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# Freshwater corridor networks in the conterminous US: a coarse-filter approach based on lake-stream networks

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km north-south stream distance), indicating that the functional connectivity of the largest potential freshwater corridor networks in the conterminous US currently may be diminished compared to smaller, undammed networks. Network lakes and hubs were protected at similar rates nationally across different levels of protection (8-18% and 6-20%, respectively), but were generally more protected in the western US. Our results indicate that conterminous US protection of major freshwater corridor networks and the hubs that maintain them generally fell short of the international conservation goal of protecting an ecologically representative, well-connected set of fresh waters (≥ 17%) by 2020 (Aichi Target 11). Conservation planning efforts might consider focusing on restoring natural hydrologic connectivity at or near hubs, particularly in larger networks, less protected or biodiverse regions, to support freshwater biodiversity conservation under climate change.

**Running head**

Freshwater corridor networks

**Title**

Freshwater corridor networks in the conterminous US: a coarse-filter approach based on lake-stream networks

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**Open research**: All data, metadata, and R analysis scripts are currently available at https://github.com/cont-limno/TripleC. Upon publication, this repository will be permanently archived in a publicly accessible online location and cited in our methods.

**Abstract**

Maintaining regional-scale freshwater connectivity is challenging owing to the dendritic, easily fragmented structure of freshwater networks, but is essential for promoting ecological resilience under climate change. Although the importance of stream network connectivity has been recognized, lake-stream network connectivity has largely been ignored. Furthermore, protected areas are generally not designed to maintain or encompass entire freshwater networks. We analyzed freshwater corridor networks, disproportionately important network lakes (i.e., "hubs"), and their protection status in the conterminous US. We calculated connectivity scores for 385 freshwater networks with > 4 lakes (≥ 1 ha) and identified 2080 hub lakes (2% of all network lakes) that are critical for maintaining intact networks. Freshwater connectivity scores were not correlated with any type of protection. Just 3% of networks received high connectivity scores based on their large size and structure (medians of 1303 lakes, 498.6 km north-south stream distance), but these also contained a median of 454 dams. In contrast, undammed networks (17% of networks) were considerably smaller (medians of 6 lakes, 7.2 km north-south stream distance), indicating that the functional connectivity of the largest potential freshwater corridor networks in the conterminous US currently may be diminished compared to smaller, undammed networks. Network lakes and hubs were protected at similar rates nationally across different levels of protection (8-18% and 6-20%, respectively), but were generally more

protected in the western US. Our results indicate that conterminous US protection of major freshwater corridor networks and the hubs that maintain them generally fell short of the international conservation goal of protecting an ecologically representative, well-connected set of fresh waters (≥ 17%) by 2020 (Aichi Target 11). Conservation planning efforts might consider focusing on restoring natural hydrologic connectivity at or near hubs, particularly in larger networks, less protected or biodiverse regions, to support freshwater biodiversity conservation under climate change.

**Key Words**

Climate change, coarse-filter, connectivity, corridors, graph theory, lakes, network, protected areas, rivers, streams

## Introduction

Connectivity is important for numerous ecological processes, including gene flow, migrations, and species range shifts, and is therefore often key for promoting ecological resilience under climate change (Heller and Zavaleta 2009). Such processes operate over a range of spatial and temporal scales from local to continental and transient to macroevolutionary (Littlefield et al. 2019, Armstrong et al. 2021). As habitats are increasingly lost, degraded, or fragmented, maintaining connectivity among habitats at these various spatial and temporal scales becomes particularly challenging (Fischer and Lindenmayer 2007). From a biodiversity conservation perspective, it is often critical to identify, create, or protect corridors to ensure long-term population maintenance and the potential for species range shifts under climate change (Beier & Noss 1998, Stralberg et al. 2020).

Corridors are natural or human-created features (habitat or non-habitat) that facilitate connectivity among two or more habitat patches (Beier & Noss 1998, Costanza and Terando 2019). Numerous studies have attempted to identify corridors for conservation purposes. Many earlier studies focused on landscape-scale modeling of least cost pathways or cost surfaces for select species among core habitats (often protected areas) based on various methods including expert opinion, literature review, or observed species-habitat relationships (Beier et al. 2008, Pullinger and Johnson 2010). Similarly, other studies have applied graph theory to model connectivity across landscapes reflecting the spatial arrangement of numerous habitat patches and potential corridors across the underlying landscape (Urban and Keitt 2001, Urban et al. 2009). Over time, graph-based studies have been adapted to incorporate more nuanced information on the characteristics of both patches (e.g., shape) and the landscape (e.g., permeability gradients) (Rayfield et al. 2011).

Whereas such approaches have been successfully applied for landscape-scale conservation planning, researchers have encountered limitations when applying them at larger spatial scales, including computational constraints, inability to resolve patch characteristics (e.g., shape, habitat quality), and the fact that well-studied, candidate focal species rarely range across large spatial extents or adequately represent regional biodiversity (Theobald et al. 2012). Coarse-filter corridor mapping approaches represent a common solution to these challenges for regional- to continental-scale conservation planning, particularly when the goals are to link distant protected areas for multiple taxa (Beier et al. 2011). Such approaches build off fine-filter graph-based or least-cost approaches, but instead rely on generalized surfaces of landscape permeability as a function of natural vegetation or lack of human presence (Theobald et al. 2012). Although such larger-scale, coarse-filter studies often have to make simplifying assumptions about connectivity (e.g., that human presence is broadly representative of fine-scale features such as fences and roads that restrict movements) (Lawler et al. 2013, Nuñez et al. 2013, Belote et al. 2016), coarse-filter approaches can be useful when prioritizing efficiency, relatively mobile, larger-bodied, or generalist species, or diverse abiotic habitat conditions that promote biodiversity (Brost and Beier 2012, Krosby et al. 2014, Costanza and Terando 2019). In more recent years, some studies have also incorporated climate change projections into landscape permeability models to account for climate change effects on habitat distribution and accessibility (i.e., “climate connectivity”) (McGuire et al. 2016, Carroll et al. 2018, Parks et al. 2020).

Although there is a rich and growing conservation literature on coarse-filter corridor mapping at broad spatial scales, most of this progress has occurred in the terrestrial realm. Despite the fact that the freshwater biodiversity crisis was identified decades ago (Abell 2002, Dudgeon et al. 2006), freshwater biodiversity continues to experience greater rates of endangerment and extinction than marine or terrestrial biodiversity (Collen et al. 2014, McRae et al. 2017, Williams-Subiza and Epele 2021). Many studies have demonstrated the importance of connectivity within freshwater networks for maintaining freshwater populations and community structure across taxa (Altermatt and Fronhofer 2018, de Mendoza et al. 2018, Schmera et al. 2018). Of existing freshwater corridor mapping studies, the majority has focused on river and stream networks at landscape, watershed, or regional scales, without incorporating lentic waterbodies (Collier 2011, Saunders et al. 2016, but also see Gardner et al. 2019, Harvey and Schmadel 2021).

The lack of broad-scale freshwater corridor studies across both lotic and lentic ecosystems may be explained somewhat by the dendritic nature of freshwater landscapes (i.e., networks of streams, rivers, and lakes). Freshwater networks are easily fragmented by numerous anthropogenic (e.g., impoundments, hydrologic alterations) or natural (e.g., flow direction, seasonal hydrology) factors (Erős et al. 2012, LeMoine et al. 2020), many of which are difficult to represent spatially across multiple regions. One previous study quantified stream network fragmentation across the conterminous US based on dam locations and found that dams have created over 48,000 new stream segments compared to historical, undammed conditions (Cooper et al. 2017). Although this study is particularly valuable given its large spatial extent and quantitative comparison of current vs. historical network conditions, it did not specifically consider the role of lakes in potential network fragmentation. Therefore, there is a need for broad-scale freshwater corridor studies that consider dam-mediated network connectivity based on both lakes and streams.

Another key consideration in freshwater corridor mapping is the imperfect translatability of the terrestrial graph-based approaches to freshwater networks of lakes, streams, and rivers (Nel et al. 2009, Hermoso et al. 2018). Topologically, lakes resemble nodes (i.e., patches) and streams and rivers resemble edges (i.e., corridors) in a traditional graph theory framework, but lakes, streams, or rivers may each represent preferred habitat, with others functioning as marginal habitat or non-habitat corridors depending on the taxa of interest (Tonn and Magnuson 1982, Jones 2010, Heim et al. 2019). Regardless, it is important to consider lakes, streams, and rivers together when mapping freshwater corridors due to their important structural and ecological linkages (Saunders et al. 2016, McCullough et al. 2019a, King et al. 2021a). Moreover, such freshwater networks represent the only possible corridors for strictly freshwater taxa without human intervention in the absence of overland or vector-mediated dispersal (e.g., transport by wind or waterfowl). In light of these facts, coarse-filter approaches focused on network structural characteristics that broadly influence connectivity among lakes, streams, and rivers may represent a promising avenue for identifying potential freshwater corridors for conservation purposes over large areas.

A concept from terrestrial graph theory that potentially translates well to fresh waters is the important role of particular nodes in maintaining structural landscape connectivity (Urban and Keitt 2001, Rayfield et al. 2011). We refer to these as “hubs”: major nodes within freshwater networks that disproportionately influence and reinforce whole-network structural connectivity (Muirhead & MacIsaac 2005) (Figure 1a). Because effects of lakes on network connectivity are generally ignored in many stream and river connectivity studies at broad spatial scales (e.g., Cooper et al. 2017, Kuemmerlen et al. 2019, Barbarossa et al. 2020), we considered lakes as nodes and streams as edges and therefore lakes as potential hubs, but recognize that it may make sense to designate stream reaches as nodes under some circumstances (e.g., regions with detailed stream habitat data or few lakes). Furthermore, major dams are commonly associated with lakes (and reservoirs), so an analysis of critical nodes can indicate where network connectivity is most compromised, vulnerable to anthropogenic alterations, or could benefit from restoration. Regardless, conceptually, network fragmentation increases and whole-network connectivity is considerably reduced if hubs become compromised due to factors such as impoundments or other hydrologic alterations, water quality declines, biological invasions, or shoreline developments (Figure 1b). Terrestrial studies have demonstrated the importance of particular nodes for maintaining network structure, including stepping-stone nodes that represent lower quality habitat (Saura et al. 2014, Dilts et al. 2016). Therefore, protecting and managing hubs to maintain intact freshwater networks for lotic-associated species may be advisable, particularly in a climate change context. For example, loss or degradation of hubs could threaten access to seasonal thermal refuges (Armstrong et al. 2021) or persistent waterbodies in dry landscapes (Jaeger et al. 2014), or the potential for species range shifts (Comte et al. 2013, Lynch et al. 2016, Ebersole et al. 2020). Future work is needed, however, to examine directly the biological importance of hubs within freshwater networks.

Finally, a major impetus for coarse-filter connectivity mapping is to identify, create, or protect corridors among protected areas (Costanza and Terando 2019). Protected areas, however, are generally focused on terrestrial biodiversity and have therefore provided mixed benefits for freshwater biodiversity and ecosystems (Saunders et al. 2002, Abell et al. 2007). Past research has focused largely on the lack of representation of freshwater biodiversity and ecosystems in protected areas (Jenkins et al. 2015, Bastin et al. 2019, McCullough et al. 2019b) rather than freshwater connectivity. Notably, global protection targets for freshwater ecosystems (Aichi

Target 11; CBD 2010) have been only somewhat achieved. In 2020, the 5th Global Biodiversity Outlook deemed Target 11 as “partially achieved”: the 17% protection target was likely achieved globally, but not necessarily based on ecologically representative, well-connected fresh waters (Secretariat of the Convention on Biological Diversity 2020). Therefore, protection of freshwater corridors may currently be insufficient in many regions and countries. Although maintaining and restoring freshwater connectivity is a major priority for freshwater biodiversity conservation worldwide, research is still needed to investigate to what extent protected areas help maintain freshwater connectivity (Harper et al. 2021).

Our objective was to provide a national-scale, coarse-filter assessment of freshwater corridors in the conterminous US, encompassing characteristics of freshwater networks, potential corridor networks, and their protected status with respect to the 17% Aichi conservation target. We focus on freshwater corridor networks, which link numerous local corridors to achieve regional-scale connectivity (Beier et al. 2008, Beier et al. 2011). This work builds upon the primarily terrestrially-focused coarse-filter connectivity literature for conservation purposes by extending these practices to fresh waters and explicitly considering the role of major nodes (i.e., hubs) in corridor networks. This work also represents the first conterminous US-wide analysis of freshwater corridor protection, another topic that has been a major focus in the terrestrial realm. Specifically, we asked:

1. What freshwater networks can best represent freshwater corridor networks?
2. What lakes represent freshwater network hubs?
3. How well protected are these freshwater corridor networks and hubs?

Generally, we expected most freshwater networks to be relatively small, heavily dammed, and susceptible to fragmentation, limiting the availability of regional freshwater corridor networks in the conterminous US. We also expected hub lakes to be more prevalent in regions with more lakes overall and for protection of hub lakes and freshwater corridor networks to fall below the 17% Aichi target nationally, except in the western US where large protected areas are concentrated. This analysis represents an important step for freshwater biodiversity conservation in a climate change context and is intended to facilitate future biodiversity-centered work, including observations of species and genetic diversity, as well as important processes of gene flow, migrations, and range shifts.



## Methods

### Freshwater connectivity metrics and scoring criteria

A challenge associated with assessing conterminous US-scale freshwater connectivity is obtaining data at ecologically appropriate resolutions across such a large spatial extent. We applied a novel, conterminous US-scale dataset, LAGOS-US-NETWORKS v1.0, that represents graph-based freshwater networks with lakes as nodes and streams as edges (King et al. 2021b, c). This dataset contains 86511 on-network lakes $\geq$ 1ha in surface area and approximately 39.5 million stream reaches that comprise a total of 898 networks (Fig 2a). Lakes were defined as permanent, lentic waterbodies $\geq$ 1ha (both natural lakes and reservoirs) with a geographically defined polygon in the National Hydrography Dataset v2 (Cheruvelil et al. 2021, Smith et al. 2021). LAGOS-US-NETWORKS also includes on-network dams (n = 49525) and metrics for the number of total dams within each network and the number of upstream or downstream dams from individual lakes. We calculated additional connectivity metrics described below using all pairs of connected lakes and the stream distances connecting them.

In our representation of freshwater networks, edges were weighted by the total stream course distance (km) and were undirected connections between pairs of nodes such that travel through each network was irrespective of streamflow direction. Although we did not weight individual nodes, we analyzed the relationship among nodes within networks using several metrics that broadly represented the density of edges and nodes, accessibility of nodes, susceptibility of networks to fragmentation, and climatic heterogeneity within networks (see Table 1 for individual variable descriptions and justifications). All network connectivity metrics were calculated using the igraph R package (Csardi & Nepusz 2006). We prioritized variables that reflected these phenomena to represent coarse-filter structural connectivity in a climate change context. Although we recognize that only relatively mobile taxa are potentially capable of traveling throughout larger networks (e.g., to reach cooler habitats at higher latitudes), many of our connectivity metrics are also relevant to slow-dispersing taxa whose resilience under climate change relies more on localized movements. Specifically, our study includes network variables that represent susceptibility to fragmentation (minimum cuts, percent articulation points), network position (edge density, betweenness centrality), and average dispersal distance between habitats (average lake distance) (Table 1). Given that these are also important considerations for fast-dispersing taxa, our analysis can be used to represent connectivity for diverse freshwater taxa. Therefore, a coarse-filter structural connectivity analysis of these networks generally represents a useful step for freshwater biodiversity conservation in a climate change context.

Coarse-filter, broad-scale connectivity studies in the terrestrial realm often require simplifying assumptions at this scale (e.g., that snapshot metrics of generalized human presence reflect landscape permeability; Theobald et al. 2012). Therefore, in the freshwater realm, we made various, similar assumptions about what our freshwater connectivity metrics represent at the scale of the conterminous US. Such assumptions may require revision for studies at finer spatial scales when different data are available or for specific taxa of interest. Specifically, we assumed static hydrology (i.e. not accounting for seasonal or interannual variation) and that all dams are structurally similar and well represented across the US, and we do not include fine-scale barriers such as waterfalls, culverts, or slope gradients. We also do not account for networks that crossed international borders due to data constraints.

We integrated the various freshwater connectivity metrics (all variables described and defined in Table 1) into a composite network connectivity score that could easily be compared across networks using a principal component analysis (PCA). We only performed this analysis for networks with > 4 lakes (n = 385); however, we excluded the Mississippi River network due to its exceptional size (containing 37.9% of all network lakes). Prior to the PCA, dam rate and percent articulation points were rescaled such that higher values represented fewer barriers and greater resistance to network fragmentation, respectively (and therefore greater overall connectivity). We then Z-score normalized all input variables (mean of 0 and standard deviation of 1) before PCA calculations. We used 2 principal components, which explained 60% of variation in the data, to calculate connectivity scores. We opted to use 2 components based on agreement between the Kaiser criterion and Horn's parallel analysis for component retention (Dinmo 2018). To facilitate usefulness of our study for management and policy decision-making processes, we analyzed freshwater connectivity scores across 9 ecoregions used by the US Environmental Protection Agency National Aquatic Resource Survey (NARS) (Herlihy et al. 2008) (Figure 2b). For networks that spanned multiple ecoregions, we assigned ecoregions based on the majority of nodes within those networks.

**Hub lake determination**

Conceptually, per graph theory, hubs within a freshwater network are vital for maintaining connectivity across large expanses. Hub lakes were determined based on individual metrics of lake nodes within networks. We defined hub lakes as lakes that jointly satisfied three conditions of node importance: 1) articulation points in their network, 2) in the top quintile of vertex strength (i.e., the weighted degree of a node), and 3) in the top quintile of betweenness centrality within their network (Figure 3). Hence, each network with ≥ 5 lakes will contain at least one hub lake using our definition as long as an articulation point exists in the network. Articulation points are by definition bridges among two or more subnetworks, meaning that an organism must travel through an articulation point to move aquatically from one subnetwork to another. High vertex strength for a lake indicates that it connects a high total network distance among lakes, whether through a multitude of short streams or a handful of long streams. Lakes with high betweenness centrality have shorter aquatic travel distances crossing through them and are more likely to be stepping stones for organisms moving within a network. Combined, these metrics indicate a lake that is necessary for network movement and connects long distances while being a more likely path for biota than other lakes in a network. Finally, although we did not differentiate between natural lakes and reservoirs in aforementioned connectivity metrics, we reported differences in the prevalence of natural lake hubs versus reservoir hubs for waterbodies ≥ 4 ha. This size cutoff is based on LAGOS-US-RESERVOIR, a database of all 137,465 natural lakes and reservoirs ≥ 4 ha classified by machine learning image interpretation (Polus et al. 2021). This dataset classifies reservoirs as waterbodies directly influenced by impoundments (lakes resulting from river impoundments and pre-existing lakes with large water control structures whose influence goes beyond water level control). Smaller waterbodies < 4 ha could not be reliably classified, but are less likely to be reservoirs (Polus et al. 2021).

**Analysis of protected networks, network lakes, and hub lakes**

Because protected areas are usually established for terrestrial ecosystems, defining protected freshwater ecosystems depends on different levels of land protection and what constitutes freshwater ecosystem protection (i.e., waterbody itself or waterbody and its watershed). Therefore, we considered both strict (i.e., managed for biodiversity; Gap Analysis Program (GAP) status 1-2) and multi-use (i.e., managed for both biodiversity and natural resource extraction; GAP status 1-3) protection (Fig 2c) in the US Protected Areas Database v2.0 (US Geological Survey 2018). We also considered protection based on lakes occurring within protected areas (i.e., based on lake centers) and on at least 80% of lake watersheds occurring within protected areas given the importance of watersheds for maintaining freshwater habitats (sensu McCullough et al. 2019b). Under these different definitions of protection, the narrowest is based on strict 80% watershed protection, whereas the loosest is based on lake centers occurring within either strict or multi-use protected areas. Watersheds were based on LAGOS-US-LOCUS v1.0 (Cheruvelil et al. 2021, Smith et al. 2021). Using these definitions, we calculated the percentage of lakes in each network currently protected. Similarly, we analyzed current protection of hub lakes using these same definitions and compared protection of hub lakes to protection of all network lakes. We also compared natural log-transformed network connectivity scores to proportions of networks protected under all definitions of protection using Pearson's correlation coefficients. Finally, we analyzed protection status of whole networks, network lakes, and hub lakes with respect to the 17% Aichi target both nationally and by NARS ecoregions.

All data, metadata, and R analysis scripts are currently available at https://github.com/cont-limno/TripleC. We used R version 4.0.4 for analyses (R Core Team 2021). Upon publication, this repository will be permanently archived in a publicly accessible online location and cited in our methods.

## Results

### Freshwater network characteristics

Of the 898 freshwater networks across the conterminous US, most were relatively small (medians of 3 lakes, 5.6 km N-S stream distance, and 1 dam). In contrast, larger networks were relatively rare: just 10.0% and 7.6% of networks contained at least 50 lakes or spanned at least 100 km of N-S stream distance, respectively. The Mississippi River network contained 37.9% of all network lakes (32811 lakes) and 51.2% of all network dams (24986 dams). Larger networks also tended to have more dams: number of dams was positively correlated with number of lakes and N-S stream distance across all networks (Pearson's $r = 0.94$ and 0.74, respectively, $p < 0.001$) (excluding the Mississippi River network). Aside from dams, larger networks were also generally more susceptible to fragmentation: 32.8% of network lakes were articulation points in networks with > 3 lakes, whereas this value was 18.5% across all networks (Table S1). Similarly, maximum N-S stream connectivity within networks was also susceptible to fragmentation with a median of 1 network cut necessary to undermine the full latitudinal breadth of all networks, as well as those with > 3 lakes. Freshwater network statistics across NARS ecoregions are reported in Table S1. In summary and as expected, our analysis of freshwater networks across the conterminous US indicates that most networks are relatively small and that larger networks generally have more dams and are structurally more susceptible to habitat fragmentation. In other words, the large networks potentially able to represent regional freshwater corridor networks are relatively few in number, heavily dammed, and particularly prone to habitat fragmentation.

**Hub lakes: distribution and characteristics**

We identified 2080 hub lakes across the conterminous US, representing 2.4% of network lakes (Table S1, Figure 4a). This percentage varied marginally across most ecoregions, but was just 0.1% in the Northern Plains (NPL) ecoregion and 1.5 - 3.6% across all other ecoregions. Across NARS ecoregions, abundance of hub lakes was positively correlated with abundance of networks (Pearson's $r = 0.79$, $p = 0.01$). Hubs were generally most abundant in the 3 ecoregions with the most networks (Central Plains (CPL): 528 hubs, Northern Appalachians (NAP): 451 hubs, Upper Midwest (UMW): 260 hubs). Ecoregions with fewer networks were generally dominated by the Mississippi River network and also had generally fewer hubs (NPL: 28 networks/5 hubs, Southern Appalachians (SAP): 10 networks/295 hubs, Southern Plains (SPL): 8 networks/103 hubs, Temperate Plains (TPL): 58 networks/190 hubs). In the western US, which is mostly outside the Mississippi River network, the Western Mountains (WMT) and Xeric (XER) ecoregions had 169 and 79 hubs, respectively. Overall, hub lakes were found throughout the conterminous US, but were generally more abundant in regions with more freshwater networks, consistent with our expectations.

Of all 2080 hub lakes, 1616 (77.7%) ≥ 4 ha could be classified as either reservoirs or natural lakes, of which 1168 (72.3%) were reservoirs and 448 (27.7%) were natural lakes. Therefore, hub lakes were considerably more likely to be reservoirs than the general population of lakes; 43.5% of 137465 lakes in the conterminous US ≥ 4 ha are classified as reservoirs. Of the 246 networks with hub lakes, just 27 networks (11.0%) had no dams. We found that 357

(21.5%) and 6 (0.4%) hub lakes (excluding the Mississippi network) had one dam or multiple dams directly on the lake, respectively. Additionally, even if a dam was not directly on a hub lake, there were 0 - 301 dams upstream and 1 - 18 dams downstream from hub lakes within the network, respectively. Hub lake surface area was a median of 15.4 ha (min = 1.0 ha; max = 107534.6 ha; Figure S3) compared with a median surface area of 4.0 ha (min = 1.0 ha; max = 129612.0 ha) for all network lakes.

**Network connectivity scores**

Network connectivity scores followed a left-skewed distribution (Figure 4a, b, S2). Of the 385 assessed networks with > 4 lakes (excluding the Mississippi River network), 286 (67.5%) received scores < 2 (low), 112 (29.1%) received scores between 2 and 4 (medium), and 13 (3.4%) received scores > 4 (high). Cutoffs for low, medium, and high scores were determined by visual inspection of the score distribution (Figure S2). In general, networks received high, medium, and low scores throughout the conterminous US, but greater concentrations of high-scoring networks were found in the western US (Figure 4a, b). Of the 13 networks with high scores, there were 3 in the WMT ecoregion, 2 each in the CPL, SAP, SPL, and XER ecoregions, and 1 each in the NAP and UMW ecoregions (Table 2). The 3 highest-scoring networks were the Colorado River (WMT), Rio Grande (SPL), and Columbia River (WMT) networks. The NPL and TPL ecoregions had no high-scoring networks. Connectivity scores and network characteristics for all 385 scored networks are provided in Table S2.

High-scoring networks were generally larger and contained more lakes and dams (Tables 2, S2). The 13 highest-scoring networks spanned 29.3 - 1330.3 km stream distance N-S (median = 498.6 km) and had 15 - 3241 lakes (median = 1303 lakes) and 0 - 1760 dams (median = 454 dams). Conversely, low- to medium-scoring networks ranged 0.9 - 553.9 km of stream distance N-S (median = 22.4 km) and had 5 - 2604 lakes (median = 13 lakes) and 0 - 1612 dams (median = 4 dams). Similarly, dam rate ranged 0.0 - 88.6% (median = 47.1%) across high-scoring networks and ranged 0.0 - 269.2% (median = 33.3%) across low- to medium-scoring networks. Dam rate was 100% or greater (i.e., at least as many dams as lakes) in 21 (5.5%) of scored networks. Just 66 (17.1%) of scored networks contained no dams, but these networks were relatively small in terms of lakes (5 - 64 lakes; median = 6 lakes) and N - S stream distance (0.9 - 186.4 km; median = 7.2 km). Finally, high-scoring networks had 0 - 72 hub lakes (median = 24) and low- to medium-scoring networks had 0 - 46 hub lakes (median = 1).

