drainage (Fig. 1G), vulnerable fish and amphibians are also common in watersheds throughout the southwest and California (Fig. 1F, E). Species rarity is more widely distributed; overall rarity is again high in the Southern Appalachian region, but even higher concentrations of rare freshwater species are observed in the southwest, California, and mountain west (Fig. 1L). Highest watershed rarity scores are generally observed in the western US for all taxonomic groups (Fig. 1I–K).

Non-native species richness (plants and animals) is concentrated in Florida, California, Southern New England south through the Chesapeake Bay region, and the states bordering the Great Lakes in the Ohio and Upper Mississippi River drainages (Fig. 2A). CIP shows a similar overall pattern, highlighting California, Florida, Southern New England, and Southern Lake Michigan, with additional highly stressed watersheds in the central Mississippi River basin.

Our Priority Index highlights 58 watersheds that we consider most in need of conservation intervention based on the combination of native species vulnerability and CIP (Fig. 3). These watersheds cluster into 11 priority areas, although some of these comprise only a single watershed (Fig. 3 and Table 1): (from west to east) the San Francisco Bay Area, Southern California, Lake Mead, Coronado National Forest, Central Mississippi River drainage, Southern Lake Michigan, the Tennessee River basin (Southern Appalachia), Atlantic Florida, New York Finger Lakes, Northern Chesapeake Bay, and Southern New England. Priority areas exhibit a mean NBI of 0.15 (SD = 0.11) and a mean CIP of 7.31 (SD = 0.67); as expected, these values are significantly higher than mean index values for non-priority watersheds (0.05 ± 0.05 and 4.75 ± 1.66 , respectively, $p < 0.001$, by a one-tailed t-test with Welch's correction; Table 1). Mean count of T&E species and mean watershed rarity are also significantly higher in priority than in non-priority watersheds. The highest mean priority score was observed in the Tennessee River Basin (PI = 0.54), the combined watersheds of which provide habitat for 499 unique species (33% of the total richness), including 72 T&E species (21% of total) and 56 rare species (15%). However, NBI and CIP ranged broadly across priority areas; in some cases, extremely high CIP values led to prioritization of watersheds with only moderately elevated NBI (e.g. the Finger Lakes and San Francisco Bay). Priority areas harbor a total of 843 native freshwater species, or 56% of the overall animal species richness in our dataset, despite representing only 3.05% of the total watershed area across the US, and they provide habitat for 37% of the T&E species in the dataset and 26% of the rare species.

According to categorization of lands by the USGS, most permanently protected lands lie in the western half of the country (Fig. 4). After overlaying the priority region boundaries, we find that the priority watersheds tend to be less protected on average than the non-priority watersheds ($p < 0.05$, Table 1), although protected status varies widely across priority areas. Eight priority areas experience a lower mean percent coverage by protected areas than the mean for non-priority watersheds, while three priority areas are actually better protected than the average non-priority watershed. Those latter areas include watersheds that are protected either as US National Forest (Coronado), National Recreation Area (Lake Mead), or National Park (Channel Islands National Park, included in the Southern California priority area). We also overlaid the priority regions with projected land cover for the year 2060. From the year 2000 to 2060, the increase in development will be widespread, with hotspots in several urban areas including San Francisco Bay Area, Chicago, Atlanta, Charlotte, Central Florida, and the Northeast. Identified priority watersheds are expected to experience a significantly higher rate of development than non-priority watersheds (mean increase of 9.98% vs. 2.32%, $p < 0.001$; Table 1). By priority area, all but one (Lake Mead) is projected to experience a higher-than-average change in the percent area developed, with one area (Atlantic Florida) expected to exhibit nearly ten times the mean increase in development of non-priority watersheds (Table 1).

4. Discussion

Given the widely recognized negative impacts of invasive species on native biodiversity, identification of areas where vulnerable native species are likely to experience high invasion pressure could substantially aid in the prioritization of conservation efforts. The utility of

this approach has been illustrated by several recent studies, which have applied species distribution modeling to predict conflict areas between known invasive species and either particular species of concern (Vicente et al., 2011; Vicente et al., 2013) or sensitive ecological areas (Thalmann et al., 2015). Other analyses have more broadly modeled the overlap between native and non-native species richness at national scales, in attempts to ascertain areas where intervention to manage non-native species may have particular benefits for the conservation of native biodiversity (Carpio et al., 2017; Padalia and Bahuguna, 2017). For instance, one recent study utilized a metric of Invasion Risk Impact together with a measure of habitat vulnerability to map lakes in New Zealand most at risk of losing conservation value as a result of invasive fish impacts (Collier et al., 2017).

