

LETTER

No lake left behind: How well do U.S. protected areas meet lake conservation targets?

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Scientific Significance Statement

In 2010, the Convention on Biological Diversity (CBD) recommended protecting 17% or more of freshwaters globally by 2020 to sustain freshwater biodiversity and ecosystem services. The CBD sought to meet this target at national and subnational levels with an ecologically representative, well-connected set of protected areas. Due to its large size, U.S. participation is important for meeting the global target. However, only 7.5% of the 280,000 lakes in the continental U.S. currently have $\geq 80\%$ of their catchment protected and these are disproportionately located in lake-poor regions. Meeting the CBD target in the U.S. requires protecting thousands of additional lakes and their catchments across diverse ecological settings, particularly in lake-rich regions. We recommend revising conservation targets for lakes to incorporate lake catchments and connectivity.

Abstract

The Convention on Biological Diversity (<https://www.cbd.int/>) recommends globally protecting $\geq 17\%$ of ecologically representative freshwaters by 2020 to sustain critical ecosystem services and rapidly declining freshwater biodiversity. We examined whether current conservation efforts meet this target for lakes (≥ 1 ha) across the continental U.S. and Environmental Protection Agency ecoregions using the U.S. Protected Areas Database. How one defines lake protection matters: 17.8% of lakes fell within multiuse or strictly protected areas, but only 7.5% of lakes had $\geq 80\%$ of their catchments in strictly protected areas. Protected lakes occurred disproportionately in the lake-poor western U.S. and most lake-rich regions fell short of the 17% target. Lakes connected to streams and other lakes were disproportionately protected relative to headwater and isolated lakes, which are important for ecosystem services and biodiversity. Meeting conservation targets requires protecting thousands of additional U.S. lakes and catchments across more diverse ecological settings and explicitly considering connectivity.

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Freshwaters provide important ecosystem services such as drinking water, fisheries, climate regulation, and recreation (Wilson and Carpenter 1999; Dodds et al. 2013), but these ecosystems and the high biodiversity they support are rapidly declining worldwide (Abell 2002; Collen et al. 2014). To ensure long-term protection of freshwater biodiversity and ecosystem services, the Convention on Biological Diversity (CBD) recommended protecting at least 17% of freshwaters by 2020 (CBD 2010). Additionally, the CBD suggested this target be achieved through “ecologically representative and well-connected systems of protected areas and other effective area-based conservation measures” that are “implemented primarily through activities at the national and subnational level” (CBD 2010). Therefore, nations and subnational governing bodies (e.g., states or provinces) should strive to meet the CBD target not by protecting any 17% of waterbodies, but by considering connectivity and ecological representation.

Recent global estimates of freshwater representation in protected areas range from 15% to 20.7% of waterbodies (Juffe-Bignoli et al. 2014; Bastin et al. 2019), suggesting that existing protected areas may meet the CBD target. However, defining a protected waterbody is not straightforward and may be affecting these estimates. Many past studies consider a waterbody protected if it is within a protected area boundary (Juffe-Bignoli et al. 2014; Bastin et al. 2019). However, because waterbodies are a direct reflection of their surrounding landscapes (Hynes 1975; Kratz et al. 1997), a better definition of protection would include both a waterbody and its catchment. Negative effects of lakeshore development on littoral food webs provide evidence that freshwater conservation must consider surrounding land, particularly areas near waterbodies. For example, increasing lakeshore development has been shown to reduce abundance of aquatic plants, macroinvertebrates, and fish in littoral areas by reducing coarse woody debris, nutrient cycling, and habitat diversity (Brauns et al. 2011; Dustin and Vondracek 2017). However, previous studies have shown mismatches between protected waterbodies and protected catchments. Lawrence et al. (2011) found that 41% of U.S. national parks have $\geq 90\%$ of their upstream catchments outside park boundaries. Similarly, protected areas cover only 12% of the Tennessee and Cumberland River basins and approximately half of all protected areas do not provide whole catchment protection to any outflowing streams (Thieme et al. 2016). These studies demonstrate that protected areas, which are usually designated for terrestrial features (Saunders et al. 2002; Abell et al. 2007; Herbert et al. 2010), may not protect freshwaters and their catchments. In fact, digitized catchments are not commonly available across large areas, nor are they often part of protected area design (Geist 2011). Therefore, it is unknown to what extent the globally estimated 15–20.7% of protected freshwaters exist within protected catchments.