**Protection of freshwater networks, network lakes, and hub lakes**

Whole freshwater networks are poorly protected across the conterminous US (Tables 3, S3, Figure 5). Median network protection was 0.0% across all networks, except under the loosest definition of protection (14.4%; strict + multi-use, lake center protection) (Figure 5a, c). Fully protected networks were relatively rare and varied across definitions of protection (28 - 122 networks; 3.1 - 13.6% of networks). Under the narrowest and loosest definitions of protection, the WMT (10.1%, 22.0%), CPL (3.3%, 19.8%), and XER (2.3%, 22.1%) ecoregions had the highest rates of full network protection, respectively, and the SAP and SPL ecoregions had no fully protected networks based on any definition of protection. Approximately 13.4 - 47.6% of networks had at least 17% of their lakes protected from the narrowest to loosest definitions of protection, respectively. Across all ecoregions, the CPL ecoregion had the highest number of networks meeting the 17% Aichi target based on lake center protection, whereas the UMW, WMT, and XER ecoregions had the highest, most consistent percentage of networks meeting the

17% Aichi target across all definitions of protection. The SAP and SPL ecoregions consistently had the fewest networks meeting the 17% Aichi target across definitions of protection. The Mississippi River network, approximately 10 times larger than the next-largest network in terms of number of lakes, was 4.3 - 15.1% protected across all definitions of protection. Additionally, network connectivity scores (natural log-transformed) were not correlated with the percent of network protection under all definitions of protection (absolute Pearson's $r < 0.1$, $p = 0.21$ - $0.72$). Overall, although whole network protection varied widely across ecoregions and definitions of protection, most networks were poorly protected as a whole and there is little association between freshwater connectivity and protection. As expected, however, protection rates of whole networks were generally greater in the western US.



Across all network lakes, protection varied from 8.2 - 18.4% from the narrowest to loosest definition of protection (Table S4). Therefore, lake protection in the conterminous US only narrowly met the 17% Aichi target under a generous definition of protection. Network lake protection varied across ecoregions from a low of 0.8% in the SAP and TPL ecoregions to highs of 55.6% in the NPL and 61.4% in WMT ecoregions under the narrowest and loosest definitions of protection, respectively. The WMT and NPL ecoregions were the only ecoregions that met the 17% Aichi target across all definitions of protection. In contrast, The CPL, NAP, SAP, SPL, TPL, and XER ecoregions did not meet the 17% Aichi target under any definition of protection and were often near or below 5% protection. The UMW ecoregion met the 17% Aichi target only when considering both strict and multi-use protected areas.

Of the 2080 hub lakes in the conterminous US, 118 (5.7%) and 413 (19.8%) were protected under the narrowest and loosest definitions of protection, respectively, similar to protection levels of all network lakes (Figure 5b, d, Table S4). Therefore, the 17% Aichi target was only met for hub lakes under the loosest definition of protection. Across ecoregions, the WMT (36.1%), UMW (8.8%), and TPL (3.2%) ecoregions had the highest rates of hub lake protection under the narrowest definition of protection, whereas the WMT (68.0%), UMW (30.0%), and XER (31.6%) ecoregions had the highest rates of hub lake protection under the loosest definition of protection. These results were broadly consistent with our expectation of greater hub lake protection in the western US. The WMT ecoregion actually had a slightly higher hub lake protection rate under strict + multi-use 80% watershed protection (69.8%) than lake center protection, indicating that a few hubs themselves were not protected, but their watersheds largely were. Notably, the NPL ecoregion had only 5 hub lakes, one of which was protected based on both strict and multi-use lake center protection.



## Discussion

### Freshwater connectivity and dams

We found that the networks with the highest structural connectivity scores tended to be geographically expansive (median = 498.6 km north-south), but with higher dam rates (median = 47.1%). Presumably, dams represent human-made barriers within freshwater corridor networks. Aside from the 12 of 13 networks with high connectivity scores despite dams, the 66 smaller, undammed networks (median = 7.2 km N-S stream distance) provide relatively unimpeded localized corridor networks for organisms and species to move throughout networks. Importantly, many undammed networks were found along the West, East, and Great Lakes Coasts (Figure S1). These networks are important for many species, particularly diadromous fishes that use both fresh and saltwater for different life stages, and potamodromous fishes that use both the Great Lakes and inland waters for various life stages (D’Amelio et al. 2008, Hall et al. 2011). Nonetheless, our broad-scale analysis suggests that the largest freshwater corridor networks in the conterminous US generally contain abundant dams and may therefore limit functional connectivity, particularly for long-distance migrations and species range shifts under climate change.

Our analysis of freshwater network structure and network hubs indicates not only which networks are highly impacted, but also those most likely to benefit from restoration, particularly by focusing on hubs. Our finding that most hub lakes were reservoirs (72.3%) is not surprising, as reservoirs tend to fall on large rivers and are therefore likely central in freshwater networks. This suggests that connectivity within many networks may be considerably compromised due to the location of dams on or near hub lakes, likely due to a combination of altered hydrology and water chemistry, elevated water temperatures, and/or invasive species (Johnson et al. 2008). Therefore, regular monitoring at and near these centralized hubs can assist in early detection of invasive species and mitigation of further degradation of freshwater networks. Although outright removal of large reservoir dams is often societally challenging or unfeasible, connectivity mitigation measures (e.g., fish ladders, lifts) or dam modifications to enhance natural flow regimes at or near hubs could help restore some functionality in freshwater corridor networks (Renöfält et al. 2009, Muir & Williams 2012, McKay et al. 2013). Similarly, our identification of network hub lakes indicates where additional impoundments would most likely further reduce connectivity, especially for natural lakes whose natural hydrology is more intact compared to reservoirs. Conversely, the 27 hub lakes currently within undammed networks may be of particularly high conservation value for maintaining connectivity (Figure S1).

## Graph theory applications for freshwater conservation

Graph theory has previously been applied toward conservation in river networks (Erős et al. 2011, Erős & Lowe 2019), including to predict current and future species' ranges (Chaput-Bardy et al. 2017), but few studies have applied a similar framework to lakes (Saunders et al. 2016). Thus, our integration of both lake and stream variables in quantifying overall freshwater network connectivity represents a novel, coarse-filter approach to identifying potential freshwater corridor networks across multiple regions of the conterminous US. This repeatable approach leverages publicly available data and can be adjusted to accommodate specific taxa of interest or new or different connectivity variables at different spatial or temporal scales.

A way in which our work advances graph theory applications for freshwater ecology and conservation is through the use of hubs, which in our case were major lake nodes that disproportionately influenced freshwater network structure. The concept of hubs in freshwater ecology (Muirhead and MacIsaac 2005, Bishop-Taylor et al. 2015) or general landscape ecology (Minor & Urban 2008) as highly connected nodes is not new, but our characterization using multiple axes of lake-stream network analysis allows for a unified definition across all freshwater networks in the conterminous US and could be similarly applied elsewhere. Critical nodes, conceptually similar to hubs, have been previously identified for river networks, but without consideration of lakes (Sarker et al. 2019). Analogous efforts to identify important nodes have a longer history for terrestrial landscapes (e.g., Estrada & Bodin 2008, Saura & Rubio 2010), which have also often included ecological attributes of nodes (Saura & Torné 2009) unlike our species-neutral hub identification. "Stepping stone" characterization has been previously quantified using betweenness centrality (Zetterberg et al. 2010) and articulation points (Keitt et al. 1997), and our usage of total vertex strength is an extension of using the degree of a node with the added weight of the distance of those connections. Thus, our multi-metric approach to identifying lakes within a network that are potentially more important for maintaining corridor networks across large expanses extends past research and can help prioritize individual locations for conservation, particularly when whole-network conservation is impractical. Finally, although previous studies on patterns of freshwater biodiversity in relation to hub lakes and small ponds have only been conducted at landscape to regional scales, our flexible, continental-scale approach and dataset opens the door for broader-scale studies of freshwater biodiversity and connectivity.

**Implications for conservation planning under climate change**

Whereas all freshwater corridor networks can potentially play important roles in supporting the resilience of biodiversity under climate change, many such networks in the conterminous US are relatively small, contain many dams, and are susceptible to fragmentation. The relatively small number of large corridor networks, which are likely the only networks capable of supporting regional-scale migrations or species range shifts under climate change, generally are even more heavily dammed and structurally prone to fragmentation. Moreover, most freshwater corridor networks are currently poorly protected, not only falling short of the 17% Aichi target under most types of protection, but particularly so in regions with high freshwater biodiversity (i.e., southern, central, and eastern US). These findings indicate that considerable conservation effort may be required to facilitate important phenomena such as gene flow, migrations, and range shifts for freshwater biodiversity in the conterminous US. Moreover, water level fluctuations further threaten network connectivity as societal demands for water increase and droughts intensify under climate change, especially in the western US. Therefore, even "protected" waterbodies are not immune to changing hydrology owing to upstream water withdrawals or climate change.

Given limited or unpredictable resources for conservation, prioritizing the monitoring and protection of network hubs could represent a relatively efficient strategy for maintaining freshwater corridor networks, but our analysis shows that current protection levels of hub lakes are not only similar to all network lakes in general, but are also relatively low (19.9%; only meeting the 17% Aichi target under combined strict and multi-use, non-watershed protection). Nonetheless, our finding that hub lakes are predominantly reservoirs, indicates that the "well-connected" conservation objective within Aichi Target 11 is difficult to achieve when many network hubs are likely highly impacted in terms of hydrology, water temperature, water quality, and invasive species. All of these stressors are expected to worsen under climate change. As such, successful hub ecosystem conservation efforts might help restore and maintain network connectivity by striving to mitigate these negative consequences of impoundments, particularly given the general lack of representation of waterbodies and their watersheds in protected areas. Although connectivity broadly benefits biodiversity under climate change, it is important to consider that in the freshwater realm, this generally means connectivity associated with more natural hydrologic regimes.



The 2020 assessment of progress toward the 17% Aichi conservation target for fresh waters identified current gaps in ecological representation and connectivity globally. Our analysis reinforces the notion that current US protected areas do not contain an ecologically representative portfolio of fresh waters (Jenkins et al. 2015, McCullough et al. 2019b), but also shows that considerable work is still needed to promote and improve protection of freshwater connectivity. Under a changing climate, ensuring functional connectivity for freshwater biodiversity is a key priority. Across the 13 high-scoring freshwater networks, 4 networks met the 17% Aichi target across all definitions of protection, 6 networks did not meet the target under any definition of protection, whereas results were mixed for the remaining 3 networks. This generally reflects the concentration of large protected areas in the western US. For example, the Savannah-Santee, Suwannee River, and James River networks in the eastern US (ranked #7, 9 and 11 nationally by connectivity score, respectively; Figure 4a, b) are 0.0 - 5.2% protected across all definitions of protection (Table 2). In contrast, the 3 highest-scoring networks in the WMT ecoregion (Colorado River, Columbia River, and San Francisco Bay networks, ranked #1, 2, and 4, respectively) were 32.5 - 72.6% protected across all definitions of protection. These findings not only reinforce the previously identified national-scale mismatches between protected areas and freshwater biodiversity (Jenkins et al. 2015), but also indicate regional mismatches between protected areas and freshwater connectivity in the southern, central, and eastern US (Fig 3). On the positive side, however, overlap between freshwater biodiversity and several large freshwater corridor networks in these regions suggests that efforts to maintain or enhance these corridor networks could help support populations and the resilience of regional freshwater biodiversity to climate change (e.g., facilitate seasonal migrations and range shifts). Moreover, conservation prioritization of hub lakes may be disproportionately more beneficial and cost-effective for conservation under climate change as generalized percent network protection targets (17% or otherwise) given their large effects on network intactness.

We envision our data, concepts of freshwater corridor networks and hubs, and analytical approach making foundational contributions to future conservation efforts, including fully data-driven systematic conservation planning or more participatory structured decision-making involving managers and stakeholders. Our use of basic computational techniques (i.e., PCA) and public data at scales of both individual lakes and whole lake-stream networks creates flexibility for future studies to integrate other relevant datasets at different spatial and temporal scales or to tailor their approaches to species, taxa, or functional groups of interest. For example, the average lake distance variable (Table 1) could be parameterized to identify lakes or networks that are more accessible for dispersal-limited species or particularly vulnerable to rapid spread of invasive species. Our coarse-filter approach targeting generalized structural connectivity in a climate change context is only one example of many potential applications. For example, studies interested in restoring anadromous fish migrations could integrate a similar structural connectivity scoring approach with more localized data on features such as waterfalls and culverts to identify networks most likely to benefit from interventions to enhance connectivity. Additionally, studies interested in maintaining access to permanent waterbodies in dry climates could integrate structural connectivity data with seasonal hydrology or other habitat data (e.g., lake or stream depth). Moreover, there is potential to analyze the joint freshwater-terrestrial conservation benefits of freshwater corridor networks, given that riparian areas often represent terrestrial corridor networks (Krosby et al. 2018) and regulate water temperature, chemistry, and physical habitat characteristics (Johnson and Almlof 2016). Although such efforts are beyond the scope of this current study, our study and approach demonstrate the potential for future connectivity studies to help advance conservation planning under climate change, particularly for freshwater biodiversity and ecosystems.



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## Tables

Table 1. Description of network-scale freshwater connectivity metrics and ecological justification for their use in broad-scale freshwater corridor identification

| Variable name | Description | Ecological Justification |
|---|---|---|
| Edge density | Ratio of stream reaches connecting lakes to the maximum number of potential stream reaches in a theoretical, complete network | Represents availability of pathways for traveling within a network |
| Average lake distance (km) | Average stream-course distance between lakes | Represents density and accessibility of lakes within a network |
| Dam rate | Ratio between the number of lakes and number of dams* | Represents density of connectivity barriers within networks |
| Elevation range (m) | Maximum minus minimum elevation among network lakes | Represents more localized climatic heterogeneity accessible within a network for both relatively mobile and sessile species |
| Maximum north-south distance (km) | Maximum north-south distance spanned by the network based on lake and stream connections | Represents large-scale climatic heterogeneity accessible within a network for relatively mobile species |
| Minimum cuts | Minimum number of stream reaches to cut needed to undermine maximum north-south distance | Represents susceptibility of a network to fragmentation, particularly in climatic context for relatively mobile species |
| Percent articulation points | The percent of lakes in the network that are articulation points, which are the lakes in the graph that prevent separation into multiple subnetworks* | Represents susceptibility of a network to fragmentation |
| Average betweenness centrality | The number of shortest-distance pairwise stream paths in a network that pass through a lake, averaged across network lakes after normalization by the number of lakes within a network (N) using the formula (2BC)/(N*N-3N+2) | Represents lake importance according to position within a network and the convergence of stream pathways |

*variable rescaled such that higher values represent greater connectivity

Table 2. Freshwater network connectivity scores and statistics and protection status of networks and hub lakes in the conterminous US for high-scoring networks

| Rank | Score | Network | Ecoregion | Lakes | Hubs | Dams | Dam rate* | North-South distance (km) |
|---|---|---|---|---|---|---|---|---|
| 1 | 12.02 | Colorado River | WMT | 2027 | 42 | 954 | 47.1% | 1,330.34 |
| 2 | 9.49 | Rio Grande | SPL | 536 | 13 | 388 | 72.4% | 1,312.70 |
| 3 | 8.10 | Columbia River | WMT | 2397 | 55 | 915 | 38.2% | 820.36 |
| 4 | 6.70 | Sacramento/San Joaquin | WMT | 1780 | 49 | 484 | 27.2% | 629.52 |
| 5 | 6.21 | Brazos River | SPL | 1529 | 22 | 1273 | 83.3% | 611.93 |
| 6 | 5.67 | Susquehanna-Hudson | NAP | 2659 | 71 | 1099 | 41.3% | 505.40 |
| 7 | 5.19 | Savannah-Santee | CPL | 3241 | 72 | 1760 | 54.3% | 491.73 |
| 8 | 5.19 | Potomac River | SAP | 420 | 9 | 372 | 88.6% | 238.12 |
| 9 | 4.94 | Suwannee | CPL | 1076 | 38 | 268 | 24.9% | 245.86 |
| 10 | 4.84 | Red River | UMW | 754 | 16 | 250 | 33.2% | 380.41 |
| 11 | 4.40 | James River | SAP | 765 | 24 | 424 | 55.4% | 173.63 |
| 12 | 4.03 | Lake Creek | XER | 15 | 0 | 0 | 0.0% | 29.30 |
| 13 | 4.01 | Humboldt River | XER | 21 | 1 | 43 | 204.8% | 146.39 |

*Dam rate = number of dams/number of lakes. CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT-Western Mountains, XER=Xeric. Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)

Table 3. Protection status of networks and hub lakes in the conterminous US for high-scoring networks

| | | Network protection | | | | Hub protection | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Network | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed |
| 1 | Colorado River | 41.1% | 68.9% | 39.1% | 72.6% | 26.2% | 83.3% | 26.2% | 76.2% |
| 2 | Rio Grande | 17.2% | 30.4% | 11.2% | 30.0% | 0.0% | 23.1% | 0.0% | 30.8% |
| 3 | Columbia River | 36.3% | 67.0% | 32.5% | 67.0% | 12.7% | 43.6% | 16.4% | 47.3% |
| 4 | Sacramento/San Joaquin | 52.9% | 65.3% | 51.5% | 62.4% | 46.9% | 59.2% | 42.9% | 46.9% |
| 5 | Brazos River | 1.8% | 2.4% | 0.9% | 1.0% | 22.7% | 22.7% | 9.1% | 9.1% |
| 6 | Susquehanna-Hudson | 5.3% | 11.7% | 11.9% | 15.8% | 12.7% | 19.7% | 4.2% | 9.9% |
| 7 | Savannah-Santee | 1.8% | 2.7% | 0.6% | 1.2% | 6.9% | 6.9% | 0.0% | 0.0% |
| 8 | Potomac River | 5.2% | 11.7% | 5.5% | 10.0% | 11.1% | 33.3% | 11.1% | 22.2% |
| 9 | Suwannee | 0.5% | 1.2% | 0.0% | 0.2% | 2.6% | 7.9% | 0.0% | 0.0% |
| 10 | Red River | 17.1% | 23.9% | 3.3% | 4.4% | 18.8% | 18.8% | 6.3% | 12.5% |
| 11 | James River | 2.7% | 5.2% | 0.7% | 3.0% | 0.0% | 8.3% | 0.0% | 0.0% |
| 12 | Lake Creek | 6.7% | 53.3% | 0.0% | 20.0% | NA | NA | NA | NA |
| 13 | Humboldt River | 28.6% | 47.6% | 23.8% | 76.2% | 0.0% | 0.0% | 0.0% | 100.0% |

CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT-Western Mountains, XER=Xeric. Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)

**Figure Captions**

**Figure. 1.** Freshwater connectivity in Michigan, USA based on (a) an intact network with an operational hub lake and (b) a compromised hub lake, which results in network fragmentation and possible upstream habitat loss for freshwater biodiversity. Upstream streams are grayed out in (b) to represent loss of stream habitat. Isolated lakes are not accessible through networks.

**Figure. 2. (**a) Freshwater networks of the conterminous US based on LAGOS-US-NETWORKS v1.0 (King et al. 2021 b, c). Contiguous colors represent individual networks (the largest of which is the Mississippi River basin in green in the central US). Shown are 898 unique networks containing a total of 86511 lakes ≥ 1 ha. (b) Ecoregions used by the US Environmental Protection Agency National Aquatic Resource Survey (Herlihy et al. 2008). CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric. (c) Strict (managed for biodiversity; GAPS 1-2) and multi-use (managed for biodiversity and natural resource extraction; GAP 3) protected areas based on the US Protected Areas Database v2.0 (US Geological Survey 2018).



**Figure. 3.** Graphical depiction of a hypothetical network showing the three network metrics used to define a hub lake: (a) vertex strength of each lake colored by quintile, (b) betweenness centrality of each lake colored by quintile, (c) lakes that are articulation points outlined in green and showing the subnetworks created by the removal of the central lake marked by “X”. Hub lakes for the network (d) are those that are in the top quintile of vertex strength, the top quintile of betweenness centrality, and are articulation points.

**Figure. 4.** (a) Freshwater network connectivity scores (for networks > 4 lakes) and hub lakes (n = 2080). The Mississippi River network (unscored) is shown in light blue dots. (b) Highest-ranking freshwater network connectivity scores. Unique mapped colors represent individual, contiguous networks with high connectivity scores (n = 13), which are ranked by connectivity score (1 = highest).

**Figure. 5.** Percent of freshwater networks (lakes within networks) and hub lakes protected by NARS ecoregion and different levels of protection. The Mississippi River network (considered separately) has 7.6% and 15.1% of its lakes protected, respectively, under strict and strict + multi-use lake center protection (a), and 4.3% and 13.8% of its lakes protected, respectively, under strict and strict + multi-use 80% watershed protection, respectively (c). Mississippi River network hubs are reflected in (b) and (d). Dashed lines represent the 17% Aichi conservation target. See Table S1 for number of networks and hub lakes per ecoregion. CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric.

## Figures

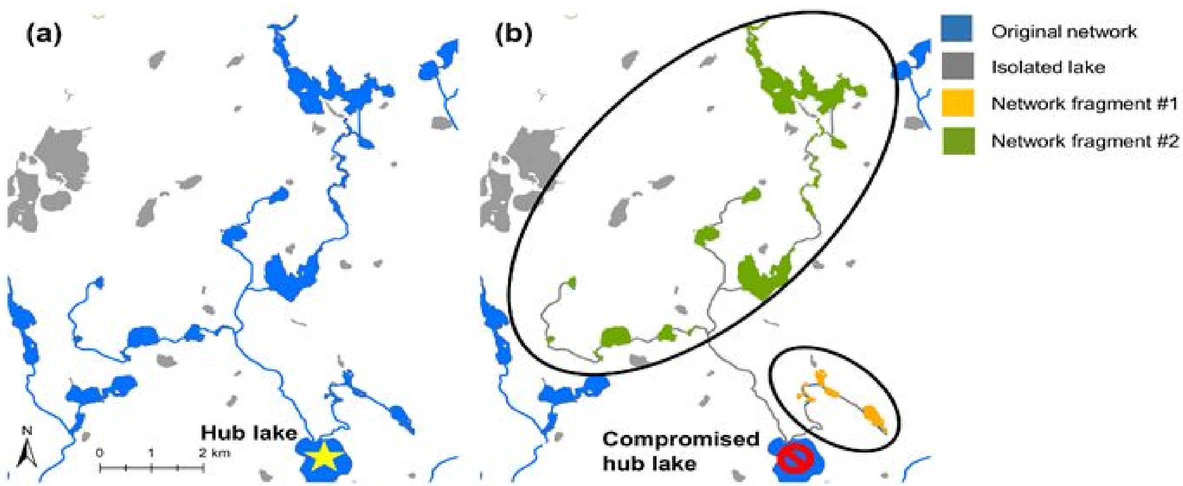



**Figure. 1.** Freshwater connectivity in Michigan, USA based on (a) an intact network with an operational hub lake and (b) a compromised hub lake, which results in network fragmentation and possible upstream habitat loss for freshwater biodiversity. Upstream streams are grayed out in (b) to represent loss of stream habitat. Isolated lakes are not accessible through networks.

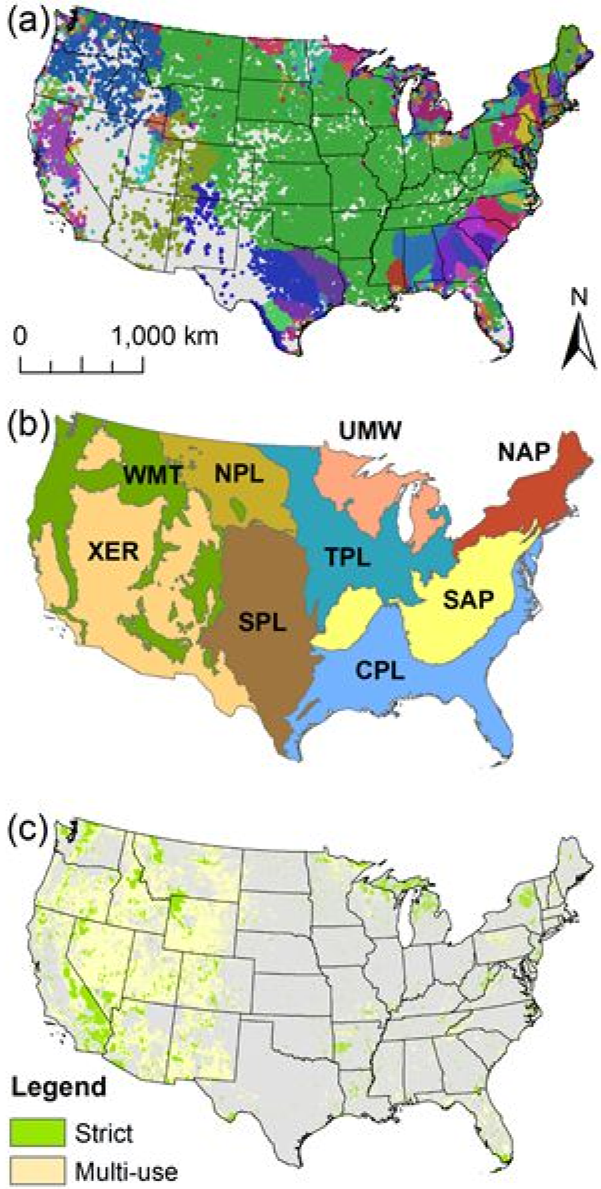



**Figure. 2.** (a) Freshwater networks of the conterminous US based on LAGOS-US-NETWORKS v1.0 (King et al. 2021 b, c). Contiguous colors represent individual networks (the largest of which is the Mississippi River basin in green in the central US). Shown are 898 unique networks containing a total of 86511 lakes ≥ 1 ha. (b) Ecoregions used by the US Environmental Protection Agency National Aquatic Resource Survey (Herlihy et al. 2008). CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, WMT=Western Mountains, UMW=Upper Midwest, XER=Xeric. (c) Strict (managed for biodiversity; GAPS 1-2) and multi-use (managed for biodiversity and natural resource extraction; GAP 3) protected areas based on the US Protected Areas Database v2.0 (US Geological Survey 2018).