Here we adopt a similar approach, incorporating explicit information on native species diversity (T&E status and rarity) to determine where NAS introductions are most likely to have negative impacts on native freshwater species. Mapping of our priority index allowed identification of a small number of watershed clusters that exhibit both high rates of non-native species introductions and elevated vulnerability of native freshwater taxa. Although overall native species richness is concentrated primarily in the eastern US, particularly in the central Mississippi River drainage (Fig. 1D), priority watersheds exhibited a much broader geographic distribution, including regions in California, the Southwest, and the Northeast. Nevertheless, the priority watersheds still disproportionately represent the nation's native freshwater richness overall, as well as imperiled freshwater biodiversity. These watersheds represent a mix of regions previously recognized as freshwater diversity hotspots as well as additional regions that are highly threatened by non-native aquatic species. For instance, the highest overall mean priority score was recorded for a cluster of watersheds comprising most of the Tennessee River drainage in Southern Appalachia. This area is renowned as a global center of diversity across multiple freshwater taxa, including fish (Leveque et al., 2008), amphibians (Milanovich et al., 2010), and invertebrates (Crandall and Buhay, 2007), and exhibits extremely high levels of native diversity, T& E species, and species rarity in our metrics (Table 1). The Tennessee River drainage exhibits the lowest mean CIP score of all priority areas, and prioritization of this region is clearly dependent primarily on extremely high mean NBI; however, the region does also experience elevated CIP relative to the national average for non-priority watersheds (mean CIP of 6.06 vs. 4.75), harboring 39 non-native species across the priority area. Watersheds in the Central Mississippi River priority area similarly exhibit low CIP values relative to other priority areas, but reside in a center of freshwater US biodiversity. In contrast, other priority areas are recognized more for the extreme pressure exhibited by non-native species. Watersheds feeding the San Francisco Bay from the Sacramento/San Joaquin River Delta, while known to support surprisingly high levels of imperiled freshwater diversity despite considerable anthropogenic modification (Wickham et al., 2013), have been identified here largely as a consequence of being a globally recognized bioinvasion hotspot (Cohen and Carlton, 1995), with the second highest mean CIP score of any priority area. Highly invaded watersheds in Southern New England and Northern Chesapeake Bay likewise exhibit relatively modest, though significantly elevated, native biodiversity indices, and are prioritized primarily due to extremely elevated CIP.

Although our approaches differed, the priority areas identified here are comparable to those observed in several previously published studies. Jenkins et al. (2015a) adopted an analysis of species rarity and protected status to prioritize US locations based on diversity across multiple terrestrial and freshwater taxa. That analysis highlighted a number of regions in the south-central US (particularly Southern Appalachia) and California consistent with our priority mapping. Notably, the inclusion of mammals and birds significantly shifted prioritization in that analysis toward the western US compared with the freshwater focus presented in our study. Similar emphasis on the western US was observed in an earlier study looking exclusively at T&E species and including terrestrial taxa (Dobson et al., 1997). Another study exclusive to freshwater biodiversity revealed distributions of richness, vulnerability, and rarity similar to those observed here, but sought to identify broad global patterns and did not attempt prioritization at a smaller scale (Collen et al., 2014). Wickham et al. (2013) used conservation status rankings of aquatic-dependent species across the US to explore areas with overlapping needs for biodiversity and drinking water protection. That study identified watersheds in California and the southeastern US exhibiting considerable overlap with those highlighted in the current study. Absent from the previous studies are watersheds in the northeastern US. In general, priority indices based on vulnerable native species alone have not recognized areas in the mid-Atlantic, Great Lakes, and New England, which we have determined to be priority areas (4, 5, 7, and 9) that harbor moderate richness but unusually high invasion pressure.

The difference between our results and previous analyses highlights the importance of incorporating priority mapping into more broadly strategic approaches to conservation decision-making. The practice of identifying species and places as targets of conservation has been criticized for failing to identify explicit aims for conservation and ignoring potential economic, social, and political constraints on management action (Brown et al., 2015; Game et al., 2013). Nevertheless, mapping biodiversity vulnerability can be an important tool, particularly when incorporated into conservation strategies with clear management objectives and guidelines for assessment of outcomes (Tulloch et al., 2015). Our results indicate that explicit consideration of widely recognized threats to freshwater biodiversity (non-native species in this case) can significantly shift priority maps, identifying areas not recognized by assessment of native species threat status alone. Emphasis on non-native species further enables specification of management approaches with potential benefit in those priority areas (i.e. invasive species prevention and control). Recent studies have demonstrated that invasive species management can have significant positive impacts on native biodiversity in both terrestrial and aquatic systems (Jones et al., 2016; McNeish et al., 2017). Alternatively, prioritization schemes that incorporate non-native species impacts could provide managers with means to direct limited resources to prevention of future introductions to already stressed ecosystems (Collier et al., 2017; Leathwick et al., 2016).