Another important consideration in the definition of protected waterbodies is the level of land protection (e.g., International Union for the Conservation of Nature global categories, U.S. Gap Analysis Program [GAP] status). For example, GAP status 1–2 lands (e.g., national parks, wilderness areas) are both strictly managed for biodiversity, whereas GAP status 3 lands (e.g., national forests) are multiuse and allow some resource extraction and off-highway vehicles (U.S. Protected Areas Database v 1.4; USGS 2016). Currently, 7.5% and 17.7% of the continental U.S. are under strict and multiuse protection, respectively, with large multiuse areas particularly prevalent in the western U.S. (Supporting Information Fig. S1). Estimates of protected freshwaters with respect to the CBD target are uncertain because previous estimates did not take into account different levels of protection.

The CBD also emphasized the need to consider connectivity when protecting freshwaters. Protecting waterbodies across the full range of freshwater connectivity (i.e., hydrologically isolated to highly connected) is important for both biodiversity and ecosystem services. For example, aquatic surface connections facilitate species' movements, gene flow, and range shifts (Hermoso et al. 2012; Mushet et al. 2019). In contrast, waterbodies that are isolated from surface connections often support unique taxa or high biodiversity (Scheffer et al. 2006). Additionally, headwaters are disproportionately important for downstream water quality (Saunders et al. 2002). Explicitly considering freshwater connectivity in conservation planning has been difficult due to the high computational and data requirements of quantifying freshwater connectivity at broad scales (Fergus et al. 2017; Hermoso et al. 2018), the need to consider multiple forms of connectivity (e.g., structural, functional) across diverse taxa (i.e., aquatic, semiaquatic) (Mushet et al. 2019), and threats of invasive species associated with increased connectivity (Panlasigui et al. 2018). Fortunately, information on freshwater connectivity is becoming increasingly available, particularly in the U.S., to assess freshwater connectivity in relation to the CBD target.

Finally, the CBD recognized that protected waterbodies should be ecologically representative. In the U.S., protected areas are most prevalent in economically and/or ecologically unproductive locations (e.g., remote mountain ranges) and do not contain a representative set of terrestrial biodiversity and ecosystems (Scott et al. 2001; Aycrigg et al. 2013; Jenkins et al. 2015). The same may be true for freshwater biodiversity and ecosystems. For example, U.S. national parks contain 62% of fish species, but only 18% of imperiled fish species (Lawrence et al. 2011). Furthermore, the southeastern U.S. contains the greatest diversity of fish, reptiles, and amphibians, but disproportionately few protected areas (Jenkins et al. 2015). Studies outside the U.S. have found mixed associations between freshwater protection and representation of freshwater biodiversity (Abraham and Kelkar 2012; Chessman 2013; Guareschi et al. 2015; Dobler et al. 2019). Therefore,

protected areas may not only insufficiently protect freshwaters, but also the full breadth of freshwater ecosystems and biodiversity.

We examined how well U.S. protected areas meet the CBD target for permanent lakes, ponds, and reservoirs ≥ 1 ha in surface area (hereafter, lakes). We quantified protection of lakes and their catchments in the continental U.S. to ask:

1. How does the definition of protection determine the percent of lakes that is considered protected?
2. How connected are protected lakes?
3. How ecologically representative are protected lakes of all lakes in the continental U.S.?

Methods

We used the NHDPlus v. 2 data set of all U.S. lakes (280,950 lakes ≥ 1 ha) (USGS 2018). Local lake catchments and upstream network watersheds were based on StreamCat (Hill et al. 2016) for lakes connected to stream networks, and LakeCat (Hill et al. 2018) for hydrologically isolated lakes (“non-network” lakes). Per LakeCat, catchments were designated as the immediate contributing drainage area, whereas watersheds encompassed the local catchment and other connected upstream catchments. Because catchment and watershed protection were highly correlated across all lakes (Pearson’s $r = 0.96$ and 0.94 for strict and multiuse, respectively), we only presented results for catchment protection. We used the U.S. Protected Areas Database v. 1.4 (USGS 2016) for land protection status (strict vs. multiuse).

We classified protected lakes into four groups based on different definitions of protection. The first two groups contained lakes with centers in either strictly or multiuse protected areas, referred to as “lake center protection.” The other two groups contained lakes with catchments that are $\geq 80\%$ protected in either strictly or multiuse protected areas, referred to as “80% catchment protection.” We used these groups to compare characteristics across the range from highly protected lakes (i.e., 80% catchment protection in strictly protected areas) to less protected lakes (i.e., lake center protection in multiuse protected areas). Because the CBD prescribed no formal guidelines for catchment protection, we chose the 80% threshold based on frequency distributions of catchment protection (strict and multiuse) for center-protected lakes (Fig. 1). Therefore, the two groups of highly protected lakes include those with the greatest level of catchment protection across all lakes in the continental U.S. Although we originally considered using a 100% catchment protection threshold as a best-case scenario point of comparison, we ultimately omitted these results because they were qualitatively similar to the 80% threshold and represented an unrealistic conservation standard. We considered all lakes with centers outside of protected areas to be unprotected.