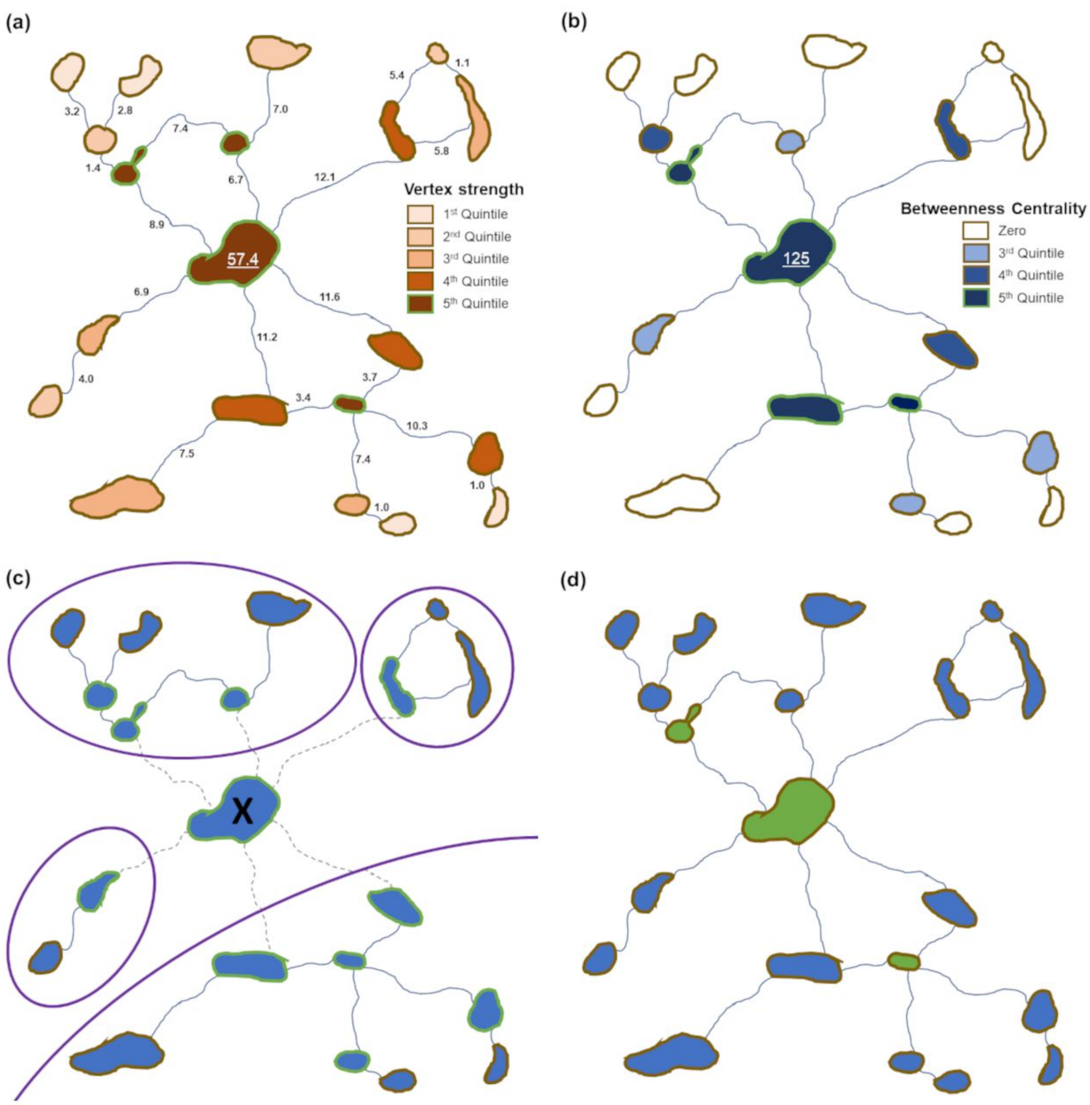
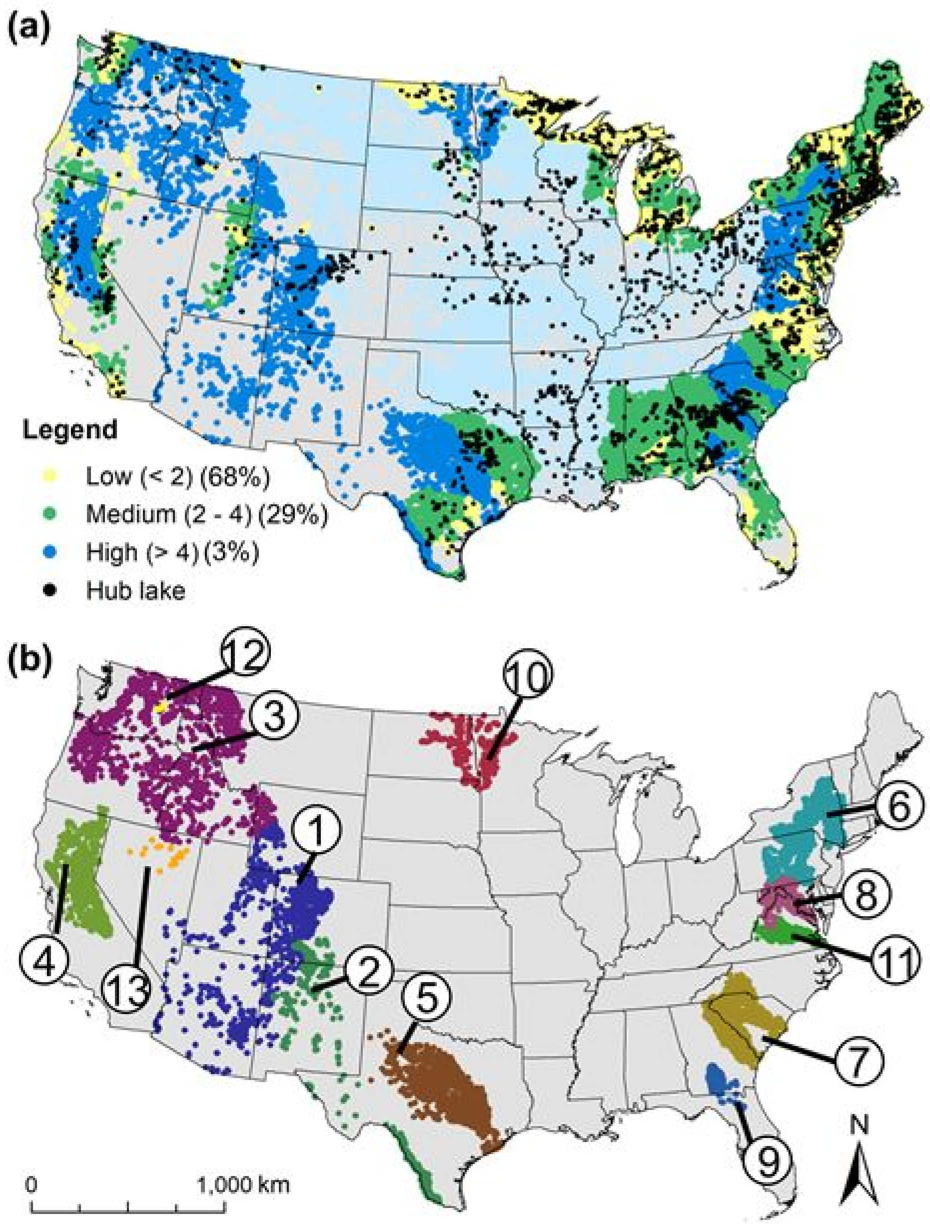



**Figure. 3.** Graphical depiction of a hypothetical network showing the three network importance metrics used to define a hub lake: (a) vertex strength of each lake colored by quintile, (b) betweenness centrality of each lake colored by quintile, (c) lakes that are articulation points outlined in green and showing the subnetworks created by the removal of the central lake marked by "X". Hub lakes for the network (d) are those that are in the top quintile of vertex strength, the top quintile of betweenness centrality, and are articulation points.

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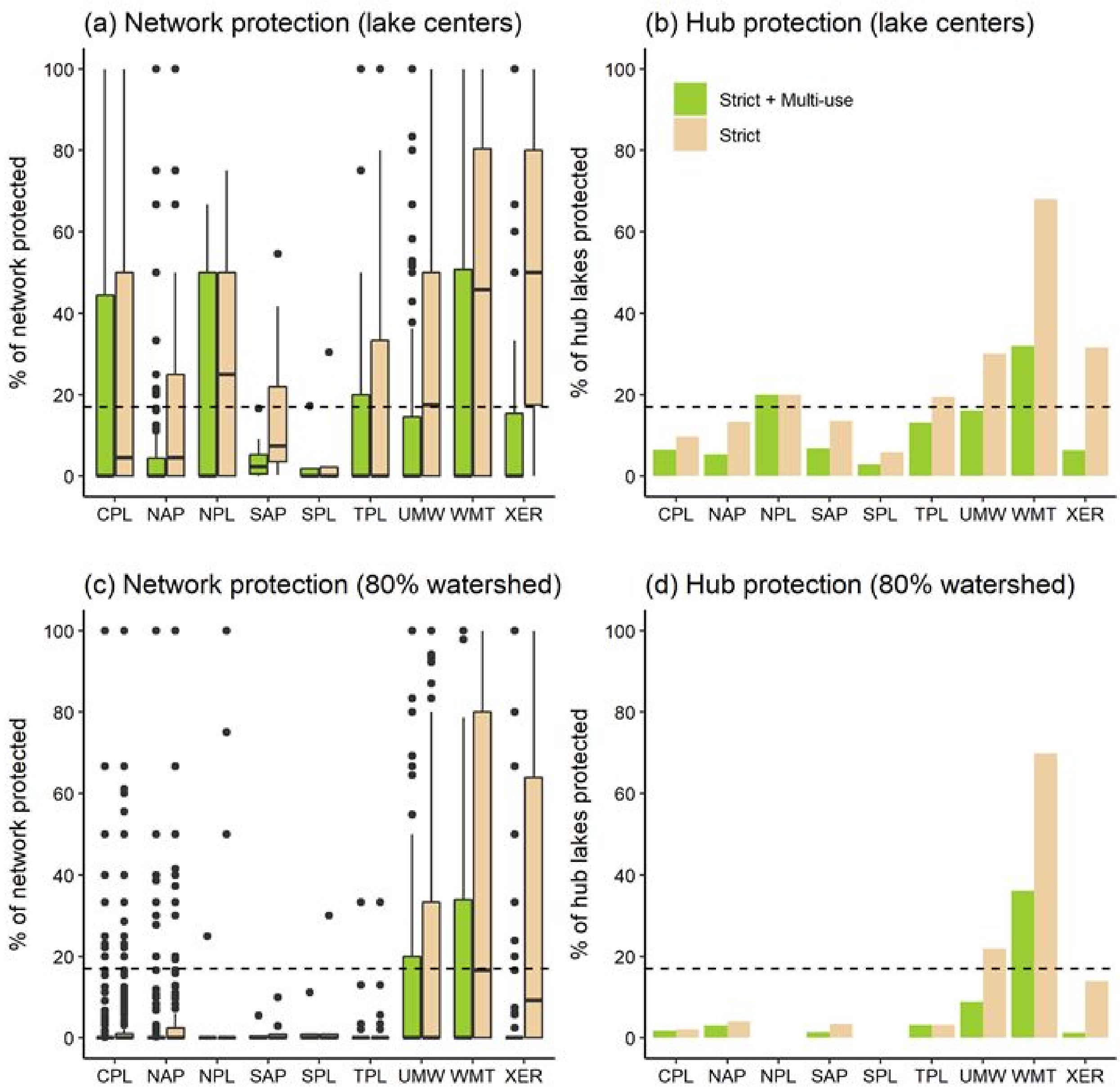


**Figure. 5.** Percent of freshwater networks (lakes within networks) and hub lakes protected by NARS ecoregion and different levels of protection. The Mississippi River network (considered separately) has 7.6% and 15.1% of its lakes protected, respectively, under strict and strict + multi-use lake center protection (a), and 4.3% and 13.8% of its lakes protected, respectively, under strict and strict + multi-use 80% watershed protection, respectively (c). Mississippi River network hubs are reflected in (b) and (d). Dashed lines represent the 17% Aichi conservation target. See Table S1 for number of networks and hub lakes per ecoregion. CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric.

**Supporting information**

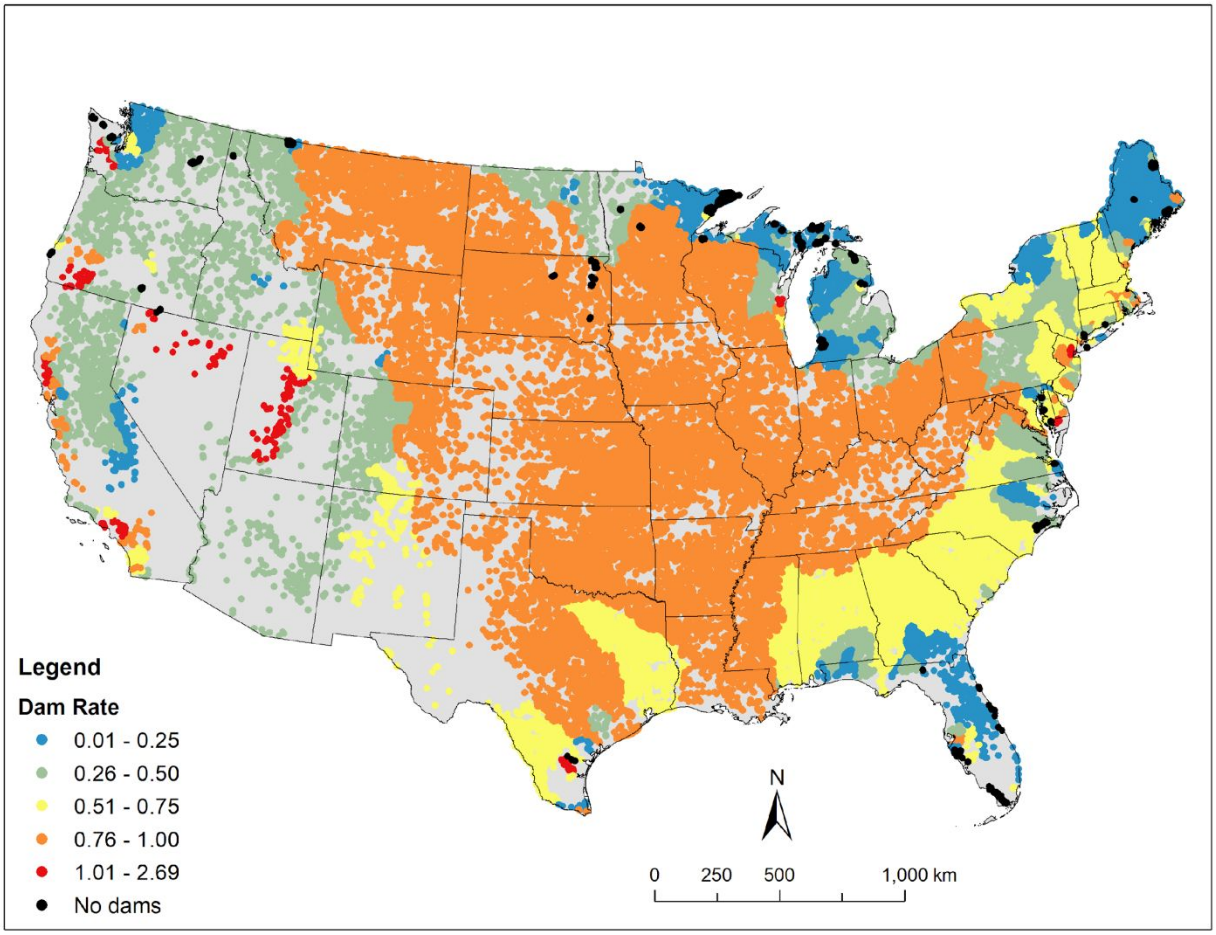


**Figure. S1.** Dam rate (number of lakes ≥ 1 ha divided by number of dams; unmodified before use in principal component analysis) in freshwater networks of the conterminous US. Shown are networks with > 4 lakes ≥ 1 ha per network (386 networks). Of these, 66 have no dams.

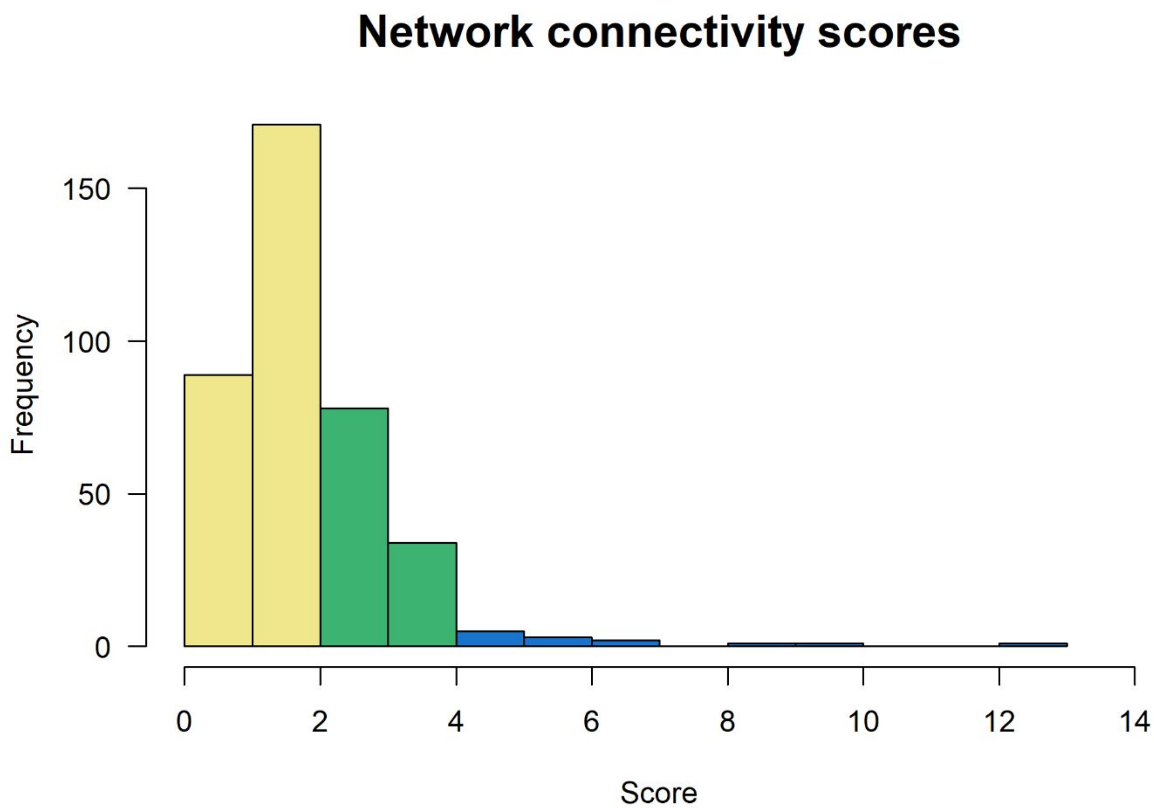


**Figure. S2.** Frequency distribution of freshwater network connectivity scores (n=385). Colors correspond to Fig. 4a.

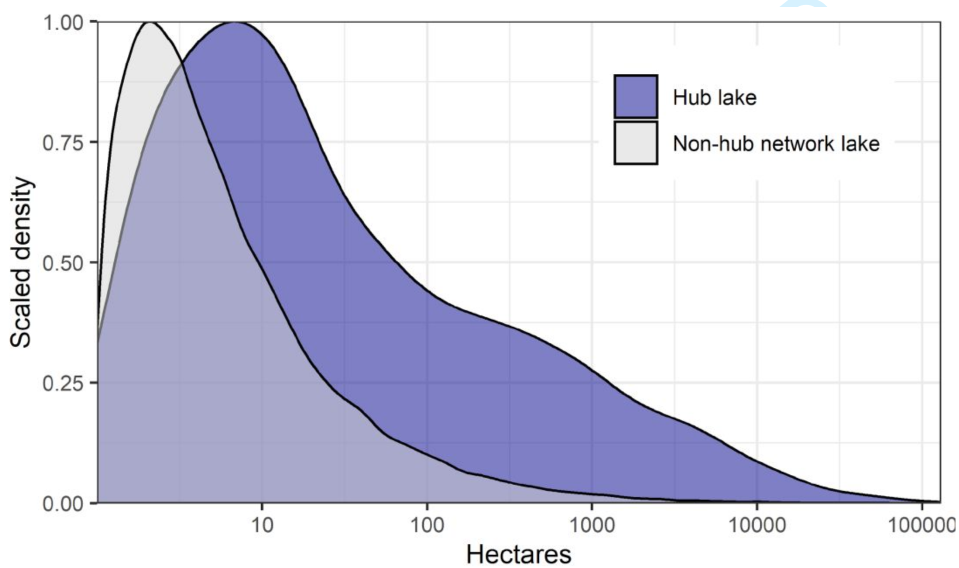


**Figure. S3.** Scaled density plot of the surface area (ha) of hub lakes (n = 2080) and non-hub lakes (n = 84431) in freshwater networks.

Table S1. Descriptive statistics of freshwater networks in the conterminous US

| Ecoregion[a] | Total Networks[b] | Number of lakes (min, median, max) | North-South distance (km) (min, median, max) | Number of dams (min, median, max) | % Articulation points (min, median, max) | Min cuts to disrupt max N-S distance (min, median, max) | Network lakes (number and % outside of MS River network) | Total network lakes (including MS River network) | Total hub lakes | % Hub lakes |
|---|---|---|---|---|---|---|---|---|---|---|
| CPL | 243 | 2, 3, 3241 | 0.0, 3.1, 539.4 | 0, 1, 1760 | 0.0, 0.0, 77.8 | 1, 1, 550 | 14862 (81.1%) | 18336 | 528 | 2.9% |
| NAP | 206 | 2, 4, 2659 | 0.0, 7.0, 505.4 | 0, 2, 1099 | 0.0, 31.2, 62.5 | 1, 1, 44 | 11934 (95.8%) | 12464 | 451 | 3.6% |
| NPL | 28 | 2, 2, 6 | 0.2, 2.5, 15.1 | 0, 0, 2 | 0.0, 0.0, 66.7 | 1, 1, 3 | 93 (1.1%) | 8166 | 5 | 0.1% |
| SAP | 10 | 11, 362, 1665 | 27.4, 139.7, 553.9 | 3, 159, 944 | 10.2, 21.1, 66.7 | 1, 4, 426 | 8287 (69.8%) | 11872 | 295 | 2.5% |
| SPL | 8 | 2, 166, 1529 | 0.6, 97.3, 1312.7 | 1, 132, 1273 | 0.0, 22.3, 40.0 | 1, 1, 65 | 2692 (39.2%) | 6871 | 103 | 1.5% |
| TPL | 58 | 2, 3, 0147 | 0.2, 4.4, 147.5 | 0, 0, 58 | 0.0, 33.3, 77.8 | 1, 1, 84 | 1073 (12.9%) | 8297 | 190 | 2.3% |
| UMW | 150 | 2, 4, 1190 | 0.0, 7.4, 380.4 | 0, 0, 250 | 0.0, 25.0, 75.0 | 1, 1, 30 | 6115 (63.1%) | 9691 | 260 | 2.7% |
| WMT | 108 | 2, 3, 2397 | 0.0, 8.5, 1330.3 | 0, 1, 954 | 0.0, 0.0, 60.0 | 1, 1, 131 | 6614 (78.0%) | 8476 | 169 | 2.0% |
| XER | 86 | 2, 3, 0105 | 0.2, 13.3, 216.8 | 0, 2, 68 | 0.0, 11.0, 86.7 | 1, 1, 18 | 2030 (86.8%) | 2338 | 79 | 3.4% |
| Overall | 897 | 2, 3, 3241 | 0.0, 5.9, 1330.3 | 0, 1, 1760 | 0.0, 21.1, 86.7 | 1, 1, 550 | 53700 (62.07%) | 86511 | 2080 | 2.4% |

[a]CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, XER=Xeric

[b]Mississippi River basin network removed (32811 lakes, 24986 dams) in calculating columns 2-7