Mapping of cumulative threats can be particularly valuable for determining where mitigation might best protect vulnerable native diversity (Mokany et al., 2014; Tulloch et al., 2015). We explored this approach by overlaying our priority areas onto maps of both protected lands (Fig. 4A) and projected future land use change (per cent change in developed land; Fig. 4B). Despite most of the vulnerable freshwater biodiversity lying in the eastern US, protected lands that incorporate management for biodiversity (GAP status codes 1, 2,

and 3) lie predominantly in the western half of the country. The result is that the mean proportion of protected land in a watershed is on average lower in our priority areas than it is across all non-priority watersheds (Table 1). This is despite several priority areas receiving above-average protection coverage as a result of their status as national protected areas (e.g. the Channel Islands in Southern California, Lake Mead, and Coronado National Forest). Of particular concern is the low proportion of protected watershed in the Tennessee River drainage, notwithstanding its globally recognized status as a center of freshwater biodiversity. Interestingly, Lake Mead is highlighted as one of our priority areas despite significant protection coverage (over 63%, Table 1). This may underscore differences in conservation practice across protection categories. Lake Mead National Recreation Area is managed to promote public recreation and use in a manner consistent with preservation of scenic, historic, scientific, and other park attributes; these competing mandates, as well as the accessibility of the park to major population centers, lead to substantial anthropogenic stress and ultimately high invasion pressure despite the park's protected status (Hickey, 2010).

It is important to note that GAP status does not provide a complete representation of conservation protection; for instance, PAD-US incorporates data from the National Conservation Easement Database (NCED; <https://www.conservationeasement.us>), which has an estimated completeness of only 49% of publicly-held easements across the US, with incompleteness particularly high in northeastern states. Nevertheless, previous studies have similarly recognized the failure of protected lands to account for priorities in biodiversity protection in the US and elsewhere (Jenkins et al., 2015b; Rodrigues et al., 2004; Sanchez-Fernandez et al., 2017). There is growing evidence of locational bias, indicating that protected areas around the globe do not match biological conservation targets (Brum et al., 2017; Quan et al., 2017) and tend to be designated on lands with lower economic value (Andam et al., 2008; Joppa and Pfaff, 2009). In the US, previous studies have similarly found below-target representation of the country's diverse ecological systems within the protected areas (Aycrigg et al., 2013; Scott et al., 2001), and similar disconnects have been observed in other regions (Sanchez-Fernandez et al., 2017). This incongruence between need for protection and enacted protection illustrates the importance of policy that is better targeted toward safeguarding native freshwater diversity, and in particular toward mitigating the ecological impacts of invasive species threatening that diversity. Perhaps of greatest concern in the context of the current study is the acknowledged limitation of protected lands in adequately representing freshwater ecosystems (Abell et al., 2007; Herbert et al., 2010). Our analysis thus represents an imperfect assessment of the degree to which priority areas are protected by existing conservation frameworks.

Unfortunately, it is clear that future urban expansion will continue to threaten freshwater biodiversity in the US, as evidenced by high projected land use change in priority areas (Fig. 4B, Table 1). Only the Lake Mead priority area is expected to experience land use change lower than the national average for non-priority areas, and in several cases land use change is projected to be dramatically higher than the mean; Atlantic Florida, in particular, is expected to experience development roughly 10 times the non-priority average. This observation is consistent with the conclusions of Martinuzzi et al. (2014), who also recognized urban expansion as a major threat to freshwater biodiversity. Urban

expansion is associated with habitat loss, fragmentation through hydrological alteration, and increased pollution, all important drivers of native biodiversity decline (Dudgeon, 2014; Garcia-Moreno et al., 2014; Martinuzzi et al., 2014). These physical effects are compounded by the fact that anthropogenically altered landscapes are conduits for spread of non-native species, as human activity strongly influences the introduction and establishment of non-native species, and metrics reflecting human presence (e.g. population density, distance to transportation hubs, intensity of global trade) have been shown to be strong predictors of invasion pressure (Bellard et al., 2016b; Gallardo et al., 2015; Westphal et al., 2007). Urban expansion can thus be expected to further the expansion of NAS, particularly through human vectors associated with intra-continental spread such as recreational fishing, aquaculture, aquarium release, and escape from ornamental gardens (Bobeldyk et al., 2014; Davis et al., 2017; Padilla and Williams, 2004). At the same time, the physical disturbances associated with land use and land cover change frequently create conditions that enable invasive species to outcompete native species (Bradley et al., 2010; Larson et al., 2009). In some cases, the establishment of non-native species may be better long-term predictors of native biodiversity loss than the disturbances that facilitate invasion (Hermoso et al., 2001).