We quantified connectivity for all U.S. lakes using four lake connectivity classes sensu Soranno et al. (2015): (1) lakes with inflow streams and at least one upstream lake (drainage lake/stream), (2) lakes with inflow streams (drainage stream), (3) lakes at the headwaters of stream networks with at least one outflow stream (headwater), and (4) lakes without inflows or outflows (isolated). Due to differences in lake mapping methods between the connectivity analysis and the NHDPlus (i.e., lake polygon updates due to reclassification of waterbodies, hydrologic regime shifts, and improved aerial photography), we could assign a connectivity class to only 73% of lakes. However, because the distribution of connectivity classes in this 73% of lakes was similar to the overall lake population, we were confident that the results applied to all lakes.

We assessed ecological representativeness of protected lakes by quantifying protection across ecoregions, U.S. states, and ecological characteristics that are known to drive variation among lakes. For ecoregions, we used the U.S. Environmental Protection Agency’s National Aquatic Resource Survey because this regionalization is used for national U.S. lake assessments (Herlihy et al. 2008). We provided a similar analysis for U.S. states because state management agencies can influence lake protection and are responsible for managing lake water quality and biodiversity. Next, we compared characteristics of protected lakes to those of unprotected lakes. Characteristics were lake area, drainage ratio (approximates water residence time; calculated as lake area/watershed area ratio), and several catchment variables: area, elevation, topographic wetness index, mean annual air temperature and precipitation, land use/cover (forest, agriculture, wetlands, road density, and impervious surface), atmospheric deposition (sulfur + nitrogen), forest loss, and hydrology (runoff and baseflow). We considered, but ultimately excluded dam density due to the high abundance of 0 values ($> 75\%$ across all groups of lake protection). All of the above variables were from LakeCat, except for lake area and elevation, which came from the NHDPlus (Supporting Information Table S1).

Data analysis and modeling

We calculated the percent of lakes in the four protection groups by connectivity class, ecoregion, and U.S. state. To examine the ecological representativeness of protected lakes, we used logistic regression to estimate the univariate region-specific relationship, β , between each of the above ecological characteristics, x , and the probability of lake protection according to the four protection groups, p (Eq. 1). Separate models were generated for each combination of ecological characteristic ($n = 17$), lake protection group ($n = 4$), and ecoregion ($n = 9$). Data and code are available at <https://doi.org/10.5281/zenodo.3361750> (McCullough and Skaff 2019) and all analyses were performed in R version 3.5.1 (R Core Team 2018).

$$\text{logit}(p) = a + \beta x + \varepsilon \quad (1)$$

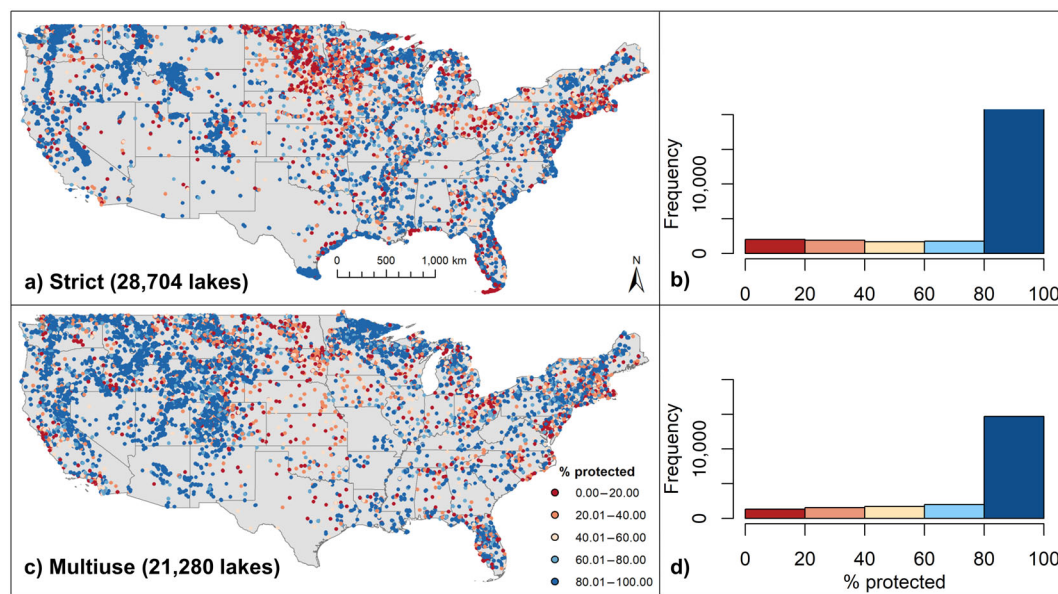


Fig. 1. Spatial and frequency distributions of percent lake catchment protected for lakes ≥ 1 ha that occur in (a, b) strictly and (c, d) multiuse protected areas. Lakes were considered protected if their centers occurred within protected areas in the U.S. Protected Areas Database v. 1.4 (USGS 2016).