Table S2. Freshwater network connectivity scores and statistics and protection status[a] of networks and hub lakes in the conterminous US

| | | | | | | | | | | Network protection | | | | Hub protection | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Net ID[b] | Rank | Score | Level | Ecoregion[c] | Lakes | Hubs | Dams | Dam rate[d] | North-South distance (km) | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed |
| 3 | 1 | 12.02 | High | WMT | 2027 | 42 | 954 | 47.1% | 1,330.34 | 41.1% | 68.9% | 39.1% | 72.6% | 26.2% | 83.3% | 26.2% | 76.2% |
| 52 | 2 | 9.49 | High | SPL | 536 | 13 | 388 | 72.4% | 1,312.70 | 17.2% | 30.4% | 11.2% | 30.0% | 0.0% | 23.1% | 0.0% | 30.8% |
| 34 | 3 | 8.10 | High | WMT | 2397 | 55 | 915 | 38.2% | 820.36 | 36.3% | 67.0% | 32.5% | 67.0% | 12.7% | 43.6% | 16.4% | 47.3% |
| 59 | 4 | 6.70 | High | WMT | 1780 | 49 | 484 | 27.2% | 629.52 | 52.9% | 65.3% | 51.5% | 62.4% | 46.9% | 59.2% | 42.9% | 46.9% |
| 50 | 5 | 6.21 | High | SPL | 1529 | 22 | 1273 | 83.3% | 611.93 | 1.8% | 2.4% | 0.9% | 1.0% | 22.7% | 22.7% | 9.1% | 9.1% |
| 10 | 6 | 5.67 | High | NAP | 2659 | 71 | 1099 | 41.3% | 505.40 | 5.3% | 11.7% | 11.9% | 15.8% | 12.7% | 19.7% | 4.2% | 9.9% |
| 2 | 7 | 5.19 | High | CPL | 3241 | 72 | 1760 | 54.3% | 491.73 | 1.8% | 2.7% | 0.6% | 1.2% | 6.9% | 6.9% | 0.0% | 0.0% |
| 90 | 8 | 5.19 | High | SAP | 420 | 9 | 372 | 88.6% | 238.12 | 5.2% | 11.7% | 5.5% | 10.0% | 11.1% | 33.3% | 11.1% | 22.2% |
| 36 | 9 | 4.94 | High | CPL | 1076 | 38 | 268 | 24.9% | 245.86 | 0.5% | 1.2% | 0.0% | 0.2% | 2.6% | 7.9% | 0.0% | 0.0% |
| 11 | 10 | 4.84 | High | UMW | 754 | 16 | 250 | 33.2% | 380.41 | 17.1% | 23.9% | 3.3% | 4.4% | 18.8% | 18.8% | 6.3% | 12.5% |
| 15 | 11 | 4.40 | High | SAP | 765 | 24 | 424 | 55.4% | 173.63 | 2.7% | 5.2% | 0.7% | 3.0% | 0.0% | 8.3% | 0.0% | 0.0% |
| 106 | 12 | 4.03 | High | XER | 15 | 0 | 0 | 0.0% | 29.30 | 6.7% | 53.3% | 0.0% | 20.0% | NA | NA | NA | NA |
| 95 | 13 | 4.01 | High | XER | 21 | 1 | 43 | 204.8 % | 146.39 | 28.6% | 47.6% | 23.8% | 76.2% | 0.0% | 0.0% | 0.0% | 100.0% |
| 6 | 14 | 3.67 | Medium | CPL | 2604 | 66 | 1612 | 61.9% | 482.56 | 1.3% | 2.0% | 1.1% | 2.1% | 1.5% | 3.0% | 0.0% | 0.0% |
| 20 | 15 | 3.63 | Medium | NAP | 1118 | 37 | 746 | 66.7% | 434.21 | 4.4% | 22.4% | 1.5% | 9.7% | 0.0% | 10.8% | 0.0% | 0.0% |
| 279 | 16 | 3.59 | Medium | TPL | 9 | 0 | 1 | 11.1% | 4.48 | 11.1% | 33.3% | 0.0% | 0.0% | NA | NA | NA | NA |
| 24 | 17 | 3.58 | Medium | CPL | 1810 | 61 | 910 | 50.3% | 316.38 | 2.5% | 3.3% | 1.0% | 1.6% | 8.2% | 9.8% | 4.9% | 4.9% |
| 313 | 18 | 3.49 | Medium | UMW | 8 | 0 | 0 | 0.0% | 6.67 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 112 | 19 | 3.49 | Medium | TPL | 5 | 0 | 9 | 180.0 % | 17.39 | 20.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 28 | 20 | 3.46 | Medium | SAP | 1665 | 37 | 944 | 56.7% | 553.87 | 2.0% | 2.6% | 0.5% | 0.9% | 0.0% | 0.0% | 0.0% | 0.0% |
| 47 | 21 | 3.40 | Medium | NAP | 1463 | 38 | 754 | 51.5% | 355.69 | 6.4% | 13.7% | 2.3% | 4.2% | 7.9% | 13.2% | 2.6% | 2.6% |
| 32 | 22 | 3.40 | Medium | WMT | 122 | 6 | 49 | 40.2% | 289.10 | 55.7% | 71.3% | 52.5% | 65.6% | 16.7% | 50.0% | 16.7% | 33.3% |
| 21 | 23 | 3.38 | Medium | CPL | 516 | 7 | 107 | 20.7% | 539.44 | 3.9% | 10.1% | 1.7% | 6.4% | 14.3% | 28.6% | 0.0% | 0.0% |
| 192 | 24 | 3.37 | Medium | CPL | 26 | 0 | 18 | 69.2% | 30.59 | 0.0% | 7.7% | 0.0% | 11.5% | NA | NA | NA | NA |
| 423 | 25 | 3.33 | Medium | CPL | 9 | 0 | 7 | 77.8% | 8.36 | 100.0% | 100.0% | 22.2% | 22.2% | NA | NA | NA | NA |
| 766 | 26 | 3.32 | Medium | CPL | 5 | 0 | 0 | 0.0% | 3.92 | 20.0% | 40.0% | 0.0% | 60.0% | NA | NA | NA | NA |
| 721 | 27 | 3.32 | Medium | CPL | 5 | 0 | 0 | 0.0% | 3.13 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 247 | 28 | 3.32 | Medium | NAP | 6 | 0 | 2 | 33.3% | 6.29 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 627 | 29 | 3.30 | Medium | CPL | 6 | 0 | 1 | 16.7% | 13.85 | 0.0% | 0.0% | 0.0% | 16.7% | NA | NA | NA | NA |
| 48 | 30 | 3.30 | Medium | CPL | 1603 | 67 | 1176 | 73.4% | 452.01 | 0.9% | 2.6% | 0.6% | 0.9% | 0.0% | 0.0% | 0.0% | 0.0% |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 406 | 31 | 3.30 | Medium | UMW | 10 | 0 | 1 | 10.0% | 8.35 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 342 | 32 | 3.30 | Medium | CPL | 8 | 0 | 2 | 25.0% | 16.62 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 77 | 33 | 3.29 | Medium | TPL | 7 | 0 | 2 | 28.6% | 22.42 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 355 | 34 | 3.27 | Medium | CPL | 10 | 0 | 5 | 50.0% | 44.63 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 248 | 35 | 3.27 | Medium | CPL | 6 | 0 | 2 | 33.3% | 20.58 | 0.0% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 382 | 36 | 3.27 | Medium | WMT | 5 | 0 | 2 | 40.0% | 19.30 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 411 | 37 | 3.26 | Medium | CPL | 9 | 0 | 0 | 0.0% | 18.43 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 256 | 38 | 3.25 | Medium | CPL | 5 | 0 | 0 | 0.0% | 18.09 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 132 | 39 | 3.24 | Medium | WMT | 108 | 4 | 12 | 11.1% | 206.64 | 71.3% | 97.2% | 78.7% | 95.4% | 0.0% | 75.0% | 25.0% | 75.0% |
| 9 | 40 | 3.23 | Medium | CPL | 2247 | 36 | 1209 | 53.8% | 315.88 | 1.5% | 4.5% | 1.2% | 1.7% | 5.6% | 11.1% | 0.0% | 0.0% |
| 673 | 41 | 3.20 | Medium | WMT | 6 | 0 | 2 | 33.3% | 17.11 | 0.0% | 33.3% | 0.0% | 33.3% | NA | NA | NA | NA |
| 100 | 42 | 3.18 | Medium | CPL | 249 | 11 | 93 | 37.3% | 187.67 | 0.8% | 1.2% | 0.4% | 0.8% | 0.0% | 0.0% | 0.0% | 0.0% |
| 58 | 43 | 3.14 | Medium | CPL | 441 | 12 | 255 | 57.8% | 260.08 | 4.3% | 5.2% | 1.8% | 3.2% | 0.0% | 0.0% | 0.0% | 0.0% |
| 376 | 44 | 3.13 | Medium | CPL | 9 | 0 | 0 | 0.0% | 186.40 | 44.4% | 66.7% | 33.3% | 55.6% | NA | NA | NA | NA |
| 33 | 45 | 3.07 | Medium | NAP | 1731 | 76 | 286 | 16.5% | 392.07 | 3.8% | 8.4% | 6.8% | 11.1% | 1.3% | 5.3% | 2.6% | 2.6% |
| 66 | 46 | 3.07 | Medium | NPL | 6 | 0 | 0 | 0.0% | 5.12 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 94 | 47 | 3.04 | Medium | CPL | 7 | 0 | 5 | 71.4% | 7.46 | 14.3% | 14.3% | 0.0% | 28.6% | NA | NA | NA | NA |
| 371 | 48 | 2.99 | Medium | WMT | 16 | 0 | 17 | 106.3% | 91.36 | 0.0% | 18.8% | 0.0% | 6.3% | NA | NA | NA | NA |
| 64 | 49 | 2.98 | Medium | UMW | 825 | 16 | 220 | 26.7% | 266.80 | 2.2% | 7.6% | 1.0% | 1.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 69 | 50 | 2.98 | Medium | CPL | 26 | 0 | 11 | 42.3% | 38.73 | 3.8% | 3.8% | 0.0% | 0.0% | NA | NA | NA | NA |
| 189 | 51 | 2.93 | Medium | WMT | 133 | 7 | 2 | 1.5% | 141.71 | 97.7% | 99.2% | 97.7% | 98.5% | 100.0% | 100.0% | 100.0% | 100.0% |
| 93 | 52 | 2.93 | Medium | CPL | 23 | 0 | 9 | 39.1% | 36.70 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 136 | 53 | 2.92 | Medium | XER | 21 | 1 | 30 | 142.9% | 101.57 | 4.8% | 9.5% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 99 | 54 | 2.89 | Medium | XER | 105 | 3 | 68 | 64.8% | 216.83 | 13.3% | 29.5% | 5.7% | 31.4% | 0.0% | 0.0% | 0.0% | 0.0% |
| 800 | 55 | 2.80 | Medium | CPL | 5 | 0 | 0 | 0.0% | 0.86 | 100.0% | 100.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 407 | 56 | 2.79 | Medium | NAP | 5 | 0 | 0 | 0.0% | 3.31 | 20.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 685 | 57 | 2.79 | Medium | CPL | 5 | 1 | 0 | 0.0% | 3.37 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 550 | 58 | 2.79 | Medium | TPL | 5 | 0 | 0 | 0.0% | 4.63 | 20.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 287 | 59 | 2.78 | Medium | TPL | 5 | 0 | 0 | 0.0% | 5.51 | 20.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 364 | 60 | 2.78 | Medium | TPL | 5 | 0 | 0 | 0.0% | 6.43 | 20.0% | 80.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 457 | 61 | 2.76 | Medium | TPL | 5 | 0 | 0 | 0.0% | 7.27 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 314 | 62 | 2.75 | Medium | CPL | 72 | 1 | 9 | 12.5% | 29.84 | 100.0% | 100.0% | 4.2% | 4.2% | 100.0% | 100.0% | 0.0% | 0.0% |
| 762 | 63 | 2.73 | Medium | XER | 5 | 0 | 0 | 0.0% | 17.56 | 0.0% | 80.0% | 0.0% | 100.0% | NA | NA | NA | NA |
| 264 | 64 | 2.72 | Medium | WMT | 5 | 0 | 0 | 0.0% | 5.26 | 0.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 282 | 65 | 2.72 | Medium | NAP | 5 | 1 | 0 | 0.0% | 3.05 | 0.0% | 0.0% | 40.0% | 40.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 30 | 66 | 2.68 | Medium | UMW | 20 | 1 | 4 | 20.0% | 46.90 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 516 | 67 | 2.68 | Medium | WMT | 5 | 1 | 1 | 20.0% | 2.65 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 681 | 68 | 2.63 | Medium | XER | 7 | 2 | 0 | 0.0% | 2.91 | 0.0% | 100.0% | 0.0% | 14.3% | 0.0% | 100.0% | 0.0% | 0.0% |
| 827 | 69 | 2.63 | Medium | NAP | 5 | 0 | 2 | 40.0% | 1.86 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 119 | 70 | 2.61 | Medium | WMT | 45 | 3 | 55 | 122.2% | 220.24 | 2.2% | 40.0% | 2.2% | 55.6% | 0.0% | 33.3% | 0.0% | 33.3% |
| 280 | 71 | 2.60 | Medium | NAP | 14 | 0 | 0 | 0.0% | 19.52 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 760 | 72 | 2.60 | Medium | NPL | 5 | 1 | 2 | 40.0% | 5.18 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 67 | 73 | 2.59 | Medium | TPL | 146 | 7 | 58 | 39.7% | 147.49 | 5.5% | 10.3% | 3.4% | 3.4% | 14.3% | 28.6% | 14.3% | 14.3% |
| 761 | 74 | 2.57 | Medium | NAP | 8 | 1 | 4 | 50.0% | 7.86 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 139 | 75 | 2.52 | Medium | NAP | 271 | 10 | 162 | 59.8% | 194.84 | 2.2% | 7.0% | 2.2% | 2.6% | 0.0% | 0.0% | 0.0% | 0.0% |
| 198 | 76 | 2.52 | Medium | NAP | 5 | 0 | 3 | 60.0% | 6.97 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 105 | 77 | 2.52 | Medium | CPL | 36 | 2 | 13 | 36.1% | 39.43 | 5.6% | 22.2% | 5.6% | 11.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 296 | 78 | 2.49 | Medium | UMW | 7 | 1 | 0 | 0.0% | 7.19 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 19 | 79 | 2.49 | Medium | SAP | 21 | 1 | 13 | 61.9% | 28.68 | 0.0% | 9.5% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 109 | 80 | 2.47 | Medium | WMT | 52 | 3 | 8 | 15.4% | 66.11 | 67.3% | 71.2% | 67.3% | 71.2% | 66.7% | 66.7% | 66.7% | 66.7% |
| 524 | 81 | 2.46 | Medium | CPL | 5 | 0 | 4 | 80.0% | 2.05 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 227 | 82 | 2.46 | Medium | XER | 16 | 0 | 14 | 87.5% | 54.89 | 18.8% | 50.0% | 6.3% | 6.3% | NA | NA | NA | NA |
| 178 | 83 | 2.45 | Medium | CPL | 5 | 0 | 4 | 80.0% | 8.40 | 20.0% | 20.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 65 | 84 | 2.45 | Medium | CPL | 48 | 0 | 13 | 27.1% | 54.71 | 0.0% | 8.3% | 0.0% | 8.3% | NA | NA | NA | NA |
| 152 | 85 | 2.43 | Medium | NAP | 5 | 0 | 4 | 80.0% | 7.65 | 20.0% | 20.0% | 20.0% | 20.0% | NA | NA | NA | NA |
| 31 | 86 | 2.42 | Medium | SPL | 454 | 14 | 288 | 63.4% | 253.01 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 427 | 87 | 2.40 | Medium | NAP | 10 | 0 | 9 | 90.0% | 34.10 | 0.0% | 10.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 150 | 88 | 2.39 | Medium | NAP | 29 | 0 | 11 | 37.9% | 30.82 | 3.4% | 10.3% | 0.0% | 0.0% | NA | NA | NA | NA |
| 40 | 89 | 2.38 | Medium | WMT | 200 | 1 | 13 | 6.5% | 72.84 | 70.5% | 77.5% | 60.5% | 65.5% | 100.0% | 100.0% | 100.0% | 100.0% |
| 210 | 90 | 2.36 | Medium | TPL | 7 | 0 | 0 | 0.0% | 3.46 | 0.0% | 28.6% | 0.0% | 0.0% | NA | NA | NA | NA |
| 277 | 91 | 2.34 | Medium | UMW | 50 | 3 | 0 | 0.0% | 15.35 | 36.0% | 96.0% | 26.0% | 100.0% | 33.3% | 100.0% | 33.3% | 100.0% |
| 45 | 92 | 2.31 | Medium | SPL | 326 | 11 | 261 | 80.1% | 185.41 | 2.1% | 2.1% | 0.9% | 0.9% | 9.1% | 9.1% | 0.0% | 0.0% |
| 781 | 93 | 2.30 | Medium | CPL | 7 | 0 | 4 | 57.1% | 3.54 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 57 | 94 | 2.29 | Medium | NAP | 749 | 23 | 436 | 58.2% | 215.67 | 1.2% | 14.6% | 0.4% | 6.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 108 | 95 | 2.29 | Medium | XER | 5 | 0 | 5 | 100.0% | 14.52 | 100.0% | 100.0% | 0.0% | 80.0% | NA | NA | NA | NA |
| 78 | 96 | 2.27 | Medium | NAP | 16 | 0 | 15 | 93.8% | 27.65 | 0.0% | 31.3% | 0.0% | 0.0% | NA | NA | NA | NA |
| 118 | 97 | 2.26 | Medium | WMT | 28 | 1 | 31 | 110.7% | 82.28 | 21.4% | 42.9% | 10.7% | 46.4% | 0.0% | 100.0% | 0.0% | 100.0% |
| 196 | 98 | 2.25 | Medium | CPL | 18 | 1 | 4 | 22.2% | 61.81 | 11.1% | 11.1% | 11.1% | 11.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 134 | 99 | 2.24 | Medium | XER | 40 | 1 | 40 | 100.0% | 70.38 | 5.0% | 42.5% | 2.5% | 15.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 35 | 100 | 2.23 | Medium | CPL | 609 | 29 | 332 | 54.5% | 179.95 | 0.5% | 0.5% | 0.2% | 0.2% | 0.0% | 0.0% | 0.0% | 0.0% |
| 156 | 101 | 2.23 | Medium | NAP | 17 | 2 | 7 | 41.2% | 25.89 | 5.9% | 17.6% | 0.0% | 5.9% | 0.0% | 50.0% | 0.0% | 0.0% |
| 648 | 102 | 2.22 | Medium | XER | 5 | 0 | 4 | 80.0% | 24.32 | 60.0% | 80.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 133 | 103 | 2.20 | Medium | CPL | 172 | 7 | 35 | 20.3% | 97.07 | 0.6% | 1.2% | 0.0% | 1.2% | 0.0% | 0.0% | 0.0% | 0.0% |
| 544 | 104 | 2.19 | Medium | WMT | 10 | 0 | 0 | 0.0% | 21.22 | 60.0% | 60.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 271 | 105 | 2.18 | Medium | NAP | 9 | 0 | 3 | 33.3% | 8.57 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 591 | 106 | 2.18 | Medium | UMW | 6 | 1 | 0 | 0.0% | 4.59 | 0.0% | 100.0% | 33.3% | 33.3% | 0.0% | 100.0% | 0.0% | 0.0% |
| 289 | 107 | 2.17 | Medium | UMW | 13 | 2 | 2 | 15.4% | 19.07 | 0.0% | 7.7% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 858 | 108 | 2.13 | Medium | TPL | 6 | 0 | 0 | 0.0% | 4.40 | 16.7% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |

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|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| 389 | 109 | 2.13 | Medium | CPL | 7 | 1 | 0 | 0.0% | 2.68 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 232 | 110 | 2.12 | Medium | WMT | 13 | 0 | 35 | 269.2% | 52.23 | 15.4% | 69.2% | 0.0% | 46.2% | NA | NA | NA | NA |
| 29 | 111 | 2.12 | Medium | NAP | 736 | 22 | 126 | 17.1% | 159.94 | 7.3% | 9.5% | 38.6% | 41.6% | 13.6% | 13.6% | 31.8% | 31.8% |
| 68 | 112 | 2.11 | Medium | UMW | 364 | 11 | 113 | 31.0% | 241.04 | 9.1% | 12.4% | 6.6% | 8.0% | 9.1% | 9.1% | 0.0% | 0.0% |
| 261 | 113 | 2.11 | Medium | WMT | 55 | 2 | 12 | 21.8% | 118.49 | 60.0% | 78.2% | 63.6% | 89.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 527 | 114 | 2.08 | Medium | WMT | 7 | 0 | 6 | 85.7% | 74.60 | 0.0% | 42.9% | 0.0% | 0.0% | NA | NA | NA | NA |
| 388 | 115 | 2.08 | Medium | XER | 16 | 1 | 4 | 25.0% | 24.53 | 6.3% | 12.5% | 6.3% | 6.3% | 0.0% | 0.0% | 0.0% | 0.0% |
| 144 | 116 | 2.08 | Medium | UMW | 15 | 0 | 0 | 0.0% | 18.11 | 0.0% | 80.0% | 0.0% | 26.7% | NA | NA | NA | NA |
| 211 | 117 | 2.06 | Medium | XER | 8 | 1 | 5 | 62.5% | 21.18 | 12.5% | 37.5% | 0.0% | 12.5% | 100.0% | 100.0% | 0.0% | 0.0% |
| 582 | 118 | 2.06 | Medium | CPL | 7 | 0 | 3 | 42.9% | 12.01 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 375 | 119 | 2.05 | Medium | NAP | 10 | 0 | 8 | 80.0% | 11.96 | 10.0% | 10.0% | 10.0% | 10.0% | NA | NA | NA | NA |
| 140 | 120 | 2.05 | Medium | WMT | 41 | 3 | 56 | 136.6% | 120.00 | 12.2% | 48.8% | 12.2% | 48.8% | 0.0% | 33.3% | 0.0% | 33.3% |
| 71 | 121 | 2.05 | Medium | WMT | 40 | 2 | 20 | 50.0% | 134.60 | 22.5% | 62.5% | 15.0% | 70.0% | 0.0% | 0.0% | 0.0% | 50.0% |
| 249 | 122 | 2.05 | Medium | NAP | 9 | 1 | 6 | 66.7% | 12.01 | 0.0% | 22.2% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 98 | 123 | 2.03 | Medium | WMT | 92 | 2 | 11 | 12.0% | 111.78 | 73.9% | 85.9% | 72.8% | 85.9% | 0.0% | 50.0% | 0.0% | 50.0% |
| 263 | 124 | 2.03 | Medium | WMT | 14 | 0 | 2 | 14.3% | 39.21 | 64.3% | 78.6% | 71.4% | 78.6% | NA | NA | NA | NA |
| 240 | 125 | 2.01 | Medium | CPL | 19 | 2 | 10 | 52.6% | 124.88 | 10.5% | 15.8% | 5.3% | 15.8% | 50.0% | 50.0% | 50.0% | 50.0% |
| 220 | 126 | 1.99 | Low | UMW | 7 | 0 | 4 | 57.1% | 9.43 | 42.9% | 71.4% | 0.0% | 0.0% | NA | NA | NA | NA |
| 164 | 127 | 1.99 | Low | UMW | 30 | 1 | 0 | 0.0% | 18.81 | 6.7% | 76.7% | 3.3% | 93.3% | 0.0% | 100.0% | 0.0% | 100.0% |
| 309 | 128 | 1.98 | Low | UMW | 27 | 1 | 4 | 14.8% | 22.47 | 0.0% | 3.7% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 145 | 129 | 1.98 | Low | WMT | 23 | 2 | 21 | 91.3% | 72.48 | 21.7% | 65.2% | 21.7% | 47.8% | 50.0% | 100.0% | 50.0% | 100.0% |
| 165 | 130 | 1.97 | Low | CPL | 24 | 2 | 8 | 33.3% | 112.31 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 238 | 131 | 1.96 | Low | TPL | 10 | 1 | 0 | 0.0% | 6.95 | 10.0% | 20.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 448 | 132 | 1.95 | Low | WMT | 12 | 2 | 11 | 91.7% | 71.45 | 8.3% | 33.3% | 8.3% | 41.7% | 0.0% | 50.0% | 0.0% | 50.0% |
| 284 | 133 | 1.95 | Low | NAP | 6 | 0 | 0 | 0.0% | 2.46 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 529 | 134 | 1.93 | Low | TPL | 6 | 0 | 0 | 0.0% | 4.90 | 33.3% | 33.3% | 0.0% | 0.0% | NA | NA | NA | NA |
| 38 | 135 | 1.92 | Low | CPL | 6 | 0 | 4 | 66.7% | 2.75 | 33.3% | 66.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 5 | 136 | 1.91 | Low | SAP | 483 | 11 | 249 | 51.6% | 168.70 | 1.2% | 3.1% | 0.2% | 0.8% | 0.0% | 9.1% | 0.0% | 0.0% |
| 357 | 137 | 1.91 | Low | NAP | 18 | 0 | 0 | 0.0% | 14.76 | 0.0% | 11.1% | 27.8% | 33.3% | NA | NA | NA | NA |
| 581 | 138 | 1.90 | Low | UMW | 6 | 0 | 0 | 0.0% | 2.91 | 0.0% | 83.3% | 0.0% | 83.3% | NA | NA | NA | NA |
| 200 | 139 | 1.89 | Low | UMW | 64 | 4 | 0 | 0.0% | 22.55 | 51.6% | 90.6% | 42.2% | 92.2% | 25.0% | 50.0% | 50.0% | 100.0% |
| 410 | 140 | 1.89 | Low | WMT | 10 | 1 | 1 | 10.0% | 26.27 | 0.0% | 70.0% | 20.0% | 80.0% | 0.0% | 0.0% | 0.0% | 100.0% |
| 158 | 141 | 1.89 | Low | CPL | 6 | 0 | 4 | 66.7% | 2.14 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 160 | 142 | 1.88 | Low | TPL | 147 | 8 | 52 | 35.4% | 122.73 | 16.3% | 19.0% | 2.0% | 2.0% | 37.5% | 37.5% | 12.5% | 12.5% |
| 14 | 143 | 1.88 | Low | WMT | 65 | 3 | 28 | 43.1% | 143.11 | 44.6% | 76.9% | 38.5% | 80.0% | 0.0% | 66.7% | 0.0% | 33.3% |
| 486 | 144 | 1.88 | Low | CPL | 7 | 2 | 0 | 0.0% | 3.16 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 633 | 145 | 1.88 | Low | CPL | 5 | 0 | 0 | 0.0% | 4.24 | 100.0% | 100.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 141 | 146 | 1.87 | Low | CPL | 25 | 2 | 2 | 8.0% | 4.04 | 40.0% | 72.0% | 4.0% | 4.0% | 100.0% | 100.0% | 0.0% | 0.0% |
| 573 | 147 | 1.86 | Low | UMW | 6 | 0 | 1 | 16.7% | 11.17 | 0.0% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 195 | 148 | 1.86 | Low | CPL | 6 | 0 | 3 | 50.0% | 8.97 | 33.3% | 50.0% | 0.0% | 0.0% | NA | NA | NA | NA |

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| 383 | 149 | 1.86 | Low | UMW | 6 | 1 | 0 | 0.0% | 7.50 | 0.0% | 0.0% | 16.7% | 16.7% | 0.0% | 0.0% | 0.0% | 0.0% |
| 437 | 150 | 1.85 | Low | UMW | 6 | 0 | 1 | 16.7% | 11.68 | 83.3% | 83.3% | 83.3% | 83.3% | NA | NA | NA | NA |
| 236 | 151 | 1.84 | Low | XER | 14 | 0 | 12 | 85.7% | 189.16 | 7.1% | 21.4% | 0.0% | 0.0% | NA | NA | NA | NA |
| 338 | 152 | 1.83 | Low | UMW | 6 | 1 | 1 | 16.7% | 9.31 | 0.0% | 16.7% | 0.0% | 33.3% | 0.0% | 0.0% | 0.0% | 100.0% |
| 443 | 153 | 1.82 | Low | WMT | 7 | 1 | 0 | 0.0% | 10.87 | 57.1% | 100.0% | 42.9% | 71.4% | 0.0% | 100.0% | 0.0% | 100.0% |
| 480 | 154 | 1.81 | Low | NAP | 6 | 0 | 2 | 33.3% | 12.69 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 324 | 155 | 1.80 | Low | CPL | 6 | 0 | 1 | 16.7% | 26.96 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 44 | 156 | 1.78 | Low | CPL | 36 | 0 | 19 | 52.8% | 66.55 | 2.8% | 2.8% | 0.0% | 5.6% | NA | NA | NA | NA |
| 42 | 157 | 1.78 | Low | NAP | 8 | 0 | 4 | 50.0% | 6.05 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 129 | 158 | 1.78 | Low | CPL | 23 | 0 | 23 | 100.0% | 45.88 | 8.7% | 21.7% | 4.3% | 4.3% | NA | NA | NA | NA |
| 465 | 159 | 1.77 | Low | NAP | 6 | 0 | 2 | 33.3% | 22.43 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 369 | 160 | 1.76 | Low | WMT | 6 | 0 | 4 | 66.7% | 23.22 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 704 | 161 | 1.76 | Low | CPL | 5 | 0 | 0 | 0.0% | 1.96 | 40.0% | 40.0% | 40.0% | 40.0% | NA | NA | NA | NA |
| 166 | 162 | 1.76 | Low | CPL | 186 | 2 | 93 | 50.0% | 143.16 | 2.7% | 2.7% | 0.5% | 0.5% | 0.0% | 0.0% | 0.0% | 0.0% |
| 253 | 163 | 1.75 | Low | WMT | 42 | 3 | 10 | 23.8% | 33.87 | 73.8% | 92.9% | 57.1% | 76.2% | 0.0% | 66.7% | 0.0% | 66.7% |
| 661 | 164 | 1.75 | Low | CPL | 6 | 0 | 3 | 50.0% | 1.07 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 463 | 165 | 1.74 | Low | XER | 5 | 0 | 0 | 0.0% | 4.67 | 0.0% | 100.0% | 0.0% | 80.0% | NA | NA | NA | NA |
| 356 | 166 | 1.74 | Low | TPL | 5 | 1 | 1 | 20.0% | 13.44 | 20.0% | 20.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 651 | 167 | 1.74 | Low | UMW | 5 | 1 | 0 | 0.0% | 5.10 | 80.0% | 80.0% | 80.0% | 80.0% | 100.0% | 100.0% | 100.0% | 100.0% |
| 272 | 168 | 1.73 | Low | UMW | 19 | 2 | 2 | 10.5% | 6.15 | 10.5% | 31.6% | 10.5% | 10.5% | 0.0% | 0.0% | 0.0% | 0.0% |
| 394 | 169 | 1.73 | Low | NAP | 6 | 0 | 5 | 83.3% | 10.68 | 16.7% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 621 | 170 | 1.72 | Low | NAP | 8 | 1 | 3 | 37.5% | 5.52 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 323 | 171 | 1.72 | Low | UMW | 5 | 1 | 1 | 20.0% | 10.41 | 0.0% | 60.0% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 366 | 172 | 1.71 | Low | NAP | 6 | 0 | 3 | 50.0% | 6.79 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 639 | 173 | 1.71 | Low | NAP | 5 | 0 | 0 | 0.0% | 2.12 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 285 | 174 | 1.70 | Low | NAP | 5 | 0 | 1 | 20.0% | 3.72 | 20.0% | 40.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 53 | 175 | 1.70 | Low | NAP | 338 | 8 | 170 | 50.3% | 187.95 | 7.7% | 17.5% | 16.6% | 19.2% | 0.0% | 25.0% | 0.0% | 0.0% |
| 75 | 176 | 1.69 | Low | CPL | 382 | 16 | 165 | 43.2% | 120.32 | 0.5% | 0.8% | 0.0% | 0.3% | 0.0% | 0.0% | 0.0% | 0.0% |
| 295 | 177 | 1.68 | Low | NAP | 5 | 0 | 2 | 40.0% | 7.03 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 293 | 178 | 1.67 | Low | UMW | 23 | 1 | 2 | 8.7% | 19.50 | 0.0% | 34.8% | 0.0% | 87.0% | 0.0% | 0.0% | 0.0% | 100.0% |
| 223 | 179 | 1.67 | Low | WMT | 14 | 1 | 0 | 0.0% | 11.57 | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% |
| 43 | 180 | 1.66 | Low | UMW | 1190 | 46 | 30 | 2.5% | 180.01 | 52.9% | 83.1% | 49.9% | 71.3% | 37.0% | 67.4% | 23.9% | 50.0% |
| 420 | 181 | 1.66 | Low | WMT | 6 | 1 | 4 | 66.7% | 18.12 | 0.0% | 0.0% | 0.0% | 16.7% | 0.0% | 0.0% | 0.0% | 0.0% |
| 126 | 182 | 1.66 | Low | SAP | 304 | 10 | 69 | 22.7% | 110.80 | 0.3% | 0.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 254 | 183 | 1.63 | Low | NAP | 22 | 1 | 7 | 31.8% | 35.87 | 4.5% | 4.5% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 60 | 184 | 1.62 | Low | SAP | 586 | 18 | 278 | 47.4% | 180.43 | 0.3% | 4.8% | 0.0% | 0.2% | 5.6% | 33.3% | 0.0% | 0.0% |
| 110 | 185 | 1.62 | Low | UMW | 142 | 8 | 31 | 21.8% | 67.97 | 4.2% | 15.5% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 543 | 186 | 1.62 | Low | XER | 5 | 1 | 0 | 0.0% | 8.28 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 16 | 187 | 1.61 | Low | CPL | 400 | 17 | 134 | 33.5% | 128.32 | 0.3% | 0.5% | 0.0% | 1.3% | 0.0% | 0.0% | 0.0% | 11.8% |
| 421 | 188 | 1.61 | Low | XER | 9 | 1 | 4 | 44.4% | 26.21 | 11.1% | 44.4% | 0.0% | 11.1% | 0.0% | 100.0% | 0.0% | 0.0% |