Increases in developed land cover in priority areas is by far highest in those areas already most heavily impacted by urban development, e.g. Southern California, Northern Chesapeake Bay, Southern New England, Atlantic Florida, and Southern Lake Michigan. Perhaps of greater concern are those priority areas that may transition in the future from low or moderate to high levels of urban impact. Research on the ecological consequences of development suggests that urbanization may have threshold effects on various measures of watershed integrity, including biodiversity (Dietz and Clausen, 2008; Wang et al., 2001), with a number of studies suggesting transitions from “sensitive” to “impacted” at approximately 10% impervious land cover (Schueler, 1994; Shuster et al., 2005). Several priority areas are projected to exceed that mark by 2060 (San Francisco Bay delta, Central Mississippi River, and Coronado National Forest) despite relatively small overall changes in percent urban land cover, suggesting the possibility of growing impacts to native freshwater biodiversity in these regions. Our analysis thus suggests not only the possibility of increasing invasion pressure to many of the priority areas identified here, but also cumulative effects associated with multiple anthropogenic stressors on native species, the mitigation of which could have substantial benefits in terms of preserving the overall freshwater biodiversity of the US.

While numerous studies attest to the value of priority mapping at national or even global scales, much conservation decision making occurs on considerably smaller spatial scales and faces complex political and socioeconomic constraints operative at those scales (Brown et al., 2015; Wickham et al., 2013). Fig. 5 illustrates scalability of the general approach of identifying conflict zones between NAS and native freshwater biodiversity. The Tennessee River watershed (USGS HUC206) comprises 89% of priority area #1. It is situated at the center of US freshwater diversity and extends across seven different states. Fig. 5B reveals that priority watersheds in our analysis predominantly follow the Tennessee River, encompassing four major metropolitan areas along that waterway. Although large portions of the overall region are protected, these areas are mostly restricted to the Great Smoky Mountains National Park and Nantahala National Forests in the east. Previous analysis

has suggested that while the overall areal coverage of protective lands in the region are consistent with global averages (i.e. between 12 and 15%), the distribution of those lands is likely inadequate to represent lowland freshwater ecosystems and the high number of imperiled and range-restricted taxa in the region (Thieme et al., 2016). Within our priority areas, we observe that protected areas are generally limited to lands immediately bordering the Tennessee River. Visualization of priority areas at this regional scale suggests the possibility that conservation protections available in National Parks and Forests have had some positive effect in limiting conflict between NAS and vulnerable native diversity, but that additional protections focused on NAS management in the more urbanized corridor along the Tennessee River, particularly in Virginia, Tennessee, and Alabama, could provide further benefits to the diverse freshwater fauna present in this region.

Analysis at this scale also highlights limitations of an approach to conservation prioritization based strictly on biodiversity metrics. For instance, Thieme et al. (2016) have previously noted that consideration of habitat connectivity and conservation value of upstream habitats can significantly improve prioritization schemes. For freshwater systems, in particular, incorporation of connectivity into decision support tools can therefore be critically important (Moilanen et al., 2008). Our analysis, even at a regional scale, thus represents only preliminary steps toward more comprehensive conservation planning. Generally, systematic conservation planning is a complex process that formally recognizes vulnerability and irreplaceability of sites (Linke et al., 2007; Wilson et al., 2005), along with consideration of ecological process (Pressey et al., 2007) and explicit recognition of conservation goals (Margules and Pressey, 2000). By incorporating data on both T&E and rare species as well as stresses associated with NAS we have attempted to address, informally, both the irreplaceability and vulnerability of watersheds across the US, and we have further explored vulnerability by investigating potential future threats and limitations to existing protections. Our research therefore captures only the early stages of conservation planning, *sensu* Margules and Pressey (2000). However, future research that more formally and comprehensively assesses important conservation-relevant attributes of freshwater systems across the US could expand considerably on the analysis presented here.

Several additional limitations of our study should also be acknowledged. First, there are multiple alternative approaches to measuring native biodiversity beyond the assessment of taxonomic richness, rarity, and vulnerability. For instance, some recent studies have used variables associated with phylogenetic and trait diversity to determine similar prioritizations for biodiversity conservation (Brum et al., 2017; Strecker et al., 2011), and others have focused on developing methods that account for species composition across sites to identify ecologically representative samples of biodiversity (Chauvenet et al., 2017). These more sophisticated metrics are challenging to implement, but could guide more effective appraisals of the spatial distribution of freshwater biodiversity value. Second, despite its widely recognized utility for determining conservation status, the IUCN Red List exhibits significant gaps in coverage; indeed, focus in the current study on freshwater animal species was driven in large part by the incompleteness of IUCN assessments for aquatic plant species. Ocampo-Peñuela et al. (2016) have found that habitat shrinkages are not well integrated into the IUCN Red List database, and that the database may therefore provide only conservative estimates of the level of endangerment. Our maps of native

vulnerability may thus offer conservative assessments of the degree to which freshwater animal species are truly threatened and endangered. Finally, attempts to delineate patterns of non-native species richness from publicly available observational records are limited by spatial and temporal bias in sampling effort, which may in some cases obscure true patterns of species introduction and spread (Davis et al., 2017). Nevertheless, the value of such data for inferring patterns of non-native species introductions has been generally recognized (Seebens et al., 2017), and priority mapping based on observational records has provided various insights relevant to conservation decision making (Bobeldyk et al., 2014; Dawson et al., 2017; Liu et al., 2017). Despite these recognized limitations, our analyses demonstrate the possibility of identifying conflict areas between vulnerable native species and NAS, a major known driver of biodiversity decline. Our results indicate that these areas may be poorly protected by existing conservation mechanisms and may experience significant additional anthropogenic stress in the future. More positively, they also suggest that active management of NAS in a small number of priority areas across the US could have a disproportionate impact on conservation of the nation's native freshwater fauna.

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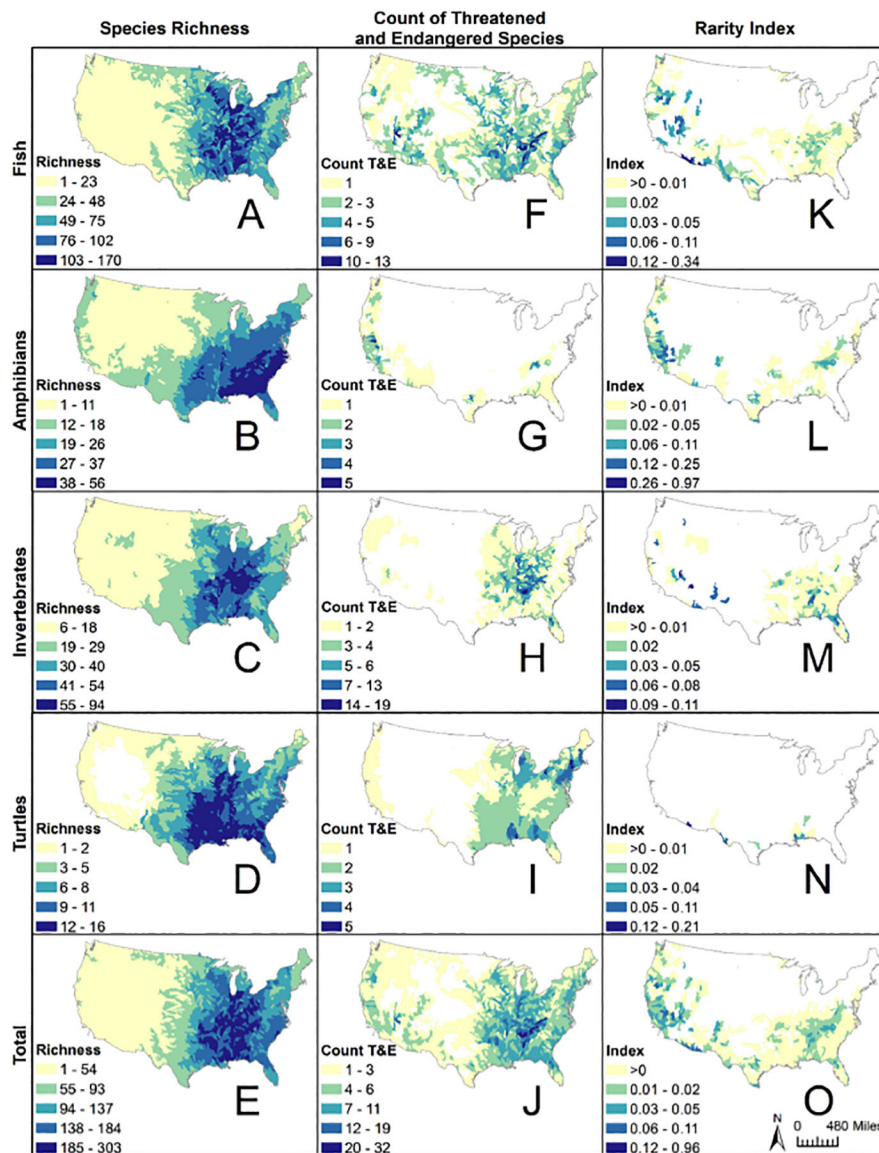