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| 450 | 189 | 1.61 | Low | CPL | 17 | 1 | 6 | 35.3% | 16.27 | 0.0% | 17.6% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 252 | 190 | 1.61 | Low | XER | 6 | 0 | 2 | 33.3% | 56.53 | 50.0% | 50.0% | 16.7% | 50.0% | NA | NA | NA | NA |
| 541 | 191 | 1.60 | Low | XER | 6 | 1 | 4 | 66.7% | 38.15 | 0.0% | 16.7% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 500 | 192 | 1.59 | Low | XER | 10 | 0 | 13 | 130.0% | 27.44 | 60.0% | 90.0% | 80.0% | 100.0% | NA | NA | NA | NA |
| 468 | 193 | 1.58 | Low | NAP | 5 | 1 | 3 | 60.0% | 6.77 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 326 | 194 | 1.58 | Low | NAP | 22 | 0 | 8 | 36.4% | 17.10 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 469 | 195 | 1.58 | Low | UMW | 5 | 1 | 0 | 0.0% | 4.98 | 20.0% | 40.0% | 20.0% | 20.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 162 | 196 | 1.57 | Low | NAP | 33 | 3 | 27 | 81.8% | 16.21 | 3.0% | 30.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 173 | 197 | 1.56 | Low | CPL | 20 | 0 | 3 | 15.0% | 27.93 | 5.0% | 15.0% | 5.0% | 10.0% | NA | NA | NA | NA |
| 588 | 198 | 1.54 | Low | UMW | 6 | 0 | 0 | 0.0% | 7.00 | 0.0% | 83.3% | 66.7% | 66.7% | NA | NA | NA | NA |
| 386 | 199 | 1.53 | Low | NPL | 5 | 1 | 2 | 40.0% | 15.13 | 40.0% | 40.0% | 0.0% | 0.0% | 100.0% | 100.0% | 0.0% | 0.0% |
| 161 | 200 | 1.53 | Low | CPL | 8 | 1 | 2 | 25.0% | 131.65 | 12.5% | 12.5% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 534 | 201 | 1.53 | Low | NAP | 5 | 0 | 3 | 60.0% | 10.32 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 593 | 202 | 1.52 | Low | CPL | 7 | 0 | 2 | 28.6% | 2.06 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 336 | 203 | 1.52 | Low | NAP | 8 | 1 | 4 | 50.0% | 13.35 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 632 | 204 | 1.52 | Low | UMW | 17 | 2 | 4 | 23.5% | 18.08 | 11.8% | 29.4% | 5.9% | 5.9% | 0.0% | 0.0% | 0.0% | 0.0% |
| 547 | 205 | 1.51 | Low | NAP | 5 | 0 | 4 | 80.0% | 7.04 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 23 | 206 | 1.50 | Low | UMW | 237 | 14 | 1 | 0.4% | 41.65 | 58.2% | 94.5% | 54.9% | 94.1% | 28.6% | 78.6% | 21.4% | 92.9% |
| 517 | 207 | 1.49 | Low | UMW | 5 | 1 | 1 | 20.0% | 3.19 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 56 | 208 | 1.48 | Low | UMW | 453 | 16 | 59 | 13.0% | 182.22 | 12.4% | 22.5% | 12.4% | 16.3% | 6.3% | 6.3% | 0.0% | 0.0% |
| 705 | 209 | 1.48 | Low | NAP | 9 | 0 | 7 | 77.8% | 8.45 | 0.0% | 44.4% | 0.0% | 0.0% | NA | NA | NA | NA |
| 354 | 210 | 1.47 | Low | SPL | 5 | 1 | 4 | 80.0% | 6.08 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 494 | 211 | 1.47 | Low | NAP | 8 | 2 | 4 | 50.0% | 14.46 | 12.5% | 12.5% | 0.0% | 0.0% | 50.0% | 50.0% | 0.0% | 0.0% |
| 821 | 212 | 1.46 | Low | XER | 5 | 0 | 5 | 100.0% | 14.66 | 0.0% | 60.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 79 | 213 | 1.45 | Low | NAP | 325 | 21 | 255 | 78.5% | 80.79 | 3.1% | 11.4% | 0.0% | 1.5% | 4.8% | 4.8% | 0.0% | 0.0% |
| 436 | 214 | 1.44 | Low | NAP | 27 | 2 | 3 | 11.1% | 38.74 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 175 | 215 | 1.43 | Low | UMW | 9 | 0 | 3 | 33.3% | 20.31 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 265 | 216 | 1.43 | Low | WMT | 20 | 1 | 1 | 5.0% | 34.29 | 15.0% | 50.0% | 10.0% | 55.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 626 | 217 | 1.42 | Low | NAP | 5 | 0 | 0 | 0.0% | 11.99 | 20.0% | 20.0% | 0.0% | 20.0% | NA | NA | NA | NA |
| 237 | 218 | 1.41 | Low | WMT | 28 | 3 | 19 | 67.9% | 106.23 | 7.1% | 17.9% | 3.6% | 10.7% | 0.0% | 33.3% | 0.0% | 0.0% |
| 379 | 219 | 1.40 | Low | UMW | 13 | 1 | 0 | 0.0% | 14.59 | 30.8% | 76.9% | 69.2% | 69.2% | 0.0% | 100.0% | 0.0% | 0.0% |
| 843 | 220 | 1.40 | Low | NAP | 6 | 1 | 4 | 66.7% | 14.90 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 83 | 221 | 1.39 | Low | TPL | 23 | 2 | 8 | 34.8% | 81.88 | 13.0% | 13.0% | 13.0% | 13.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 17 | 222 | 1.38 | Low | CPL | 222 | 10 | 66 | 29.7% | 166.94 | 0.0% | 1.4% | 0.0% | 0.5% | 0.0% | 10.0% | 0.0% | 0.0% |
| 665 | 223 | 1.37 | Low | CPL | 5 | 1 | 3 | 60.0% | 42.12 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 61 | 224 | 1.37 | Low | NAP | 9 | 1 | 5 | 55.6% | 7.72 | 11.1% | 22.2% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 403 | 225 | 1.37 | Low | CPL | 13 | 1 | 7 | 53.8% | 7.66 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 660 | 226 | 1.37 | Low | WMT | 6 | 0 | 0 | 0.0% | 14.17 | 0.0% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 91 | 227 | 1.37 | Low | CPL | 9 | 1 | 7 | 77.8% | 12.34 | 33.3% | 66.7% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 731 | 228 | 1.35 | Low | NAP | 7 | 1 | 4 | 57.1% | 6.18 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |

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| 97 | 229 | 1.33 | Low | UMW | 14 | 1 | 0 | 0.0% | 29.73 | 0.0% | 21.4% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 115 | 230 | 1.33 | Low | UMW | 47 | 2 | 1 | 2.1% | 35.97 | 36.2% | 36.2% | 31.9% | 31.9% | 100.0% | 100.0% | 0.0% | 0.0% |
| 276 | 231 | 1.33 | Low | NAP | 7 | 1 | 1 | 14.3% | 7.09 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 275 | 232 | 1.32 | Low | UMW | 11 | 0 | 8 | 72.7% | 13.16 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 202 | 233 | 1.30 | Low | CPL | 23 | 1 | 18 | 78.3% | 42.08 | 21.7% | 30.4% | 4.3% | 4.3% | 0.0% | 100.0% | 0.0% | 0.0% |
| 39 | 234 | 1.29 | Low | TPL | 7 | 0 | 0 | 0.0% | 5.33 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 604 | 235 | 1.28 | Low | WMT | 8 | 0 | 2 | 25.0% | 13.35 | 0.0% | 0.0% | 0.0% | 12.5% | NA | NA | NA | NA |
| 283 | 236 | 1.28 | Low | NAP | 6 | 1 | 0 | 0.0% | 5.90 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 63 | 237 | 1.27 | Low | UMW | 454 | 18 | 86 | 18.9% | 116.11 | 3.7% | 5.3% | 0.9% | 0.9% | 0.0% | 0.0% | 0.0% | 0.0% |
| 185 | 238 | 1.27 | Low | NAP | 14 | 1 | 5 | 35.7% | 15.75 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 188 | 239 | 1.27 | Low | CPL | 66 | 3 | 18 | 27.3% | 39.39 | 37.9% | 43.9% | 9.1% | 9.1% | 100.0% | 100.0% | 0.0% | 0.0% |
| 257 | 240 | 1.27 | Low | NAP | 113 | 3 | 76 | 67.3% | 40.10 | 5.3% | 27.4% | 0.0% | 3.5% | 0.0% | 0.0% | 0.0% | 0.0% |
| 88 | 241 | 1.26 | Low | NAP | 380 | 15 | 214 | 56.3% | 97.72 | 3.4% | 9.2% | 0.3% | 4.7% | 13.3% | 20.0% | 0.0% | 0.0% |
| 92 | 242 | 1.25 | Low | NAP | 75 | 4 | 33 | 44.0% | 50.59 | 2.7% | 8.0% | 2.7% | 2.7% | 0.0% | 25.0% | 0.0% | 0.0% |
| 435 | 243 | 1.25 | Low | NAP | 6 | 0 | 4 | 66.7% | 6.09 | 0.0% | 50.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 187 | 244 | 1.24 | Low | CPL | 25 | 1 | 2 | 8.0% | 9.01 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 114 | 245 | 1.24 | Low | UMW | 50 | 3 | 20 | 40.0% | 41.64 | 0.0% | 6.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 368 | 246 | 1.24 | Low | XER | 12 | 0 | 4 | 33.3% | 35.46 | 0.0% | 41.7% | 0.0% | 33.3% | NA | NA | NA | NA |
| 489 | 247 | 1.22 | Low | UMW | 6 | 1 | 0 | 0.0% | 8.77 | 0.0% | 16.7% | 16.7% | 16.7% | 0.0% | 100.0% | 0.0% | 0.0% |
| 363 | 248 | 1.21 | Low | WMT | 5 | 0 | 1 | 20.0% | 21.51 | 0.0% | 20.0% | 20.0% | 60.0% | NA | NA | NA | NA |
| 26 | 249 | 1.20 | Low | NAP | 418 | 11 | 225 | 53.8% | 142.51 | 4.8% | 12.9% | 2.2% | 5.7% | 0.0% | 18.2% | 0.0% | 0.0% |
| 72 | 250 | 1.19 | Low | NAP | 12 | 1 | 3 | 25.0% | 11.88 | 33.3% | 33.3% | 0.0% | 0.0% | 100.0% | 100.0% | 0.0% | 0.0% |
| 214 | 251 | 1.17 | Low | NAP | 43 | 4 | 15 | 34.9% | 55.27 | 2.3% | 2.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 440 | 252 | 1.17 | Low | XER | 9 | 1 | 8 | 88.9% | 12.79 | 11.1% | 88.9% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 204 | 253 | 1.17 | Low | NAP | 28 | 2 | 11 | 39.3% | 20.29 | 3.6% | 3.6% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 302 | 254 | 1.17 | Low | CPL | 19 | 0 | 3 | 15.8% | 91.01 | 0.0% | 21.1% | 0.0% | 10.5% | NA | NA | NA | NA |
| 522 | 255 | 1.16 | Low | CPL | 10 | 0 | 0 | 0.0% | 12.54 | 10.0% | 10.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 595 | 256 | 1.15 | Low | NAP | 13 | 1 | 6 | 46.2% | 7.82 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 570 | 257 | 1.15 | Low | UMW | 6 | 0 | 1 | 16.7% | 16.18 | 16.7% | 16.7% | 50.0% | 50.0% | NA | NA | NA | NA |
| 438 | 258 | 1.15 | Low | CPL | 6 | 0 | 0 | 0.0% | 13.52 | 33.3% | 33.3% | 16.7% | 16.7% | NA | NA | NA | NA |
| 7 | 259 | 1.15 | Low | UMW | 153 | 5 | 30 | 19.6% | 139.15 | 4.6% | 12.4% | 3.3% | 3.3% | 20.0% | 20.0% | 0.0% | 0.0% |
| 358 | 260 | 1.15 | Low | NAP | 6 | 0 | 3 | 50.0% | 10.92 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 559 | 261 | 1.15 | Low | NAP | 7 | 1 | 2 | 28.6% | 7.24 | 0.0% | 14.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 37 | 262 | 1.14 | Low | NAP | 261 | 10 | 81 | 31.0% | 98.36 | 0.8% | 5.4% | 0.8% | 3.8% | 0.0% | 0.0% | 0.0% | 0.0% |
| 266 | 263 | 1.14 | Low | CPL | 40 | 0 | 27 | 67.5% | 107.98 | 25.0% | 25.0% | 12.5% | 12.5% | NA | NA | NA | NA |
| 519 | 264 | 1.14 | Low | CPL | 7 | 1 | 7 | 100.0% | 15.29 | 0.0% | 14.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 122 | 265 | 1.14 | Low | XER | 27 | 1 | 12 | 44.4% | 90.13 | 11.1% | 22.2% | 7.4% | 7.4% | 100.0% | 100.0% | 0.0% | 0.0% |
| 13 | 266 | 1.13 | Low | UMW | 240 | 10 | 26 | 10.8% | 119.26 | 0.4% | 30.8% | 0.0% | 1.3% | 0.0% | 20.0% | 0.0% | 0.0% |
| 460 | 267 | 1.13 | Low | WMT | 6 | 0 | 2 | 33.3% | 9.69 | 0.0% | 16.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 307 | 268 | 1.12 | Low | UMW | 12 | 1 | 0 | 0.0% | 44.34 | 8.3% | 8.3% | 25.0% | 25.0% | 0.0% | 0.0% | 100.0% | 100.0% |

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| 18 | 269 | 1.11 | Low | CPL | 410 | 16 | 99 | 24.1% | 130.19 | 0.5% | 1.2% | 0.5% | 1.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 274 | 270 | 1.11 | Low | NAP | 30 | 3 | 7 | 23.3% | 16.41 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 80 | 271 | 1.11 | Low | UMW | 20 | 0 | 5 | 25.0% | 43.14 | 15.0% | 35.0% | 35.0% | 35.0% | NA | NA | NA | NA |
| 224 | 272 | 1.10 | Low | UMW | 23 | 0 | 0 | 0.0% | 32.53 | 0.0% | 4.3% | 4.3% | 4.3% | NA | NA | NA | NA |
| 62 | 273 | 1.09 | Low | NAP | 26 | 0 | 14 | 53.8% | 15.53 | 0.0% | 7.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 104 | 274 | 1.09 | Low | TPL | 17 | 1 | 14 | 82.4% | 36.14 | 5.9% | 11.8% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 125 | 275 | 1.09 | Low | NAP | 10 | 1 | 3 | 30.0% | 10.53 | 0.0% | 30.0% | 30.0% | 30.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 49 | 276 | 1.09 | Low | NAP | 62 | 3 | 38 | 61.3% | 29.95 | 16.1% | 22.6% | 3.2% | 12.9% | 0.0% | 0.0% | 0.0% | 0.0% |
| 653 | 277 | 1.08 | Low | UMW | 6 | 1 | 1 | 16.7% | 6.69 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 455 | 278 | 1.08 | Low | NAP | 12 | 2 | 1 | 8.3% | 19.58 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 752 | 279 | 1.08 | Low | UMW | 7 | 1 | 0 | 0.0% | 15.34 | 0.0% | 42.9% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 27 | 280 | 1.08 | Low | CPL | 31 | 1 | 21 | 67.7% | 48.20 | 32.3% | 35.5% | 3.2% | 3.2% | 100.0% | 100.0% | 0.0% | 0.0% |
| 565 | 281 | 1.08 | Low | UMW | 6 | 0 | 0 | 0.0% | 14.96 | 33.3% | 33.3% | 83.3% | 83.3% | NA | NA | NA | NA |
| 221 | 282 | 1.07 | Low | CPL | 15 | 0 | 1 | 6.7% | 31.04 | 13.3% | 20.0% | 6.7% | 6.7% | NA | NA | NA | NA |
| 127 | 283 | 1.06 | Low | UMW | 30 | 0 | 6 | 20.0% | 36.88 | 3.3% | 6.7% | 0.0% | 0.0% | NA | NA | NA | NA |
| 180 | 284 | 1.06 | Low | UMW | 11 | 0 | 0 | 0.0% | 16.19 | 9.1% | 90.9% | 0.0% | 36.4% | NA | NA | NA | NA |
| 452 | 285 | 1.05 | Low | UMW | 8 | 1 | 0 | 0.0% | 4.75 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 25 | 286 | 1.05 | Low | CPL | 98 | 1 | 64 | 65.3% | 129.12 | 1.0% | 3.1% | 1.0% | 2.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 344 | 287 | 1.05 | Low | UMW | 8 | 1 | 3 | 37.5% | 11.54 | 0.0% | 25.0% | 25.0% | 25.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 255 | 288 | 1.04 | Low | CPL | 5 | 0 | 5 | 100.0% | 10.05 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 184 | 289 | 1.04 | Low | CPL | 57 | 1 | 34 | 59.6% | 86.65 | 7.0% | 26.3% | 0.0% | 3.5% | 0.0% | 0.0% | 0.0% | 0.0% |
| 151 | 290 | 1.04 | Low | CPL | 22 | 3 | 24 | 109.1% | 50.63 | 4.5% | 4.5% | 0.0% | 0.0% | 33.3% | 33.3% | 0.0% | 0.0% |
| 85 | 291 | 1.04 | Low | NAP | 7 | 0 | 4 | 57.1% | 10.36 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 46 | 292 | 1.03 | Low | NAP | 258 | 14 | 175 | 67.8% | 74.07 | 6.2% | 41.9% | 1.9% | 1.9% | 0.0% | 14.3% | 0.0% | 0.0% |
| 8 | 293 | 1.02 | Low | NAP | 32 | 1 | 15 | 46.9% | 31.55 | 0.0% | 18.8% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 244 | 294 | 1.02 | Low | UMW | 50 | 4 | 14 | 28.0% | 70.12 | 6.0% | 30.0% | 28.0% | 28.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 474 | 295 | 1.01 | Low | CPL | 12 | 1 | 7 | 58.3% | 8.73 | 0.0% | 8.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 239 | 296 | 1.01 | Low | CPL | 13 | 1 | 6 | 46.2% | 13.26 | 0.0% | 30.8% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 434 | 297 | 0.97 | Low | NAP | 6 | 0 | 4 | 66.7% | 6.99 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 191 | 298 | 0.97 | Low | WMT | 8 | 0 | 2 | 25.0% | 23.91 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 113 | 299 | 0.96 | Low | CPL | 10 | 0 | 0 | 0.0% | 30.28 | 30.0% | 30.0% | 20.0% | 20.0% | NA | NA | NA | NA |
| 301 | 300 | 0.96 | Low | CPL | 7 | 0 | 10 | 142.9% | 15.53 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 387 | 301 | 0.96 | Low | CPL | 6 | 0 | 4 | 66.7% | 10.01 | 66.7% | 66.7% | 16.7% | 16.7% | NA | NA | NA | NA |
| 750 | 302 | 0.94 | Low | NAP | 6 | 0 | 5 | 83.3% | 22.62 | 33.3% | 33.3% | 16.7% | 16.7% | NA | NA | NA | NA |
| 576 | 303 | 0.93 | Low | CPL | 6 | 1 | 6 | 100.0% | 7.99 | 16.7% | 16.7% | 0.0% | 0.0% | 100.0% | 100.0% | 0.0% | 0.0% |
| 147 | 304 | 0.93 | Low | CPL | 24 | 1 | 0 | 0.0% | 47.74 | 95.8% | 100.0% | 12.5% | 12.5% | 100.0% | 100.0% | 100.0% | 100.0% |
| 225 | 305 | 0.92 | Low | NAP | 28 | 4 | 11 | 39.3% | 23.33 | 21.4% | 21.4% | 10.7% | 10.7% | 25.0% | 25.0% | 0.0% | 0.0% |
| 87 | 306 | 0.92 | Low | NAP | 181 | 5 | 18 | 9.9% | 74.97 | 1.7% | 4.4% | 1.7% | 5.5% | 20.0% | 20.0% | 20.0% | 20.0% |
| 153 | 307 | 0.92 | Low | UMW | 174 | 8 | 36 | 20.7% | 85.76 | 1.1% | 2.9% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |

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| 54 | 308 | 0.90 | Low | CPL | 18 | 1 | 1 | 5.6% | 15.30 | 44.4% | 55.6% | 22.2% | 61.1% | 0.0% | 100.0% | 0.0% | 100.0% |
| 361 | 309 | 0.90 | Low | NAP | 7 | 1 | 2 | 28.6% | 15.46 | 0.0% | 42.9% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 207 | 310 | 0.88 | Low | NAP | 83 | 6 | 8 | 9.6% | 52.00 | 20.5% | 21.7% | 27.7% | 37.3% | 16.7% | 16.7% | 16.7% | 16.7% |
| 137 | 311 | 0.87 | Low | XER | 5 | 1 | 2 | 40.0% | 8.83 | 20.0% | 20.0% | 20.0% | 40.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 230 | 312 | 0.86 | Low | NAP | 23 | 2 | 10 | 43.5% | 14.16 | 4.3% | 4.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 496 | 313 | 0.86 | Low | NAP | 10 | 0 | 5 | 50.0% | 14.77 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 490 | 314 | 0.84 | Low | XER | 7 | 0 | 3 | 42.9% | 23.39 | 0.0% | 42.9% | 0.0% | 42.9% | NA | NA | NA | NA |
| 242 | 315 | 0.84 | Low | UMW | 6 | 0 | 4 | 66.7% | 19.57 | 0.0% | 0.0% | 0.0% | 16.7% | NA | NA | NA | NA |
| 154 | 316 | 0.83 | Low | NAP | 15 | 1 | 5 | 33.3% | 29.65 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 405 | 317 | 0.83 | Low | CPL | 23 | 1 | 6 | 26.1% | 29.09 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 96 | 318 | 0.83 | Low | NAP | 13 | 1 | 2 | 15.4% | 22.38 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 545 | 319 | 0.83 | Low | XER | 7 | 1 | 7 | 100.0 % | 33.95 | 0.0% | 71.4% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 495 | 320 | 0.82 | Low | UMW | 9 | 0 | 1 | 11.1% | 22.39 | 66.7% | 66.7% | 33.3% | 33.3% | NA | NA | NA | NA |
| 103 | 321 | 0.82 | Low | CPL | 27 | 1 | 7 | 25.9% | 31.87 | 3.7% | 3.7% | 0.0% | 7.4% | 0.0% | 0.0% | 0.0% | 0.0% |
| 216 | 322 | 0.82 | Low | UMW | 7 | 1 | 1 | 14.3% | 22.78 | 0.0% | 14.3% | 0.0% | 14.3% | 0.0% | 0.0% | 0.0% | 0.0% |
| 339 | 323 | 0.81 | Low | WMT | 22 | 1 | 1 | 4.5% | 23.71 | 22.7% | 40.9% | 13.6% | 31.8% | 0.0% | 0.0% | 0.0% | 0.0% |
| 190 | 324 | 0.79 | Low | NAP | 9 | 2 | 6 | 66.7% | 10.30 | 11.1% | 22.2% | 0.0% | 0.0% | 50.0% | 50.0% | 0.0% | 0.0% |
| 209 | 325 | 0.78 | Low | NAP | 17 | 1 | 11 | 64.7% | 14.44 | 0.0% | 5.9% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 142 | 326 | 0.78 | Low | CPL | 26 | 1 | 15 | 57.7% | 19.81 | 46.2% | 46.2% | 15.4% | 15.4% | 0.0% | 0.0% | 0.0% | 0.0% |
| 51 | 327 | 0.78 | Low | CPL | 13 | 1 | 5 | 38.5% | 9.84 | 46.2% | 61.5% | 23.1% | 23.1% | 0.0% | 100.0% | 0.0% | 0.0% |
| 269 | 328 | 0.77 | Low | NAP | 8 | 1 | 6 | 75.0% | 8.10 | 12.5% | 12.5% | 0.0% | 12.5% | 0.0% | 0.0% | 0.0% | 0.0% |
| 321 | 329 | 0.76 | Low | UMW | 14 | 1 | 3 | 21.4% | 21.38 | 0.0% | 7.1% | 7.1% | 7.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 102 | 330 | 0.76 | Low | NAP | 72 | 4 | 14 | 19.4% | 87.57 | 1.4% | 2.8% | 1.4% | 2.8% | 0.0% | 0.0% | 0.0% | 0.0% |
| 643 | 331 | 0.75 | Low | XER | 8 | 1 | 2 | 25.0% | 44.44 | 0.0% | 50.0% | 0.0% | 100.0% | 0.0% | 0.0% | 0.0% | 100.0% |
| 521 | 332 | 0.75 | Low | XER | 6 | 0 | 2 | 33.3% | 19.49 | 0.0% | 16.7% | 0.0% | 33.3% | NA | NA | NA | NA |
| 148 | 333 | 0.74 | Low | CPL | 21 | 1 | 12 | 57.1% | 51.42 | 28.6% | 28.6% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 213 | 334 | 0.71 | Low | NAP | 9 | 0 | 7 | 77.8% | 5.18 | 0.0% | 11.1% | 0.0% | 33.3% | NA | NA | NA | NA |
| 41 | 335 | 0.71 | Low | UMW | 100 | 6 | 20 | 20.0% | 65.89 | 14.0% | 25.0% | 20.0% | 20.0% | 0.0% | 16.7% | 0.0% | 0.0% |
| 201 | 336 | 0.68 | Low | NAP | 39 | 4 | 20 | 51.3% | 36.94 | 2.6% | 5.1% | 0.0% | 2.6% | 0.0% | 0.0% | 0.0% | 0.0% |
| 772 | 337 | 0.67 | Low | XER | 7 | 0 | 4 | 57.1% | 58.14 | 0.0% | 57.1% | 0.0% | 85.7% | NA | NA | NA | NA |
| 317 | 338 | 0.65 | Low | CPL | 26 | 1 | 0 | 0.0% | 11.40 | 100.0% | 100.0% | 0.0% | 0.0% | 100.0% | 100.0% | 0.0% | 0.0% |
| 81 | 339 | 0.64 | Low | UMW | 15 | 2 | 2 | 13.3% | 9.03 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 390 | 340 | 0.64 | Low | NAP | 11 | 0 | 2 | 18.2% | 45.50 | 9.1% | 9.1% | 0.0% | 0.0% | NA | NA | NA | NA |
| 73 | 341 | 0.64 | Low | NAP | 74 | 5 | 38 | 51.4% | 43.47 | 8.1% | 24.3% | 0.0% | 1.4% | 0.0% | 20.0% | 0.0% | 0.0% |
| 130 | 342 | 0.63 | Low | UMW | 45 | 3 | 7 | 15.6% | 42.37 | 26.7% | 28.9% | 40.0% | 40.0% | 33.3% | 33.3% | 0.0% | 0.0% |
| 250 | 343 | 0.63 | Low | NAP | 19 | 1 | 10 | 52.6% | 16.77 | 10.5% | 15.8% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 584 | 344 | 0.63 | Low | XER | 5 | 1 | 3 | 60.0% | 13.71 | 0.0% | 40.0% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 413 | 345 | 0.62 | Low | WMT | 9 | 0 | 6 | 66.7% | 20.09 | 0.0% | 66.7% | 0.0% | 77.8% | NA | NA | NA | NA |
| 431 | 346 | 0.62 | Low | NAP | 17 | 1 | 1 | 5.9% | 18.44 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 325 | 347 | 0.62 | Low | CPL | 13 | 0 | 2 | 15.4% | 44.69 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |

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| 484 | 348 | 0.61 | Low | TPL | 9 | 2 | 1 | 11.1% | 61.15 | 11.1% | 33.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 177 | 349 | 0.61 | Low | UMW | 55 | 3 | 9 | 16.4% | 96.63 | 7.3% | 29.1% | 20.0% | 20.0% | 0.0% | 33.3% | 0.0% | 0.0% |
| 168 | 350 | 0.60 | Low | SAP | 79 | 4 | 62 | 78.5% | 72.12 | 5.1% | 25.3% | 0.0% | 0.0% | 25.0% | 50.0% | 0.0% | 0.0% |
| 536 | 351 | 0.58 | Low | UMW | 10 | 0 | 1 | 10.0% | 13.38 | 50.0% | 50.0% | 50.0% | 50.0% | NA | NA | NA | NA |
| 120 | 352 | 0.56 | Low | NAP | 134 | 7 | 72 | 53.7% | 73.69 | 3.7% | 15.7% | 0.0% | 3.7% | 14.3% | 14.3% | 0.0% | 0.0% |
| 347 | 353 | 0.56 | Low | NAP | 12 | 2 | 1 | 8.3% | 34.38 | 0.0% | 25.0% | 8.3% | 8.3% | 0.0% | 0.0% | 0.0% | 0.0% |
| 764 | 354 | 0.55 | Low | XER | 6 | 1 | 7 | 116.7 % | 12.69 | 16.7% | 33.3% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 476 | 355 | 0.55 | Low | WMT | 18 | 0 | 3 | 16.7% | 39.64 | 0.0% | 11.1% | 0.0% | 11.1% | NA | NA | NA | NA |
| 194 | 356 | 0.53 | Low | UMW | 62 | 4 | 24 | 38.7% | 57.82 | 1.6% | 16.1% | 16.1% | 16.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 359 | 357 | 0.53 | Low | NAP | 18 | 1 | 2 | 11.1% | 24.92 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 466 | 358 | 0.52 | Low | XER | 14 | 1 | 9 | 64.3% | 21.79 | 14.3% | 64.3% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 305 | 359 | 0.49 | Low | WMT | 69 | 2 | 2 | 2.9% | 44.83 | 60.9% | 60.9% | 60.9% | 60.9% | 50.0% | 50.0% | 50.0% | 50.0% |
| 117 | 360 | 0.48 | Low | UMW | 49 | 4 | 10 | 20.4% | 97.05 | 8.2% | 18.4% | 6.1% | 6.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 328 | 361 | 0.48 | Low | WMT | 20 | 1 | 0 | 0.0% | 16.99 | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% | 100.0% |
| 243 | 362 | 0.46 | Low | UMW | 15 | 1 | 5 | 33.3% | 36.36 | 0.0% | 20.0% | 0.0% | 20.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 222 | 363 | 0.46 | Low | XER | 9 | 2 | 4 | 44.4% | 30.57 | 0.0% | 55.6% | 0.0% | 55.6% | 0.0% | 100.0% | 0.0% | 100.0% |
| 123 | 364 | 0.44 | Low | UMW | 82 | 3 | 18 | 22.0% | 63.82 | 37.8% | 46.3% | 43.9% | 43.9% | 33.3% | 66.7% | 0.0% | 0.0% |
| 233 | 365 | 0.42 | Low | NAP | 47 | 2 | 9 | 19.1% | 36.80 | 2.1% | 6.4% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 419 | 366 | 0.42 | Low | SAP | 11 | 1 | 14 | 127.3 % | 27.43 | 9.1% | 54.5% | 0.0% | 0.0% | 0.0% | 100.0% | 0.0% | 0.0% |
| 215 | 367 | 0.40 | Low | SAP | 12 | 2 | 3 | 25.0% | 31.35 | 16.7% | 41.7% | 0.0% | 0.0% | 0.0% | 50.0% | 0.0% | 0.0% |
| 146 | 368 | 0.39 | Low | TPL | 33 | 1 | 14 | 42.4% | 23.79 | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% | 0.0% |
| 381 | 369 | 0.39 | Low | UMW | 28 | 3 | 7 | 25.0% | 32.49 | 14.3% | 14.3% | 0.0% | 0.0% | 33.3% | 33.3% | 0.0% | 0.0% |
| 235 | 370 | 0.39 | Low | UMW | 79 | 5 | 10 | 12.7% | 54.60 | 51.9% | 51.9% | 64.6% | 64.6% | 0.0% | 0.0% | 40.0% | 40.0% |
| 205 | 371 | 0.39 | Low | NAP | 14 | 1 | 8 | 57.1% | 30.48 | 7.1% | 21.4% | 7.1% | 7.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 478 | 372 | 0.36 | Low | WMT | 6 | 0 | 2 | 33.3% | 36.22 | 0.0% | 0.0% | 0.0% | 0.0% | NA | NA | NA | NA |
| 169 | 373 | 0.35 | Low | UMW | 34 | 2 | 1 | 2.9% | 43.10 | 14.7% | 58.8% | 41.2% | 41.2% | 50.0% | 100.0% | 0.0% | 0.0% |
| 304 | 374 | 0.35 | Low | UMW | 16 | 1 | 4 | 25.0% | 21.71 | 6.3% | 56.3% | 0.0% | 43.8% | 100.0% | 100.0% | 0.0% | 0.0% |
| 315 | 375 | 0.34 | Low | NAP | 44 | 0 | 14 | 31.8% | 42.08 | 11.4% | 22.7% | 2.3% | 2.3% | NA | NA | NA | NA |
| 74 | 376 | 0.31 | Low | UMW | 58 | 1 | 19 | 32.8% | 62.44 | 1.7% | 25.9% | 5.2% | 5.2% | 0.0% | 0.0% | 0.0% | 0.0% |
| 329 | 377 | 0.29 | Low | XER | 19 | 2 | 7 | 36.8% | 41.33 | 15.8% | 31.6% | 0.0% | 0.0% | 50.0% | 50.0% | 0.0% | 0.0% |
| 70 | 378 | 0.29 | Low | NAP | 29 | 2 | 17 | 58.6% | 20.24 | 10.3% | 27.6% | 0.0% | 3.4% | 0.0% | 0.0% | 0.0% | 0.0% |
| 199 | 379 | 0.28 | Low | NAP | 89 | 6 | 35 | 39.3% | 67.31 | 2.2% | 20.2% | 0.0% | 0.0% | 16.7% | 50.0% | 0.0% | 0.0% |
| 212 | 380 | 0.28 | Low | UMW | 33 | 2 | 5 | 15.2% | 16.51 | 12.1% | 15.2% | 12.1% | 12.1% | 0.0% | 0.0% | 0.0% | 0.0% |
| 135 | 381 | 0.25 | Low | NAP | 24 | 1 | 6 | 25.0% | 33.32 | 0.0% | 16.7% | 8.3% | 8.3% | 0.0% | 0.0% | 0.0% | 0.0% |
| 111 | 382 | 0.23 | Low | WMT | 18 | 1 | 12 | 66.7% | 54.53 | 5.6% | 5.6% | 16.7% | 16.7% | 0.0% | 0.0% | 0.0% | 0.0% |
| 353 | 383 | 0.21 | Low | NAP | 26 | 1 | 5 | 19.2% | 22.40 | 0.0% | 7.7% | 0.0% | 3.8% | 0.0% | 0.0% | 0.0% | 0.0% |
| 86 | 384 | 0.18 | Low | TPL | 36 | 2 | 19 | 52.8% | 54.77 | 5.6% | 5.6% | 0.0% | 5.6% | 0.0% | 0.0% | 0.0% | 0.0% |
| 234 | 385 | 0.12 | Low | CPL | 46 | 1 | 13 | 28.3% | 53.60 | 2.2% | 2.2% | 0.0% | 4.3% | 0.0% | 0.0% | 0.0% | 0.0% |

[a]Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)
[b] Network ID = unique network identifier in LAGOS-US-NETWORKS,

[c] CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric

[d] Dam rate = number of dams/number of lakes in a network

Table S3. Freshwater networks in the conterminous US that meet conservation targets[a]

| | 17% Aichi target | | | | 30% by 2030 | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Ecoregion[b] | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Total networks[c] |
| CPL | 88 (36.2%) | 106 (43.6%) | 21 (8.6%) | 28 (11.5%) | 81 (33.3%) | 94 (38.7%) | 16 (6.6%) | 23 (9.5%) | 243 |
| NAP | 29 (14.1%) | 73 (35.4%) | 15 (7.3%) | 26 (12.6%) | 19 (9.2%) | 48 (23.3%) | 12 (5.8%) | 23 (11.2%) | 206 |
| NPL | 11 (39.3%) | 15 (53.6%) | 1 (3.6%) | 3 (10.7%) | 10 (35.7%) | 13 (46.4%) | 0 (0.0%) | 3 (10.7%) | 28 |
| SAP | 0 (0.0%) | 3 (30.0%) | 0 (0.0%) | 0 (0.0%) | 0 (0.0%) | 2 (20.0%) | 0 (0.0%) | 0 (0.0%) | 10 |
| SPL | 1 (12.5%) | 1 (12.5%) | 0 (0.0%) | 1 (12.5%) | 0 (0.0%) | 1 (12.5%) | 0 (0.0%) | 1 (12.5%) | 8 |
| TPL | 16 (27.6%) | 23 (39.7%) | 2 (3.5%) | 2 (3.5%) | 11 (19.0%) | 16 (27.6%) | 2 (3.5%) | 2 (3.5%) | 58 |
| UMW | 35 (23.3%) | 75 (50.05%) | 39 (26.0%) | 52 (34.7%) | 30 (20.0%) | 63 (20.0%) | 32 (21.3%) | 43 (28.7%) | 150 |
| WMT | 41 (38.0%) | 67 (62.0%) | 31 (28.7%) | 53 (49.1%) | 37 (34.3%) | 63 (42.0%) | 28 (26.0%) | 53 (49.1%) | 108 |
| XER | 20 (23.3%) | 64 (74.4%) | 11 (12.8%) | 39 (45.4%) | 17 (19.8%) | 59 (68.6%) | 9 (10.5%) | 38 (44.2%) | 86 |
| Overall | 241 (26.9%) | 427 (47.6%) | 120 (13.4%) | 204 (22.7%) | 205 (22.9%) | 359 (40.0%) | 99 (11.0%) | 186 (20.7%) | 897 |

[a]Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)
[b]CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, XER=Xeric
[c]All freshwater networks in the conterminous US except the Mississippi River network

Table S4. Lake protection[a] across all freshwater networks in the conterminous US

| | Network lakes | | | | | Hub lakes | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Ecoregion[b] | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Total network lakes | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Total hub lakes |
| CPL | 636 (3.5%) | 949 (5.2%) | 203 (1.1%) | 362 (2.0%) | 18336 | 34 (6.4%) | 51 (9.7%) | 9 (1.7%) | 11 (2.1%) | 528 |
| NAP | 635 (5.1%) | 1737 (13.9%) | 917 (7.4%) | 1389 (11.1%) | 12464 | 24 (5.3%) | 60 (13.3%) | 14 (3.1%) | 18 (4.0%) | 451 |
| NPL | 2507 (30.7%) | 4981 (61.0%) | 1407 (17.2%) | 4537 (55.6%) | 8166 | 1 (20.0%) | 1 (20.0%) | 0 (0.0%) | 0 (0.0%) | 5 |
| SAP | 92 (0.8%) | 210 (1.8%) | 38 (0.3%) | 85 (0.7%) | 11872 | 20 (6.8%) | 40 (13.6%) | 4 (1.4%) | 10 (3.4%) | 295 |
| SPL | 126 (1.8%) | 207 (3.0%) | 77 (1.1%) | 179 (2.6%) | 6871 | 3 (2.9%) | 6 (5.8%) | 0 (0.0%) | 0 (0.0%) | 103 |
| TPL | 63 (0.8%) | 90 (1.1%) | 13 (0.2%) | 15 (0.2%) | 8297 | 25 (13.2%) | 37 (19.5%) | 6 (3.2%) | 6 (3.2%) | 190 |
| UMW | 1302 (13.4%) | 2304 (23.8%) | 1165 (12.0%) | 1698 (17.5%) | 9691 | 42 (16.2%) | 78 (30.0%) | 23 (8.8%) | 57 (21.9%) | 260 |
| WMT | 3430 (40.5%) | 5205 (61.4%) | 3220 (38.0%) | 5183 (61.1%) | 8476 | 54 (32.0%) | 115 (68.0%) | 61 (36.1%) | 118 (69.8%) | 169 |
| XER | 81 (3.5%) | 253 (10.8%) | 39 (1.7%) | 170 (7.3%) | 2338 | 5 (6.3%) | 25 (31.6%) | 1 (1.3%) | 11 (13.9%) | 79 |
| Overall | 8872 (10.2%) | 15936 (18.4%) | 7079 (8.2%) | 13618 (15.7%) | 86511 | 208 (10.0%) | 413 (19.9%) | 118 (5.7%) | 231 (11.1%) | 2080 |

[a]Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)

[b]CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, XER=Xeric

**Running head**

Freshwater corridor networks

**Title**

# Freshwater corridor networks in the conterminous US: a coarse-filter approach based on lake-stream networks



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**Open research**: All data, metadata, and R analysis scripts are currently available at https://github.com/cont-limno/TripleC. Upon publication, this repository will be permanently archived in a publicly accessible online location and cited in our methods.


## Abstract

Maintaining regional-scale freshwater connectivity is challenging owing to the dendritic, easily fragmented structure of freshwater networks, but is essential for promoting ecological resilience under climate change. Although the importance of stream network connectivity has been recognized, lake-stream network connectivity has largely been ignored. Furthermore, protected areas are generally not designed to maintain or encompass entire freshwater networks. We analyzed freshwater corridor networks, disproportionately important network lakes (i.e., "hubs"), and their protection status in the conterminous US. We calculated connectivity scores for 385 freshwater networks with > 4 lakes (≥ 1 ha) and identified 2080 hub lakes (2% of all network lakes) that are critical for maintaining intact networks. Freshwater connectivity scores were not correlated with any type of protection. Just 3% of networks received high connectivity scores based on their large size and structure (medians of 1303 lakes, 498.6 km north-south stream distance), but these also contained a median of 454 dams. In contrast, undammed networks (17% of networks) were considerably smaller (medians of 6 lakes, 7.2 km north-south stream distance), indicating that the functional connectivity of the largest potential freshwater corridor networks in the conterminous US currently may be diminished compared to smaller, undammed networks. Network lakes and hubs were protected at similar rates nationally across different levels of protection (8-18% and 6-20%, respectively), but were generally more

protected in the western US. Our results indicate that conterminous US protection of major freshwater corridor networks and the hubs that maintain them generally fell short of the international conservation goal of protecting an ecologically representative, well-connected set of fresh waters ($\geq$ 17%) by 2020 (Aichi Target 11). Conservation planning efforts might consider focusing on restoring natural hydrologic connectivity at or near hubs, particularly in larger networks, less protected or biodiverse regions, to support ~~connectivity for~~ freshwater biodiversity conservation under climate change.

**Key Words**

Climate change, coarse-filter, connectivity, corridors, graph theory, lakes, network, protected areas, rivers, streams

## Introduction

Connectivity is important for numerous ecological processes, including gene flow, migrations, and species range shifts, and is therefore often key for promoting ecological resilience under climate change (Heller and Zavaleta 2009). Such processes operate over a range of spatial and temporal scales from local to continental and transient to macroevolutionary (Littlefield et al. 2019, Armstrong et al. 2021). As habitats are increasingly lost, degraded, or fragmented, maintaining connectivity among habitats at these various spatial and temporal scales becomes particularly challenging (Fischer and Lindenmayer 2007). From a biodiversity conservation perspective, it is often critical to identify, create, or protect corridors to ensure long-term population maintenance and the potential for species range shifts under climate change (Beier & Noss 1998, Stralberg et al. 2020).

Corridors are natural or human-created features (habitat or non-habitat) that facilitate connectivity among two or more habitat patches (Beier & Noss 1998, Costanza and Terando 2019). Numerous studies have attempted to identify corridors for conservation purposes. Many earlier studies focused on landscape-scale modeling of least cost pathways or cost surfaces for select species among core habitats (often protected areas) based on various methods including expert opinion, literature review, or observed species-habitat relationships (Beier et al. 2008, Pullinger and Johnson 2010). Similarly, other studies have applied graph theory to model connectivity across landscapes reflecting the spatial arrangement of numerous habitat patches and potential corridors across the underlying landscape (Urban and Keitt 2001, Urban et al. 2009). Over time, graph-based studies have been adapted to incorporate more nuanced information on the characteristics of both patches (e.g., shape) and the landscape (e.g., permeability gradients) (Rayfield et al. 2011).

Whereas such approaches have been successfully applied for landscape-scale conservation planning, researchers have encountered limitations when applying them at larger spatial scales, including computational constraints, inability to resolve patch characteristics (e.g., shape, habitat quality), and the fact that well-studied, candidate focal species rarely range across large spatial extents or adequately represent regional biodiversity (Theobald et al. 2012). Coarse-filter corridor mapping approaches represent a common solution to these challenges for regional- to continental-scale conservation planning, particularly when the goals are to link distant protected areas for multiple taxa (Beier et al. 2011). Such approaches build off fine-filter graph-based or least-cost approaches, but instead rely on generalized surfaces of landscape permeability as a function of natural vegetation or lack of human presence (Theobald et al. 2012). Although such larger-scale, coarse-filter studies often have to make simplifying assumptions about connectivity (e.g., that human presence is broadly representative of fine-scale features such as fences and roads that restrict movements) (Lawler et al. 2013, Nuñez et al. 2013, Belote et al. 2016), coarse-filter approaches can be useful when prioritizing efficiency, relatively mobile, larger-bodied, or generalist species, or diverse abiotic habitat conditions that promote biodiversity (Brost and Beier 2012, Krosby et al. 2014, Costanza and Terando 2019). In more recent years, some studies have also incorporated climate change projections into landscape permeability models to account for climate change effects on habitat distribution and accessibility (i.e., “climate connectivity”) (McGuire et al. 2016, Carroll et al. 2018, Parks et al. 2020).

~~**Advancing coarse-filter freshwater corridor mapping across lakes, streams, and rivers**~~

Although there is a rich and growing conservation literature on coarse-filter corridor mapping at broad spatial scales, most of this progress has occurred in the terrestrial realm. Despite the fact that the freshwater biodiversity crisis was identified decades ago (Abell 2002, Dudgeon et al. 2006), freshwater biodiversity continues to experience greater rates of endangerment and extinction than marine or terrestrial biodiversity (Collen et al. 2014, McRae et al. 2017, Williams-Subiza and Epele 2021). Many studies have demonstrated the importance of connectivity within freshwater networks for maintaining freshwater populations and community structure across taxa (Altermatt and Fronhofer 2018, de Mendoza et al. 2018, Schmera et al. 2018). Of existing freshwater corridor mapping studies, the majority has focused on river and stream networks at landscape, watershed, or regional scales, without incorporating lentic waterbodies (Collier 2011, Saunders et al. 2016, but also see Gardner et al. 2019, Harvey and Schmadel 2021).

The lack of broad-scale freshwater corridor studies across both lotic and lentic ecosystems may be explained somewhat by the dendritic nature of freshwater landscapes (i.e., networks of streams, rivers, and lakes). Freshwater networks are easily fragmented by numerous anthropogenic (e.g., impoundments, hydrologic alterations) or natural ~~factors~~ (e.g., flow direction, seasonal hydrology) factors (Erős et al. 2012, LeMoine et al. 2020), many of which are difficult to represent spatially across multiple regions. One previous study quantified stream network fragmentation across the conterminous US based on dam locations and found that dams have created over 48,000 new stream segments compared to historical, undammed conditions (Cooper et al. 2017). Although this study is particularly valuable given its large spatial extent and quantitative comparison of current vs. historical network conditions, it did not specifically consider the role of lakes in potential network fragmentation. Therefore, there is a need for broad-scale freshwater corridor studies that consider dam-mediated network connectivity based on both lakes and streams.

Another key consideration in freshwater corridor mapping~~potential limitation~~ is the imperfect translatability of the terrestrial graph-based approaches to freshwater networks of lakes, streams, and rivers (Nel et al. 2009, Hermoso et al. 2018). Topologically, lakes resemble nodes (i.e., patches) and streams and rivers resemble edges (i.e., corridors) in a traditional graph theory framework, but lakes, streams, or rivers may each represent preferred habitat, with others functioning as marginal habitat or non-habitat corridors depending on the taxa of interest (Tonn and Magnuson 1982, Jones 2010, Heim et al. 2019). Regardless, it is important to consider lakes, streams, and rivers together when mapping freshwater corridors due to their important structural and ecological linkages (Saunders et al. 2016, McCullough et al. 2019a, King et al. 2021a). Moreover, such freshwater networks represent the only possible corridors for strictly freshwater taxa without human intervention in the absence of overland or vector-mediated dispersal (e.g., transport by wind or waterfowl). In light of these facts, coarse-filter approaches focused on network structural characteristics that broadly influence connectivity among lakes, streams, and rivers may represent a promising avenue for identifying potential freshwater corridors for conservation purposes over large areas.



A concept from terrestrial graph theory that potentially translates well to fresh waters is the important role of particular nodes in maintaining structural landscape connectivity (Urban and Keitt 2001, Rayfield et al. 2011). We refer to these as “hubs”: major nodes within freshwater networks that disproportionately influence and reinforce whole-network structural connectivity (Muirhead & MacIsaac 2005) (Figure 1a). Because effects of lakes on network connectivity are generally ignored in many stream and river connectivity studies at broad spatial scales (e.g., Cooper et al. 2017, Kuemmerlen et al. 2019, Barbarossa et al. 2020), we considered lakes as nodes and streams as edges and therefore lakes as potential hubs, but recognize that it may make sense to designate stream reaches as nodes under some circumstances (e.g., regions with detailed stream habitat data or few lakes). Furthermore, major dams are commonly associated with lakes (and reservoirs), so an analysis of critical nodes can indicate where network connectivity is most compromised, vulnerable to anthropogenic alterations, or could benefit from restoration. Regardless, conceptually, network fragmentation increases and whole-network connectivity is considerably reduced if hubs become compromised due to factors such as impoundments or other hydrologic alterations, water quality declines, biological invasions, or shoreline developments (Figure 1b). Terrestrial studies have demonstrated the importance of particular nodes for maintaining network structure, including stepping-stone nodes that represent lower quality habitat (Saura et al. 2014, Dilts et al. 2016). Therefore, protecting and managing hubs to maintain intact freshwater networks for lotic-associated species may be advisable, particularly in a climate change context. For example, loss or degradation of hubs could threaten access to seasonal thermal refuges (Armstrong et al. 2021) or persistent waterbodies in dry landscapes (Jaeger et al. 2014), or the potential for species range shifts (Comte et al. 2013, Lynch et al. 2016, Ebersole et al. 2020). Future work is needed, however, to examine directly the biological importance of hubs within freshwater networks.