Fig. 1. Native biodiversity metrics, mapped at HUC8. Metrics were calculated for major taxonomic groups, including fish (A, F, K), amphibians (B, G, L), invertebrates (crustaceans and mollusks; C, H, M), and turtles (D, I, N) and also aggregated across all taxa (E, J, O). Shown are the total richness (species count; A–E), the count of IUCN threatened and endangered species (F–J), and the summed rarity index across species (K–O). Note that the color legend varies across maps.

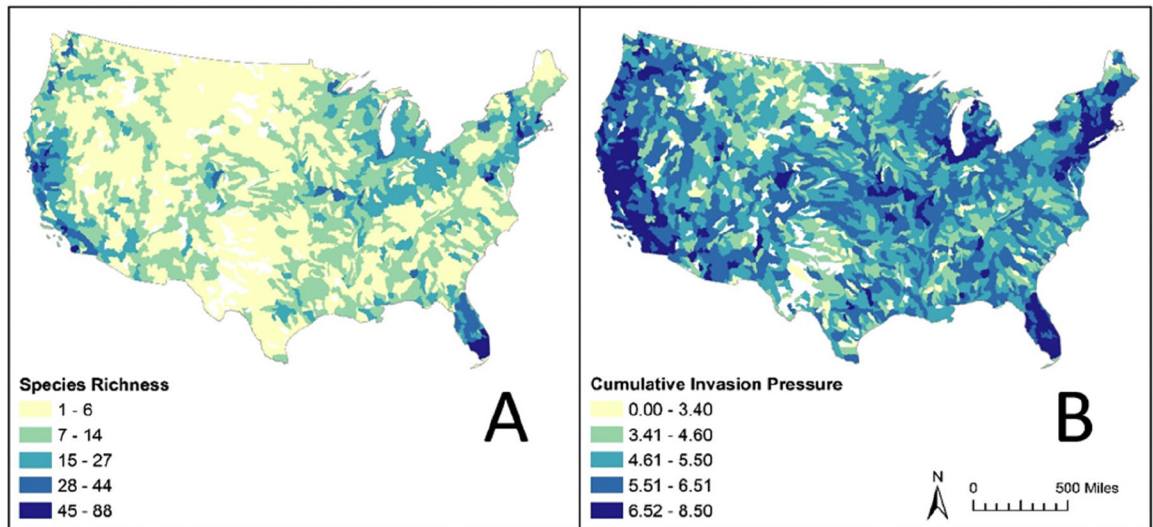


Fig. 2. Non-native species richness (A) and Cumulative Invasion Pressure (CIP; B) per HUC8. CIP is the log transformed sum of years present for all non-native species in the watershed.

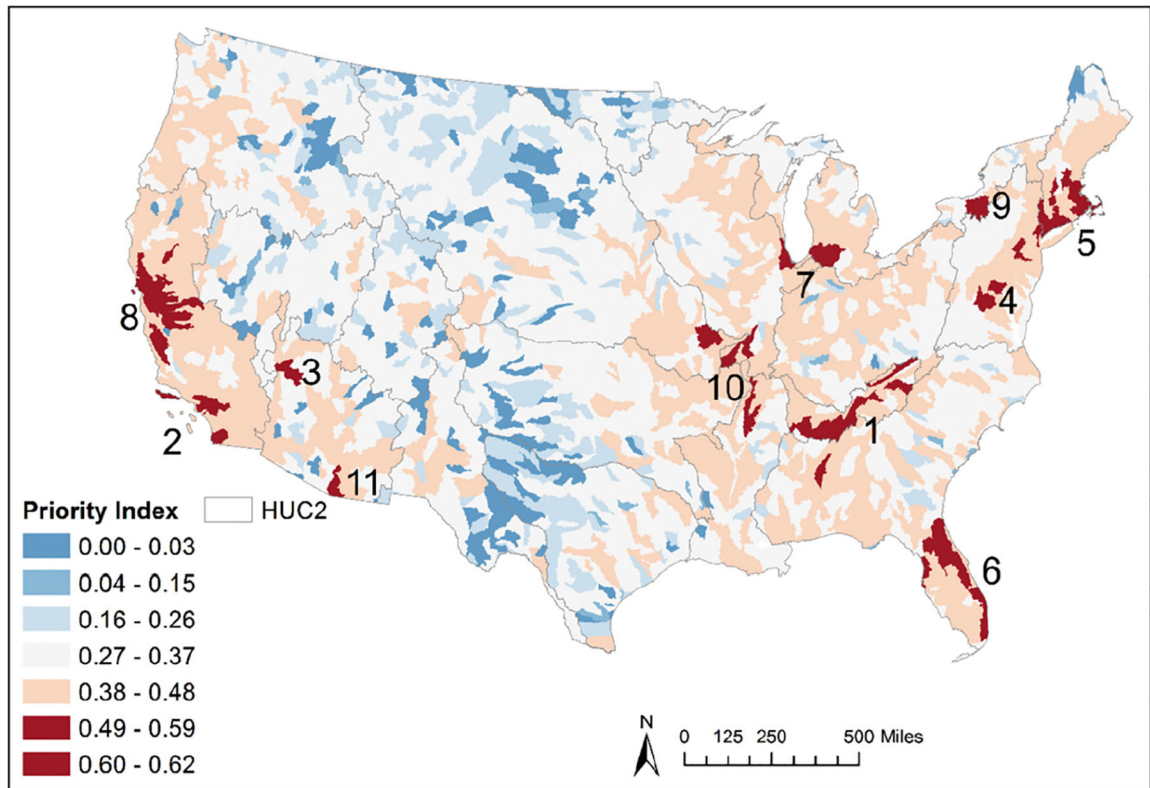


Fig. 3. Priority mapping of HUC8 watersheds. The watersheds with an index value 1.5 standard deviations above the mean or greater (priority score ≥ 0.49) are considered to be our priority areas. A total of 58 watersheds fall into 11 priority areas; region numbering corresponds to Table 1. HUC2 watershed boundaries are shown in gray.

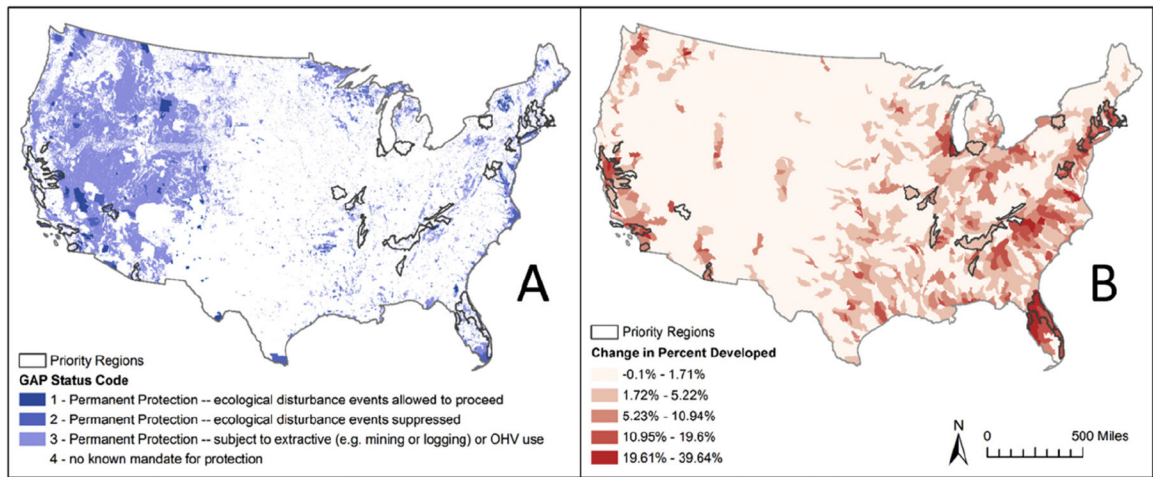


Fig. 4. The boundaries of 58 watersheds in 11 priority areas displayed over protected areas (A) and future change in development (B). The protected areas fall into three categories of protection according to the U.S. Geological Survey Gap Analysis Program (GAP). Change in percent developed per HUC8 was derived from FORE-SCE models of future land use and land cover change. The rates shown are the difference from year 2000 to 2060.