Finally, a major impetus for coarse-filter connectivity mapping is to identify, create, or protect corridors among protected areas (Costanza and Terando 2019). Protected areas, however, are generally focused on terrestrial biodiversity and have therefore provided mixed benefits for freshwater biodiversity and ecosystems (Saunders et al. 2002, Abell et al. 2007)~~; thus perhaps there has been less motivation for coarse-filter freshwater corridor mapping or conservation~~

~~prioritization~~. Past research has focused largely on the lack of representation of freshwater biodiversity and ecosystems in protected areas (Jenkins et al. 2015, Bastin et al. 2019, McCullough et al. 2019b) rather than freshwater connectivity. ~~Moreover, freshwater biodiversity and ecosystems are often poorly represented in protected areas, including across the US (Jenkins et al. 2015, Bastin et al. 2019, McCullough et al. 2019b).~~ Notably, global protection targets for freshwater ecosystems (Aichi Target 11; CBD 2010) have been only somewhat~~partly~~ achieved. In 2020, the 5th Global Biodiversity Outlook deemed Target 11 as "partially achieved": the 17% protection target was likely achieved globally, but not necessarily based on ecologically representative, well-connected fresh waters (Secretariat of the Convention on Biological Diversity 2020). Therefore, protection of freshwater corridors may currently be insufficient in many regions and countries. Although maintaining and restoring freshwater connectivity is a major priority for freshwater biodiversity conservation worldwide, research is still needed to investigate to what extent protected areas help maintain freshwater connectivity (Harper et al. 2021).

~~**Study objective and research questions**~~

Our objective was to provide a national-scale, coarse-filter assessment of freshwater corridors in the conterminous US, encompassing characteristics of freshwater networks, potential corridor networks, and their protected status with respect to the 17% Aichi conservation target. We focus on freshwater corridor networks, which ~~owing to the need to~~ link numerous local corridors to achieve regional-scale connectivity (Beier et al. 2008, Beier et al. 2011). This work builds upon the primarily terrestrially-focused coarse-filter connectivity literature for conservation purposes by extending these practices to fresh waters and explicitly considering the role of major nodes (i.e., hubs) in corridor networks. This work also represents the first conterminous US-wide analysis of freshwater corridor protection, another topic that has been a major focus in the terrestrial realm. Specifically, we asked:

1. What freshwater networks can best represent freshwater corridor networks?
2. What lakes represent freshwater network hubs?
3. How well protected are these freshwater corridor networks and hubs?

Generally, we expected most freshwater networks to be relatively small, heavily dammed, and susceptible to fragmentation, limiting the availability of regional freshwater corridor networks in the conterminous US. We also expected hub lakes to be more prevalent in regions with more lakes overall and for protection of hub lakes and freshwater corridor networks to fall below the 17% Aichi target nationally, except in the western US where large protected areas are concentrated. This analysis represents an important step for freshwater biodiversity conservation in a climate change context and is intended to facilitate future biodiversity-centered work, including observations of species and genetic diversity, as well as important processes of gene flow, migrations, and range shifts.



## Methods

### Freshwater connectivity metrics and scoring criteria

A challenge associated with assessing conterminous US-scale freshwater connectivity is obtaining data at ecologically appropriate resolutions across such a large spatial extent. We applied a novel, conterminous US-scale dataset, LAGOS-US-NETWORKS v1.0, that represents graph-based freshwater networks with lakes as nodes and streams as edges (King et al. 2021b, c). This dataset contains 86511 on-network lakes $\geq$ 1ha in surface area and approximately 39.5

million stream reaches that comprise a total of 898 networks (Fig 2a). Lakes were defined as permanent, lentic waterbodies ≥ 1ha (both natural lakes and reservoirs) with a geographically defined polygon in the National Hydrography Dataset v2 (Cheruvelil et al. 2021, Smith et al. 2021). LAGOS-US-NETWORKS also includes on-network dams (n = ~~48777~~49525) and metrics for the number of total dams within each network and the number of upstream or downstream dams from individual lakes. We calculated additional connectivity metrics described below using all pairs of connected lakes and the stream distances connecting them.

In our representation of freshwater networks, edges were weighted by the total stream course distance (km) and were undirected connections between pairs of nodes such that travel through each network was irrespective of streamflow direction. Although we did not weight individual nodes, ~~Subsequently,~~ we analyzed the relationship among nodes within networks using several metrics that broadly represented the density of edges and nodes, accessibility of nodes, susceptibility of networks to fragmentation, and climatic heterogeneity within networks (see Table 1 for individual variable descriptions and justifications). All network connectivity metrics were calculated using the igraph R package (Csardi & Nepusz 2006). We prioritized variables that reflected these phenomena to represent coarse-filter structural connectivity in a climate change context. Although we recognize that only relatively mobile taxa are potentially capable of traveling throughout larger networks (e.g., to reach cooler habitats at higher latitudes), many of our connectivity metrics ~~(e.g., susceptibility to fragmentation, distances between nodes)~~ are also relevant to slow-dispersing taxa whose resilience under climate change relies more on localized movements. Specifically, our study includes network variables that represent susceptibility to fragmentation (minimum cuts, percent articulation points), network position (edge density, betweenness centrality), and average dispersal distance between habitats (average lake distance) (Table 1). Given that these are also important considerations for fast-dispersing taxa, our analysis can be used to represent connectivity for diverse freshwater taxa. Therefore, a coarse-filter structural connectivity analysis of these networks generally represents a useful step for freshwater biodiversity conservation in a climate change context.

Coarse-filter, broad-scale connectivity studies in the terrestrial realm often require simplifying assumptions at this scale (e.g., that snapshot metrics of generalized human presence reflect landscape permeability; Theobald et al. 2012). Therefore, in the freshwater realm, we made various, similar assumptions about what our freshwater connectivity metrics represent at the scale of the conterminous US. Such assumptions may require revision for studies at finer spatial scales when different data are available or for specific taxa of interest. Specifically, we assumed static hydrology (i.e. not accounting for seasonal or interannual variation) and that all dams are structurally similar and well represented across the US, and we do not include fine-scale barriers such as waterfalls, culverts, or slope gradients. We also do~~id~~ not account for networks that crossed international borders due to data constraints.

We integrated the various freshwater connectivity metrics (all variables described and defined in Table 1) into a composite network connectivity score that could easily be compared across networks using a principal component analysis (PCA). We only performed this analysis for networks with > 4 lakes (n = 385); however, we excluded the Mississippi River network due to its exceptional size (containing 37.9% of all network lakes). Prior to the PCA, dam rate and percent articulation points were rescaled such that higher values represented fewer barriers and greater resistance to network fragmentation, respectively (and therefore greater overall connectivity). We then ~~rescaled~~ Z-score normalized all input variables (mean of 0 and standard deviation of 1) before PCA calculations. We used 2 principal components, which explained 60%

of variation in the data, to calculate connectivity scores. We opted to use 2 components based on agreement between the Kaiser criterion and Horn's parallel analysis for component retention (Dinmo 2018). To facilitate usefulness of our study for management and policy decision-making processes, we analyzed freshwater connectivity scores across 9 ecoregions used by the US Environmental Protection Agency National Aquatic Resource Survey (NARS) (Herlihy et al. 2008) (Figure 2b). For networks that spanned multiple ecoregions, we assigned ecoregions based on the majority of nodes within those networks.

**Hub lake determination**

Conceptually, per graph theory, hubs within a freshwater network are vital for maintaining connectivity across large expanses. Hub lakes were determined based on individual metrics of lake nodes within networks. We defined hub lakes as lakes that jointly satisfied three conditions of node importance:~~were~~ 1) articulation points in their network~~, and were~~ 2) in the top quintile of vertex~~total node~~ strength (i.e., the weighted degree of a node), and 3) in the top quintile of betweenness centrality within their network (Figure 3). Hence, each network with ≥ 5 lakes will contain at least one hub lake using our definition as long as an articulation point exists in the network. Articulation points are by definition bridges among two or more subnetworks, meaning that an organism must travel through an articulation point to move aquatically from one subnetwork to another. High vertex~~node~~ strength for a lake indicates that it connects a high total network distance among lakes, whether through a multitude of short streams or a handful of long streams. Lakes with high betweenness centrality have shorter aquatic travel distances crossing through them and are more likely to be stepping stones for organisms moving within a network. Combined, these metrics indicate a lake that is necessary for network movement and connects long distances while being a more likely path for biota than other lakes in a network. Finally, although we did not differentiate between natural lakes and reservoirs in aforementioned connectivity metrics, we reported differences in the prevalence of natural lake hubs ~~between~~ versus ~~natural lakes and~~ reservoir hubs~~s~~ for waterbodies ≥ 4 ha. This size cutoff is based on LAGOS-US-RESERVOIR, a database of all 137,465 natural lakes and reservoirs ≥ 4 ha classified by machine learning image interpretation (Polus et al. 2021). This dataset classifies reservoirs as waterbodies directly influenced by impoundments (lakes resulting from river impoundments and pre-existing lakes with large water control structures whose influence goes beyond water level control). Smaller waterbodies < 4 ha could not be reliably classified, but are less likely to be reservoirs (Polus et al. 2021).

**Analysis of protected networks, network lakes, and hub lakes**

Because protected areas are usually established for terrestrial ecosystems, d~~D~~efining protected freshwater ecosystems depends on different levels of land ~~legal~~ protection and what constitutes freshwater ecosystem protection (i.e., waterbody itself or waterbody and its watershed). Therefore, we considered both strict (i.e., managed for biodiversity; Gap Analysis Program (GAP) status 1-2) and multi-use (i.e., managed for both biodiversity and natural resource extraction; GAP status 1-3) protection (Fig 2c) in the US Protected Areas Database v2.0 (US Geological Survey 2018). We also considered protection based on lakes occurring within protected areas (i.e., based on lake centers) and on at least 80% of lake watersheds occurring within protected areas given the importance of watersheds for maintaining freshwater habitats (sensu McCullough et al. 2019b). Under these different definitions of protection, the narrowest is based on strict 80% watershed protection, whereas the loosest is based on lake centers occurring within either strict or multi-use protected areas. Watersheds were based on LAGOS-US-LOCUS v1.0 (Cheruvelil et al. 2021, Smith et al. 2021). Using these definitions, we calculated the percentage of lakes in each network currently protected. Similarly, we analyzed current protection of hub lakes using these same definitions and compared protection of hub lakes to protection of all network lakes. We also compared natural log-transformed network connectivity scores to proportions of networks protected under all definitions of protection using Pearson's correlation coefficients. Finally, we analyzed protection status of whole networks, network lakes, and hub lakes with respect to the 17% Aichi target both nationally and by NARS ecoregions.

All data, metadata, and R analysis scripts are currently available at https://github.com/cont-limno/TripleC. We used R version 4.0.4 for analyses (R Core Team 2021). Upon publication, this repository will be permanently archived in a publicly accessible online location and cited in our methods.

## Results

### Freshwater network characteristics

Of the 898 freshwater networks across the conterminous US, most were relatively small (medians of 3 lakes, 5.6 km N-S stream distance, and 1 dam). In contrast, larger networks were relatively rare: just 10.0% and 7.6% of networks contained at least 50 lakes or spanned at least 100 km of N-S stream distance, respectively. The Mississippi River network contained 37.9% of all network lakes (32811 lakes) and 51.2% of all network dams (24986 dams). Larger networks also tended to have more dams: number of dams was positively correlated with number of lakes and N-S stream distance across all networks (Pearson's $r = 0.94$ and 0.74, respectively, $p < 0.001$) (excluding the Mississippi River network). Aside from dams, larger networks were also generally more susceptible to fragmentation: 32.8% of network lakes were articulation points in networks with > 3 lakes, whereas this value was 18.5% across all networks (Table S1). Similarly, maximum N-S stream connectivity within networks was also susceptible to fragmentation with a median of 1 network cut necessary to undermine the full latitudinal breadth of all networks, as well as those with > 3 lakes. Freshwater network statistics across NARS ecoregions are reported in Table S1. In summary and as expected, our analysis of freshwater networks across the conterminous US indicates that most networks are relatively small and that larger networks generally have more dams and are structurally more susceptible to habitat fragmentation. In other words, the large networks potentially able to represent regional freshwater corridor networks are relatively few in number, heavily dammed, and particularly prone to habitat fragmentation.



**Hub lakes: distribution and characteristics**

We identified 2080 hub lakes across the conterminous US, representing 2.4% of network lakes (Table S1, Figure 4a). This percentage varied marginally across most ecoregions, but was just 0.1% in the Northern Plains (NPL) ecoregion and 1.5 - 3.6% across all other ecoregions. Across NARS ecoregions, abundance of hub lakes was positively correlated with abundance of networks (Pearson's $r = 0.79$, $p = 0.01$). Hubs were generally most abundant in the 3 ecoregions with the most networks (Central Plains (CPL): 528 hubs, Northern Appalachians (NAP): 451 hubs, Upper Midwest (UMW): 260 hubs). Ecoregions with fewer networks were generally dominated by the Mississippi River network and also had generally fewer hubs (NPL: 28 networks/5 hubs, Southern Appalachians (SAP): 10 networks/295 hubs, Southern Plains (SPL): 8 networks/103 hubs, Temperate Plains (TPL): 58 networks/190 hubs). In the western US, which is mostly outside the Mississippi River network, the Western Mountains (WMT) and Xeric (XER) ecoregions had 169 and 79 hubs, respectively. Overall, hub lakes were found throughout the conterminous US, but were generally more abundant in regions with more freshwater networks, consistent with our expectations.

Of all 2080 hub lakes, 1616 (77.7%) ≥ 4 ha could be classified as either reservoirs or natural lakes, of which 1168 (72.3%) were reservoirs and 448 (27.7%) were natural lakes. Therefore, hub lakes were considerably more likely to be reservoirs than the general population of lakes; 43.5% of 137465 lakes in the conterminous US ≥ 4 ha are classified as reservoirs. Of the 246 networks with hub lakes, just 27 networks (11.0%) had no dams. We found that 357 (21.5%) and 6 (0.4%) hub lakes (excluding the Mississippi network) had one dam or multiple dams directly on the lake, respectively. Additionally, even if a dam was not directly on a hub lake, there were 0 - 301 dams upstream and 1 - 18 dams downstream from hub lakes within the network, respectively. Hub lake surface area was a median of 15.4 ha (min = 1.0 ha; max = 107534.6 ha; Figure S3) compared with a median surface area of 4.0 ha (min = 1.0 ha; max = 129612.0 ha) for all network lakes.



**Network connectivity scores**

Network connectivity scores followed a left-skewed distribution (Figure 4a, b, S2). Of the 385 assessed networks with > 4 lakes (excluding the Mississippi River network), 286 (67.5%) received scores < 2 (low), 112 (29.1%) received scores between 2 and 4 (medium), and 13 (3.4%) received scores > 4 (high). Cutoffs for low, medium, and high scores were determined by visual inspection of the score distribution (Figure S2). In general, networks received high, medium, and low scores throughout the conterminous US, but greater concentrations of high-scoring networks were found in the western US (Figure 4a, b). Of the 13 networks with high scores, there were 3 in the WMT ecoregion, 2 each in the CPL, SAP, SPL, and XER ecoregions, and 1 each in the NAP and UMW ecoregions (Table 2). The 3 highest-scoring networks were the Colorado River (WMT), Rio Grande (SPL), and Columbia River (WMT) networks. The NPL and TPL ecoregions had no high-scoring networks. Connectivity scores and network characteristics for all 385 scored networks are provided in Table S2.

High-scoring networks were generally larger and contained more lakes and dams (Tables 2, S2). The 13 highest-scoring networks spanned 29.3 - 1330.3 km stream distance N-S (median = 498.6 km) and had 15 - 3241 lakes (median = 1303 lakes) and 0 - 1760 dams (median = 454 dams). Conversely, low- to medium-scoring networks ranged 0.9 - 553.9 km of stream distance N-S (median = 22.4 km) and had 5 - 2604 lakes (median = 13 lakes) and 0 - 1612 dams (median = 4 dams). Similarly, dam rate ranged 0.0 - 88.6% (median = 47.1%) across high-scoring networks and ranged 0.0 - 269.2% (median = 33.3%) across low- to medium-scoring networks. Dam rate was 100% or greater (i.e., at least as many dams as lakes) in 21 (5.5%) of scored networks. Just 66 (17.1%) of scored networks contained no dams, but these networks were relatively small in terms of lakes (5 - 64 lakes; median = 6 lakes) and N - S stream distance (0.9 - 186.4 km; median = 7.2 km). Finally, high-scoring networks had 0 - 72 hub lakes (median = 24) and low- to medium-scoring networks had 0 - 46 hub lakes (median = 1).



**Protection of freshwater networks, network lakes, and hub lakes**

Whole freshwater networks are poorly protected across the conterminous US (Tables 3, S3, Figure 5). Median network protection was 0.0% across all networks, except under the loosest definition of protection (14.4%; strict + multi-use, lake center protection) (Figure 5a, c). Fully protected networks were relatively rare and varied across definitions of protection (28 - 122 networks; 3.1 - 13.6% of networks). Under the narrowest and loosest definitions of protection, the WMT (10.1%, 22.0%), CPL (3.3%, 19.8%), and XER (2.3%, 22.1%) ecoregions had the highest rates of full network protection, respectively, and the SAP and SPL ecoregions had no fully protected networks based on any definition of protection. Approximately 13.4 - 47.6% of networks had at least 17% of their lakes protected from the narrowest to loosest definitions of protection, respectively. Across all ecoregions, the CPL ecoregion had the highest number of networks meeting the 17% Aichi target based on lake center protection, whereas the UMW, WMT, and XER ecoregions had the highest, most consistent percentage of networks meeting the 17% Aichi target across all definitions of protection. The SAP and SPL ecoregions consistently had the fewest networks meeting the 17% Aichi target across definitions of protection. The Mississippi River network, approximately 10 times larger than the next-largest network in terms of number of lakes, was 4.3 - 15.1% protected across all definitions of protection. Additionally, network connectivity scores (natural log-transformed) were not correlated with the percent of network protection under all definitions of protection (absolute Pearson's $r < 0.1$, $p = 0.21$ - $0.72$). Overall, although whole network protection varied widely across ecoregions and definitions of protection, most networks were poorly protected as a whole and there is little association between freshwater connectivity and protection. As expected, however, protection rates of whole networks were generally greater in the western US.

Across all network lakes, protection varied from 8.2 - 18.4% from the narrowest to loosest definition of protection (Table S4). Therefore, lake protection in the conterminous US only narrowly met the 17% Aichi target under a generous definition of protection. Network lake protection varied across ecoregions from a low of 0.8% in the SAP and TPL ecoregions to highs of 55.6% in the NPL and 61.4% in WMT ecoregions under the narrowest and loosest definitions of protection, respectively. The WMT and NPL ecoregions were the only ecoregions that met the 17% Aichi target across all definitions of protection. In contrast, The CPL, NAP, SAP, SPL, TPL, and XER ecoregions did not meet the 17% Aichi target under any definition of protection and were often near or below 5% protection. The UMW ecoregion met the 17% Aichi target only when considering both strict and multi-use protected areas.

Of the 2080 hub lakes in the conterminous US, 118 (5.7%) and 413 (19.8%) were protected under the narrowest and loosest definitions of protection, respectively, similar to protection levels of all network lakes (Figure 5b, d, Table S4). Therefore, the 17% Aichi target was only met for hub lakes under the loosest definition of protection. Across ecoregions, the WMT (36.1%), UMW (8.8%), and TPL (3.2%) ecoregions had the highest rates of hub lake protection under the narrowest definition of protection, whereas the WMT (68.0%), UMW (30.0%), and XER (31.6%) ecoregions had the highest rates of hub lake protection under the loosest definition of protection. These results were broadly consistent with our expectation of greater hub lake protection in the western US. The WMT ecoregion actually had a slightly higher hub lake protection rate under strict + multi-use 80% watershed protection (69.8%) than lake center protection, indicating that a few hubs themselves were not protected, but their watersheds largely were. Notably, the NPL ecoregion had only 5 hub lakes, one of which was protected based on both strict and multi-use lake center protection.

## Discussion

### Freshwater connectivity and dams

We found that the networks with the highest structural connectivity scores tended to be geographically expansive (median = 498.6 km north-south), but with higher dam rates (median =

47.1%). Presumably, dams represent human-made barriers within freshwater corridor networks. Aside from the 12 of 13 networks with high connectivity scores despite dams, the 66 smaller, undammed networks (median = 7.2 km N-S stream distance) provide relatively unimpeded localized corridor networks for organisms and species to move throughout networks. Importantly, many undammed networks were found along the West, East, and Great Lakes Coasts (Figure S1). These networks are important for many species, particularly diadromous fishes that use both fresh and saltwater for different life stages, and potamodromous fishes that use both the Great Lakes and inland waters for various life stages (D'Amelio et al. 2008, Hall et al. 2011). Nonetheless, our broad-scale analysis suggests that the largest freshwater corridor networks in the conterminous US generally contain abundant dams and may therefore limit functional connectivity, particularly for long-distance migrations and species range shifts under climate change.



Our analysis of freshwater network structure and network hubs indicates not only which networks are highly impacted, but also those most likely to benefit from restoration, particularly by focusing on hubs.~~Another important component of maintaining open freshwater corridor networks is maintaining hubs.~~ Our finding that most hub lakes were reservoirs (72.3%) is not surprising, as reservoirs tend to fall on large rivers and are therefore likely central in freshwater networks. This suggests that connectivity within many networks may be considerably compromised due to the location of dams on or near hub lakes, likely due to a combination of altered hydrology and water chemistry, elevated water temperatures, and/or invasive species~~. Likewise, the 27 hub lakes currently within undammed networks may be of high conservation value for maintaining connectivity (Figure S1). Conversely, dams can facilitate biological invasions within networks by altering habitat~~ (Johnson et al. 2008)~~, which is an important~~

~~consideration when reservoirs are central nodes in many networks~~. Therefore, regular monitoring at and near these centralized hubs can assist in early detection of invasive species and mitigation of further degradation of freshwater networks. Although outright removal of large reservoir dams is often societally challenging or unfeasible, connectivity mitigation measures (e.g., fish ladders, lifts) or dam modifications to enhance natural flow regimes at or near hubs could help restore some functionality in freshwater corridor networks (Renöfält et al. 2009, Muir & Williams 2012, McKay et al. 2013). Similarly, our identification of network hub lakes indicates where additional impoundments would most likely further reduce connectivity, especially for natural lakes whose natural hydrology is more intact compared to reservoirs. Conversely, the 27 hub lakes currently within undammed networks may be of particularly high conservation value for maintaining connectivity (Figure S1).



**Graph theory applications for freshwater conservation**

Graph theory has previously been applied toward conservation in river networks (Erős et al. 2011, Erős & Lowe 2019), including to predict current and future species' ranges (Chaput-Bardy et al. 2017), but few studies have applied a similar framework to lakes (Saunders et al. 2016). Thus, our integration of both lake and stream variables in quantifying overall freshwater network connectivity represents a novel, coarse-filter approach to identifying potential freshwater corridor networks across multiple regions of the conterminous US. This repeatable approach leverages publicly available data and can be adjusted to accommodate specific taxa of interest or new or different connectivity variables at different spatial or temporal scales.

A way in which our work advances graph theory applications for freshwater ecology and conservation is through the use of hubs, which in our case were major lake nodes that disproportionately influenced freshwater network structure. The concept of hubs in freshwater ecology (Muirhead and MacIsaac 2005, Bishop-Taylor et al. 2015) or general landscape ecology (Minor & Urban 2008) as highly connected nodes is not new, but our characterization using multiple axes of lake-stream network analysis allows for a unified definition across all freshwater networks in the conterminous US and could be similarly applied elsewhere. Critical nodes, conceptually similar to hubs, have been previously identified for river networks, but without consideration of lakes (Sarker et al. 2019). Analogous efforts to identify important nodes have a longer history for terrestrial landscapes (e.g., Estrada & Bodin 2008, Saura & Rubio 2010), which have also often included ecological attributes of nodes (Saura & Torné 2009) unlike our species-neutral hub identification. "Stepping stone" characterization has been previously quantified using betweenness centrality (Zetterberg et al. 2010) and articulation points (Keitt et al. 1997), and our usage of total vertex~~node~~ strength is an extension of using the degree of a node with the added ~~information~~ weight of the distance of those connections. Thus, our multi-metric approach to identifying lakes within a network that are potentially more important for maintaining corridor networks across large expanses extends past research and can help prioritize individual locations for conservation, particularly when whole-network conservation is impractical. Finally, although previous studies on patterns of freshwater biodiversity in relation to hub lakes and small ponds have only been conducted at landscape to regional scales, our flexible, continental-scale approach and dataset opens the door for broader-scale studies of freshwater biodiversity and connectivity.

**Implications for conservation planning under climate change**

Whereas all freshwater corridor networks can potentially play important roles in supporting the resilience of biodiversity under climate change, many such networks in the conterminous US are relatively small, contain many dams, and are susceptible to fragmentation. The relatively small number of large corridor networks, which are likely the only networks capable of supporting regional-scale migrations or species range shifts under climate change, generally are even more heavily dammed and structurally prone to fragmentation. Moreover, most freshwater corridor networks are currently poorly protected, not only falling short of the 17% Aichi target under most types of protection, but particularly so in regions with high freshwater biodiversity (i.e., southern, central, and eastern US). These findings indicate that considerable conservation effort may be required to facilitate important phenomena such as gene flow, migrations, and range shifts for freshwater biodiversity in the conterminous US. Moreover, water level fluctuations further threaten network connectivity as societal demands for water increase and droughts intensify under climate change, especially in the western US. Therefore, even “protected” waterbodies are not immune to changing hydrology owing to upstream water withdrawals or climate change.



Given limited or unpredictable resources for conservation, prioritizing the monitoring and protection of network hubs could represent a relatively efficient strategy for maintaining freshwater corridor networks, but our analysis shows that current protection levels of hub lakes are not only similar to all network lakes in general, but are also relatively low (19.9%; only meeting the 17% Aichi target under combined strict and multi-use, non-watershed protection). ~~Managers might consider prioritizing hub ecosystems for future conservation given that maintaining these lakes would help promote network functionality.~~ Nonetheless, our finding that hub lakes are predominantly reservoirs, indicates that the “well-connected” conservation objective within Aichi Target 11 is difficult to achieve when many network hubs are likely highly impacted in terms of hydrology, water temperature, water quality, and invasive species. All of these stressors are expected to worsen under climate change. As such, successful hub ecosystem conservation efforts might help restore and maintain network connectivity by striving to mitigate these negative consequences of impoundments, particularly given the general lack of representation of waterbodies and their watersheds in protected areas. Although connectivity broadly benefits biodiversity under climate change, it is important to consider that in the freshwater realm, this generally means connectivity associated with more natural hydrologic regimes.~~, regular monitoring of network hubs may assist in water quality maintenance and early detection of aquatic invasive species within networks.~~

The 2020 assessment of progress toward the 17% Aichi conservation target for fresh waters identified current gaps in ecological representation and connectivity globally. Our analysis reinforces the notion that current US protected areas do not contain an ecologically representative portfolio of fresh waters (Jenkins et al. 2015, McCullough et al. 2019b), but also shows that considerable work is still needed to promote and improve protection of freshwater connectivity. Under a changing climate, ensuring functional connectivity for freshwater biodiversity is a key priority. Across the 13 high-scoring freshwater networks, 4 networks met the 17% Aichi target across all definitions of protection, 6 networks did not meet the target under any definition of protection, whereas results were mixed for the remaining 3 networks. This generally reflects the concentration of large protected areas in the western US. For example, the Savannah-Santee, Suwannee River, and James River networks in the eastern US (ranked #7, 9 and 11 nationally by connectivity score, respectively; Figure 4a, b) are 0.0 - 5.2% protected across all definitions of protection (Table 2). In contrast, the 3 highest-scoring networks in the

WMT ecoregion (Colorado River, Columbia River, and San Francisco Bay networks, ranked #1, 2, and 4, respectively) were 32.5 - 72.6% protected across all definitions of protection. These findings not only reinforce the previously identified national-scale mismatches between protected areas and freshwater biodiversity (Jenkins et al. 2015), but also indicate regional mismatches between protected areas and freshwater connectivity in the southern, central, and eastern US (Fig 3). On the positive side, however, overlap between freshwater biodiversity and several large freshwater corridor networks in these regions suggests that efforts to maintain or enhance these corridor networks could help support populations and the resilience of regional freshwater biodiversity to climate change (e.g., facilitate seasonal migrations and range shifts). Moreover, conservation prioritization of hub lakes may be disproportionately more beneficial and cost-effective for conservation under climate change as generalized percent network protection targets (17% or otherwise) given their large effects on network intactness.

We envision our data, concepts of freshwater corridor networks and hubs, and analytical approach making foundational contributions to future conservation efforts, including fully data-driven systematic conservation planning or more participatory structured decision-making involving managers and stakeholders. Our use of basic computational techniques (i.e., PCA) and public data at scales of both individual lakes and whole lake-stream networks creates flexibility for future studies to integrate other relevant datasets at different spatial and temporal scales or to tailor their approaches to species, taxa, or functional groups of interest. For example, the average lake distance variable (Table 1) could be parameterized to identify lakes or networks that are more accessible for dispersal-limited species or particularly vulnerable to rapid spread of invasive species. Our coarse-filter approach targeting generalized structural connectivity in a climate change context is only one example of many potential applications. For example, studies interested in restoring anadromous fish migrations could integrate a similar structural connectivity scoring approach with more localized data on features such as waterfalls and culverts to identify networks most likely to benefit from interventions to enhance connectivity. Additionally, studies interested in maintaining access to permanent waterbodies in dry climates could integrate structural connectivity data with seasonal hydrology or other habitat data (e.g., lake or stream depth). Moreover, there is potential to analyze the joint freshwater-terrestrial conservation benefits of freshwater corridor networks, given that riparian areas often represent terrestrial corridor networks (Krosby et al. 2018) and regulate water temperature, chemistry, and physical habitat characteristics (Johnson and Almlof 2016). Although such efforts are beyond the scope of this current study, our study and approach demonstrate the potential for future connectivity studies to help advance conservation planning under climate change, particularly for freshwater biodiversity and ecosystems.



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**Tables**

Table 1. Description of network-scale freshwater connectivity metrics and ecological justification for their use in broad-scale freshwater corridor identification

| Variable name | Description | Ecological Justification |
|---|---|---|
| Edge density | Ratio of ~~actual~~ stream reaches ~~(edges)~~ connecting lakes to the maximum number of potential stream reaches in a theoretical, complete network | Represents availability of pathways for traveling ~~among lakes~~ within a network |
| Average lake distance (km) | Average stream-course distance between lakes ~~(nodes)~~ | Represents density and accessibility of lakes within a network |
| Dam rate | ~~Density of dams within a network, calculated as the~~ R~~r~~atio between the number of lakes ~~(nodes)~~ and number of dams*~~; rescaled such that higher values penalize network connectivity~~ | Represents density of connectivity barriers within networks |
| Elevation range (m) | Maximum minus minimum elevation among network lakes~~nodes~~ | Represents more localized climatic heterogeneity accessible~~acessible~~ within a network for both relatively mobile and sessile species |
| Maximum north-south distance (km) | Maximum north-south distance spanned by the network based on lake and stream connections | Represents large-scale climatic heterogeneity accessible within a network for relatively mobile species |
| Minimum cuts | Minimum number of stream reaches ~~(edges)~~ to cut needed to ~~separate the network into multiple networks (i.e.,~~ undermine maximum north-south distance~~)~~ | Represents susceptibility of a network to fragmentation, particularly in climatic context for relatively mobile species |
| Percent articulation points | The percent of lakes ~~(nodes)~~ in the network that are articulation points, which are the lakes in the graph that ~~when disconnected lead to~~ prevent separation into multiple subnetworks*~~; rescaled such that higher values represent greater resistance to network fragmentation~~ | Represents susceptibility of a network to fragmentation |
| Average betweenness centrality | The number of shortest-distance pairwise stream paths in a network that pass through a lake ~~(node)~~, ~~which we~~ averaged across network lakes after normalization by the number of lakes within a network (N) using the formula (2BC)/(N*N-3N+2)~~.~~ | Represents lake importance according to position within a network and the convergence of stream pathways |

~~Table 1. Description of network-scale freshwater connectivity metrics and ecological justification for their use in broad-scale freshwater corridor identification~~

| ~~Variable name~~ | ~~Description~~ | ~~Ecological Justification~~ |
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| ~~Average lake distance (km)~~ | ~~Average stream-course distance between lakes~~ | ~~Represents density and accessibility of lakes within a network~~ |
| ~~Dam rate~~ | ~~Ratio between the number of lakes and number of dams*~~ | ~~Represents density of connectivity barriers within networks~~ |
| ~~Elevation range (m)~~ | ~~Maximum minus minimum elevation among network lakes~~ | ~~Represents more localized climatic heterogeneity accessible within a network for both relatively mobile and sessile species~~ |
| ~~Maximum north-south distance (km)~~ | ~~Maximum north-south distance spanned by the network based on lake and stream connections~~ | ~~Represents large-scale climatic heterogeneity accessible within a network for relatively mobile species~~ |
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| ~~Average betweenness centrality~~ | ~~The number of shortest-distance pairwise stream paths in a network that pass through a lake, averaged across network lakes after normalization by the number of lakes within a network (N) using the formula (2BC)/(N*N-3N+2)~~ | ~~Represents lake importance according to position within a network and the convergence of stream pathways~~ |

*variable rescaled such that higher values represent greater connectivity

Table 2. Freshwater network connectivity scores and statistics and protection status of networks and hub lakes in the conterminous US for high-scoring networks

| **Rank** | **Score** | **Network** | **Ecoregion** | **Lakes** | **Hubs** | **Dams** | **Dam rate*** | **North-South distance (km)** |
|---|---|---|---|---|---|---|---|---|
| 1 | 12.02 | Colorado River | WMT | 2027 | 42 | 954 | 47.1% | 1,330.34 |
| 2 | 9.49 | Rio Grande | SPL | 536 | 13 | 388 | 72.4% | 1,312.70 |
| 3 | 8.10 | Columbia River | WMT | 2397 | 55 | 915 | 38.2% | 820.36 |
| 4 | 6.70 | Sacramento/San Joaquin~~n Francisco Bay~~ | WMT | 1780 | 49 | 484 | 27.2% | 629.52 |
| 5 | 6.21 | Brazos River | SPL | 1529 | 22 | 1273 | 83.3% | 611.93 |
| 6 | 5.67 | Susquehanna-Hudson | NAP | 2659 | 71 | 1099 | 41.3% | 505.40 |
| 7 | 5.19 | Savannah-Santee | CPL | 3241 | 72 | 1760 | 54.3% | 491.73 |
| 8 | 5.19 | Potomac River | SAP | 420 | 9 | 372 | 88.6% | 238.12 |
| 9 | 4.94 | Suwannee | CPL | 1076 | 38 | 268 | 24.9% | 245.86 |
| 10 | 4.84 | Red River | UMW | 754 | 16 | 250 | 33.2% | 380.41 |
| 11 | 4.40 | James River | SAP | 765 | 24 | 424 | 55.4% | 173.63 |
| 12 | 4.03 | Lake Creek | XER | 15 | 0 | 0 | 0.0% | 29.30 |
| 13 | 4.01 | Humboldt River | XER | 21 | 1 | 43 | 204.8% | 146.39 |

*Dam rate = number of dams/number of lakes. CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT-Western Mountains, XER=Xeric. Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)

Table 3. Protection status of networks and hub lakes in the conterminous US for high-scoring networks

| | | Network protection | | | | Hub protection | | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Network | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed | Strict, lake center | Strict + multi-use, lake center | Strict, 80% watershed | Strict + multi-use, 80% watershed |
| 1 | Colorado River | 41.1% | 68.9% | 39.1% | 72.6% | 26.2% | 83.3% | 26.2% | 76.2% |
| 2 | Rio Grande | 17.2% | 30.4% | 11.2% | 30.0% | 0.0% | 23.1% | 0.0% | 30.8% |
| 3 | Columbia River | 36.3% | 67.0% | 32.5% | 67.0% | 12.7% | 43.6% | 16.4% | 47.3% |
| 4 | Sacramento/San Joaquin~~n~~ ~~Francisco Bay~~ | 52.9% | 65.3% | 51.5% | 62.4% | 46.9% | 59.2% | 42.9% | 46.9% |
| 5 | Brazos River | 1.8% | 2.4% | 0.9% | 1.0% | 22.7% | 22.7% | 9.1% | 9.1% |
| 6 | Susquehanna-Hudson | 5.3% | 11.7% | 11.9% | 15.8% | 12.7% | 19.7% | 4.2% | 9.9% |
| 7 | Savannah-Santee | 1.8% | 2.7% | 0.6% | 1.2% | 6.9% | 6.9% | 0.0% | 0.0% |
| 8 | Potomac River | 5.2% | 11.7% | 5.5% | 10.0% | 11.1% | 33.3% | 11.1% | 22.2% |
| 9 | Suwannee | 0.5% | 1.2% | 0.0% | 0.2% | 2.6% | 7.9% | 0.0% | 0.0% |
| 10 | Red River | 17.1% | 23.9% | 3.3% | 4.4% | 18.8% | 18.8% | 6.3% | 12.5% |
| 11 | James River | 2.7% | 5.2% | 0.7% | 3.0% | 0.0% | 8.3% | 0.0% | 0.0% |
| 12 | Lake Creek | 6.7% | 53.3% | 0.0% | 20.0% | NA | NA | NA | NA |
| 13 | Humboldt River | 28.6% | 47.6% | 23.8% | 76.2% | 0.0% | 0.0% | 0.0% | 100.0% |

CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT-Western Mountains, XER=Xeric. Strict protection=managed for biodiversity (GAPS 1-2), multi-use=managed for biodiversity and natural resource extraction (GAP 3)

**Figure Captions**

**Figure. 1.** Freshwater connectivity in Michigan, USA based on (a) an intact network with an operational hub lake and (b) a compromised hub lake, which results in network fragmentation and possible upstream habitat loss for freshwater biodiversity. Upstream streams are grayed out in (b) to represent loss of stream habitat. Isolated lakes are not accessible through networks.

**Figure. 2.** (a) Freshwater networks of the conterminous US based on LAGOS-US-NETWORKS v1.0 (King et al. 2021 b, c). Contiguous colors represent individual networks (the largest of which is the Mississippi River basin in green in the central US). Shown are 898 unique networks containing a total of 86511 lakes ≥ 1 ha. (b) Ecoregions used by the US Environmental Protection Agency National Aquatic Resource Survey (Herlihy et al. 2008). CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric. (c) Strict (managed for biodiversity; GAPS 1-2) and multi-use (managed for biodiversity and natural resource extraction; GAP 3) protected areas based on the US Protected Areas Database v2.0 (US Geological Survey 2018).

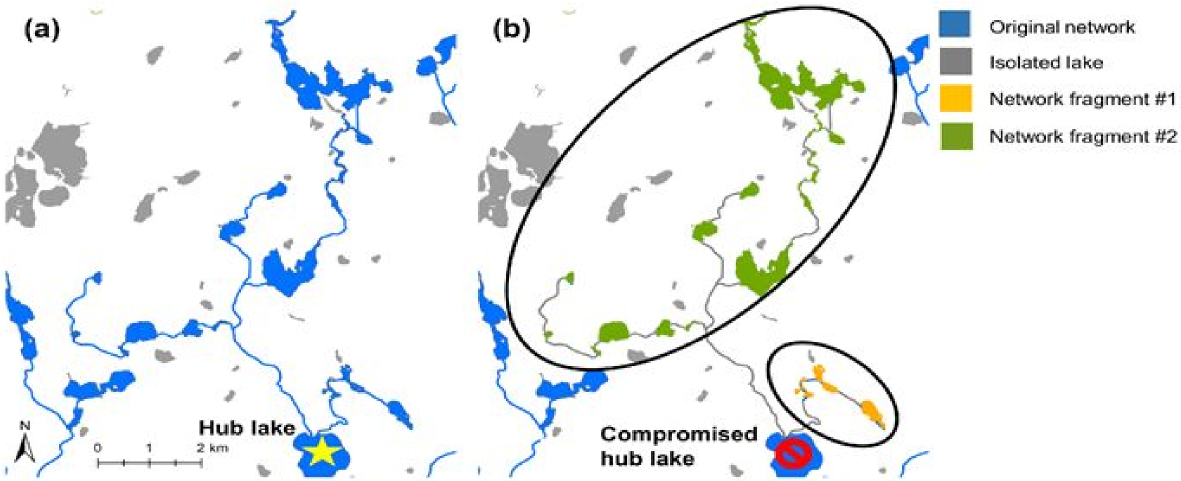


**Figure. 3.** Graphical depiction of a hypothetical network showing the three network metrics used to define a hub lake: (a) vertex strength of each lake colored by quintile, (b) betweenness centrality of each lake colored by quintile, (c) lakes that are articulation points outlined in green and showing the subnetworks created by the removal of the central lake marked by “X”. Hub lakes for the network (d) are those that are in the top quintile of vertex strength, the top quintile of betweenness centrality, and are articulation points.

**Figure. 4.** (a) Freshwater network connectivity scores (for networks > 4 lakes) and hub lakes (n = 2080). The Mississippi River network (unscored) is shown in light blue dots. (b) Highest-ranking freshwater network connectivity scores. Unique mapped colors represent individual, contiguous networks with high connectivity scores (n = 13), which are ranked by connectivity score (1 = highest).

**Figure. 5.** Percent of freshwater networks (lakes within networks) and hub lakes protected by NARS ecoregion and different levels of protection. The Mississippi River network (considered separately) has 7.6% and 15.1% of its lakes protected, respectively, under strict and strict + multi-use lake center protection (a), and 4.3% and 13.8% of its lakes protected, respectively, under strict and strict + multi-use 80% watershed protection, respectively (c). Mississippi River network hubs are reflected in (b) and (d). Dashed lines represent the 17% Aichi conservation target. See Table S1 for number of networks and hub lakes per ecoregion. CPL=Coastal Plains, NAP=Northern Appalachians, NPL=Northern Plains, SAP=Southern Appalachians, SPL=Southern Plains, TPL=Temperate Plains, UMW=Upper Midwest, WMT=Western Mountains, XER=Xeric.

**Figures**

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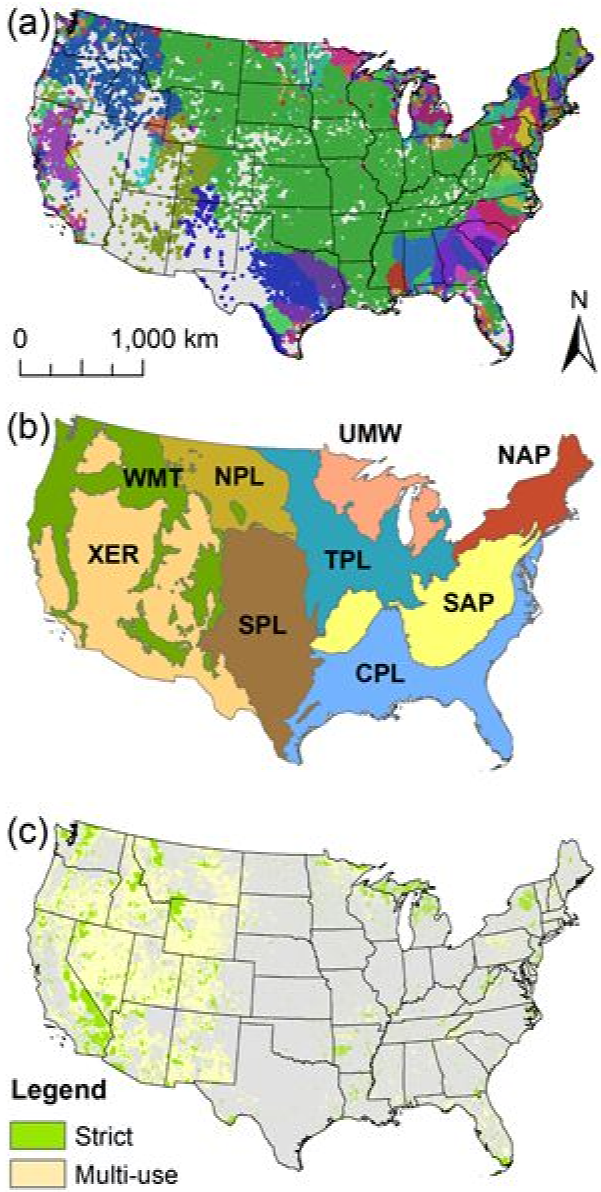


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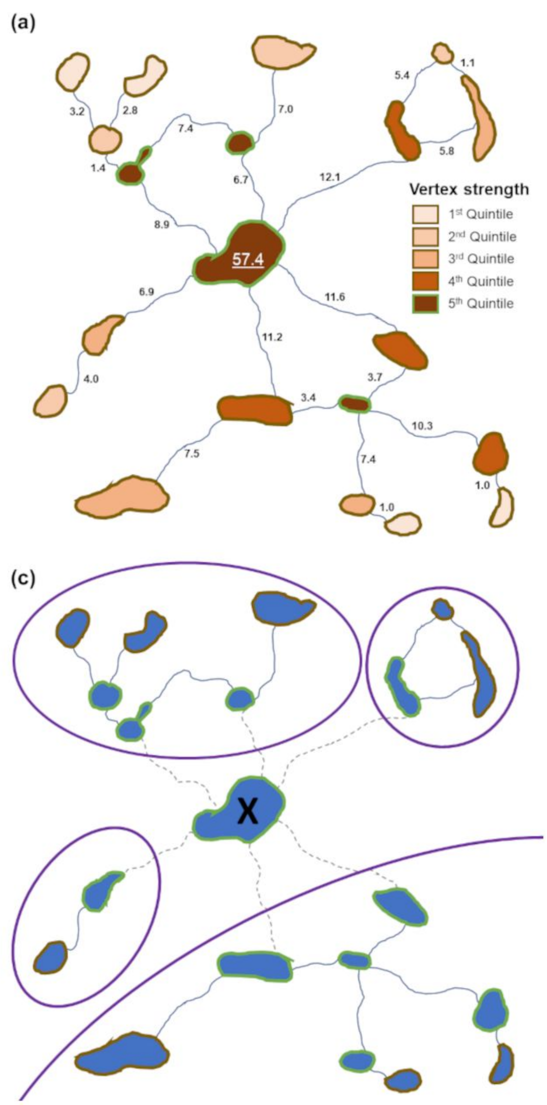


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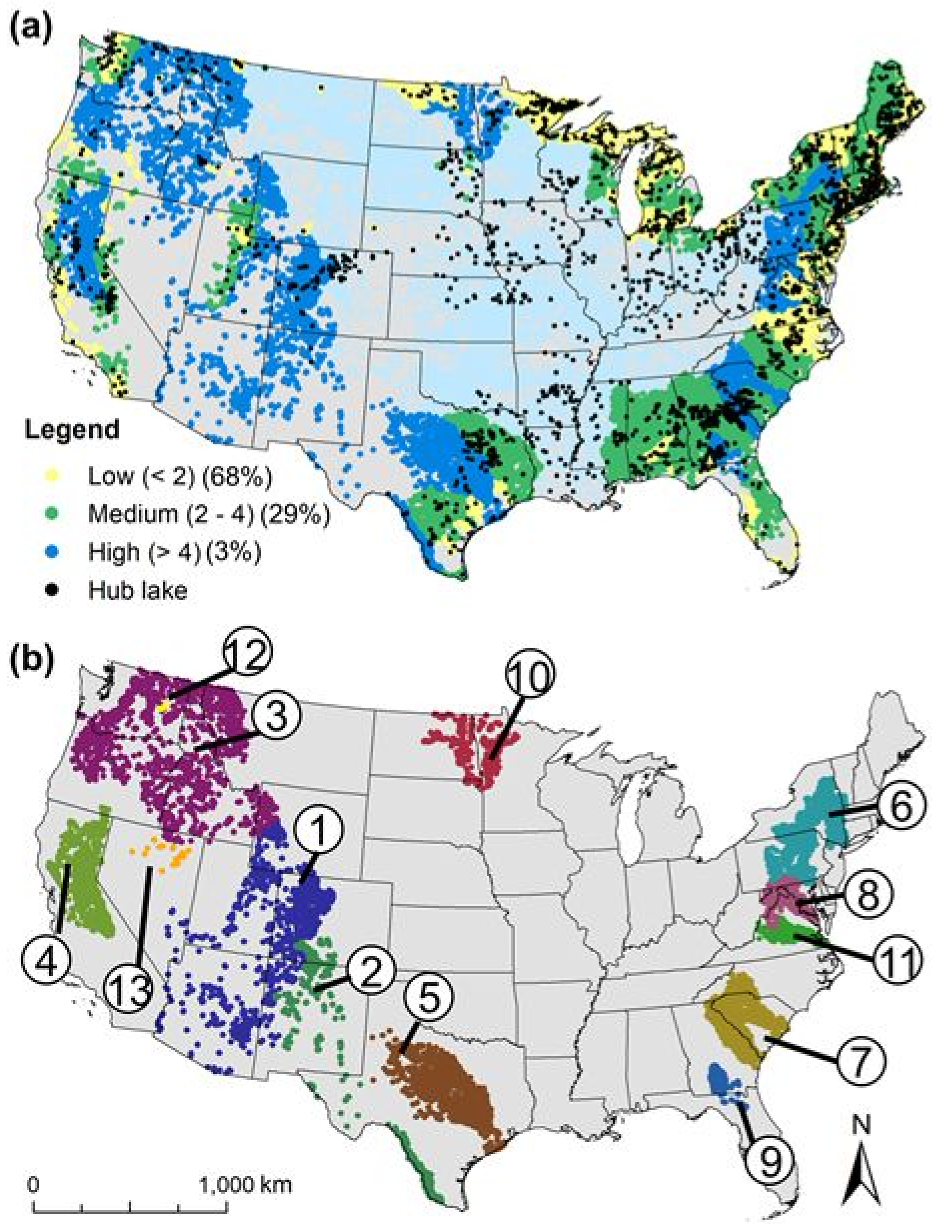


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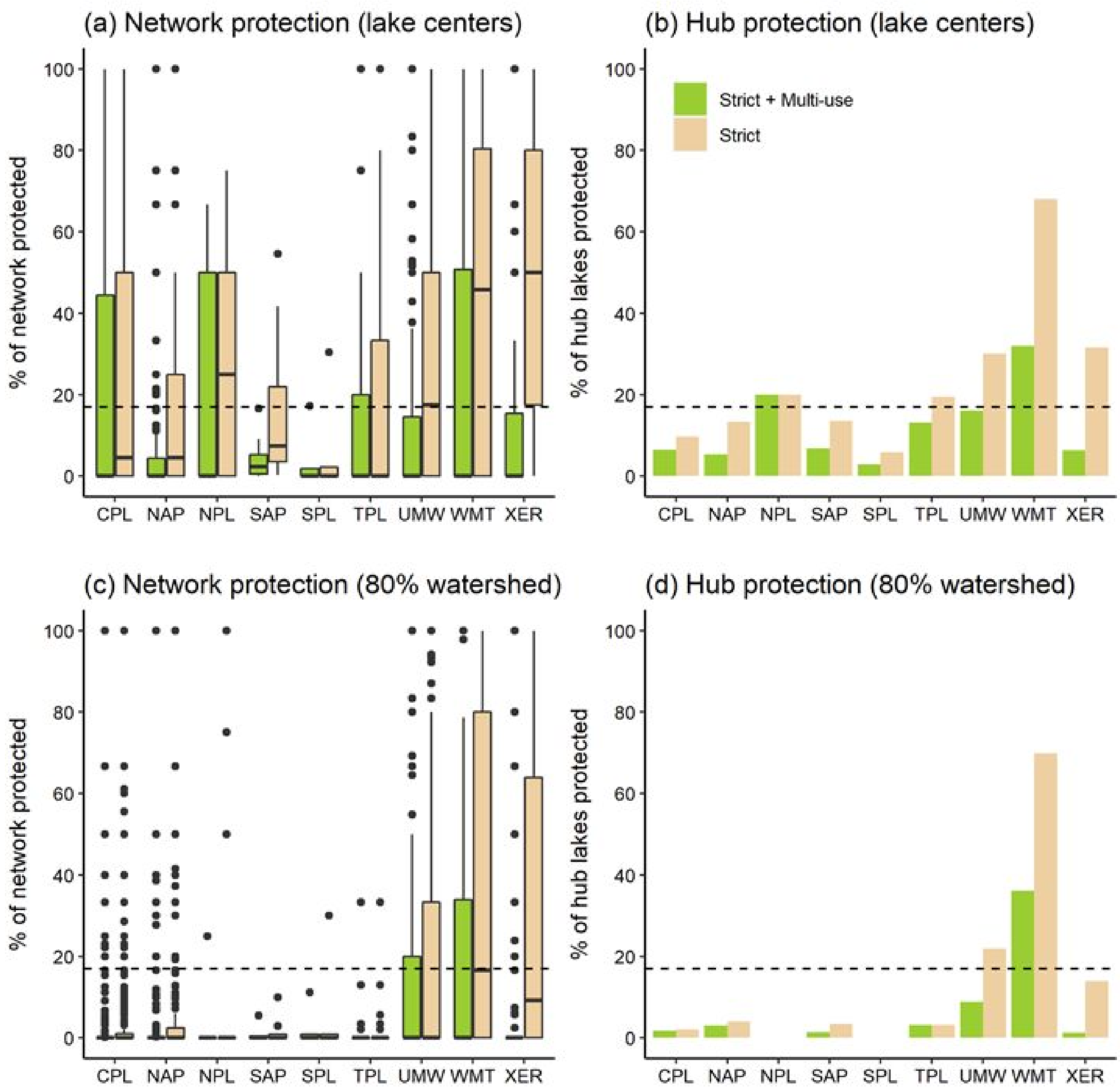


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