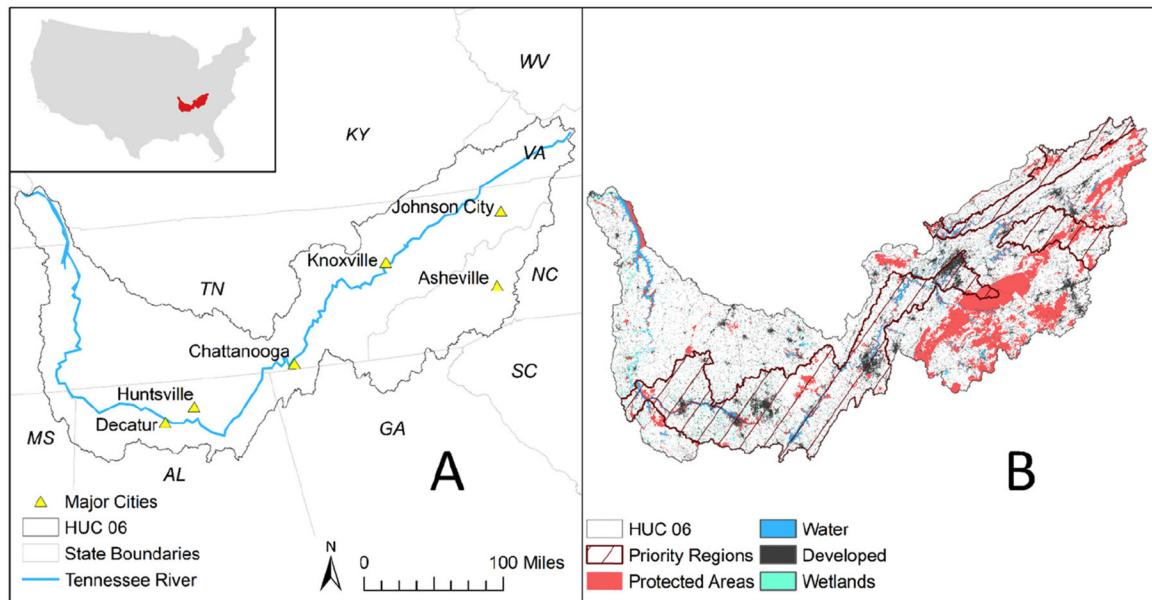


Fig. 5. Downscaled map of priority watersheds within the Tennessee River drainage, comprising the majority of priority area 1. A) Political boundaries and major geographic features; B) land cover map showing overlay with priority watersheds (red line fill). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Summary statistics for all HUC8 watersheds, for all priority watersheds, and by individual priority area. CIP, Cumulative Invasion Pressure; NBI, Native Biodiversity Index.

Priority area	Mean PI	Number of watersheds	Unique species	T&E species		Rare species		Mean CIP	Mean NBI	Mean percent protected	Mean change in percent developed
				n	Mean % per watershed	n	Mean % per watershed				
1. Tennessee River drainage	0.54	8	499	72	8.99%	56	4.51%	6.06	0.36	9.19%	3.09%
2. Southern California	0.52	5	40	6	11.26%	7	29.91%	7.43	0.17	49.52%	10.66%
3. Lake Mead	0.52	1	40	12	30.00%	7	17.50%	7.02	0.21	63.20%	0.05%
4. Northern Chesapeake Bay	0.51	3	152	8	5.20%	0	0.00%	7.78	0.1	10.28%	11.93%
5. Southern New England	0.50	13	152	9	7.44%	0	0.00%	7.71	0.1	13.37%	12.53%
6. Atlantic Florida	0.50	5	166	15	6.18%	9	1.85%	7.28	0.14	22.91%	22.23%
7. Southern Lake Michigan	0.50	3	228	11	4.17%	0	0.00%	7.4	0.13	2.26%	12.92%
8. San Francisco Bay	0.49	14	77	11	9.49%	14	6.22%	7.62	0.08	21.12%	8.82%
9. Finger Lakes	0.49	1	138	4	2.90%	0	0.00%	7.76	0.06	2.96%	3.68%
10. Central Mississippi River	0.49	4	317	15	4.80%	4	0.59%	6.93	0.16	7.59%	3.89%
11. Coronado National Forest	0.48	1	38	5	13.16%	4	10.53%	7.08	0.12	37.93%	9.54%
All priority	0.50	58	843	124	8.31% ^{***}	100	5.39% ^{***}	7.31 ^{***}	0.15 ^{***}	18.57% [*]	9.98% ^{***}
All non-priority	0.31	2050	1494	328	0.03%	362	0.01%	4.75	0.05	24.47%	2.32%

Note: Asterisks denote the level of statistical significance (one-tailed t-test with Welch's correction for unequal variance) in comparison between priority and non-priority watersheds.

* p < 0.05.

*** p < 0.001.