Results

U.S. lake protection varies according to the definition of protection

Overall lake protection in the continental U.S. depended on the definition of lake protection. For the two broader groups of lake protection (i.e., lake center protection in strictly and multiuse protected areas), 10.2% (28,704 lakes) and 7.6% (21,280 lakes) of lakes were protected, respectively (Fig. 1a,c). Combined, these lakes slightly exceeded the CBD target (17.8%; 49,984 lakes). In contrast, only 7.5% (21,018 lakes) and 5.2% (14,690 lakes) of lakes had $\geq 80\%$ catchment protection (strict and multiuse, respectively) (Supporting Information Fig. S2). Therefore, under these narrower, more ecologically relevant protection groups, lake protection in the continental U.S. was well below the CBD target, even with strict and multiuse protection combined (12.7%; 35,708 lakes).

Most lake catchments in the continental U.S. contained little protected land (Supporting Information Fig. S3): 85.1% and 85.7% of catchments were $< 1\%$ protected (median = 0%) for strictly and multiuse protected areas, respectively. However, frequency distributions indicate that most lakes whose centers occur within protected areas had relatively well-protected catchments (Fig. 1b,d). Of those with centers in strictly protected areas, median catchment protection was 100% and 73.2% of these lakes had $> 80\%$ catchment protection. For multiuse protected areas, 69.0% of lakes had $> 80\%$ catchment protection and the median catchment protection was 100%. Just 4.7% (13,213 lakes) and 2.9% (8162 lakes) had fully protected (100%) catchments in strict and multiuse protected areas, respectively (combined: 7.6%; 21,375 lakes, data not shown).

Protected U.S. lakes do not represent the full range of lake connectivity

Across all groups of lake protection, lake connectivity classes were not protected proportionally to the overall U.S. lake population. Based on lake center protection, highly connected lakes were most commonly protected (16.8% strict and 10.8% multiuse protection of drainage lake/stream lakes), but were the least common lake connectivity class in the U.S. (7.9%) (Table 1; Fig. 2a). Less connected lakes had similar percentages of protection, with 8.9–10.5% and 7.0–7.9% under strict and multiuse protection, respectively. However, these three connectivity classes were considerably more common in the U.S. (drainage stream, headwater, and isolated lakes; 14.5–44.1%). Based on 80% catchment protection, 6.6–11.5% and 4.8–6.0% of lakes were protected in strict and multiuse areas, respectively, across all four connectivity classes (Table 1; Fig. 2b). Therefore, under this more protective definition, $< 12\%$ of lakes were protected (strict and multiuse combined) and lake protection was not proportional to the distribution of lake connectivity classes in the U.S.

Protected U.S. lakes are not ecologically representative

Lake protection was geographically uneven across the continental U.S. based on ecoregions. Lake-rich ecoregions generally had fewer protected lakes and protected lakes were predominantly located in the Western Mountains, which contained only 6.5% of U.S. lakes. Based on both lake center and 80% catchment protection, the Western Mountains had the largest percent of lakes under both strict (44.5% and 42.7%) and multiuse (25.5% and 22.2%) protection, respectively (Table 1; Fig. 3a,b). Most lake-rich ecoregions in the eastern,

Table 1. Lake protection by NARS ecoregion and lake connectivity class for strict and multiuse protected areas. First number = number of protected lakes, second number in parentheses = proportion of protected lakes.

Ecoregion	Lakes ≥ 1 ha	% of total	Strict, center	Multiuse, center	Strict, 80%	Multiuse, 80%	Unprotected
Coastal Plains (CPL)	79,587	28.40%	6485 (0.08)	2832 (0.04)	5218 (0.07)	1989 (0.02)	70,270 (0.88)
Northern Appalachians (NAP)	22,465	8.02%	1191 (0.05)	1972 (0.09)	637 (0.03)	971 (0.04)	19,302 (0.86)
Northern Plains (NPL)	19,342	6.90%	969 (0.05)	1978 (0.10)	296 (0.02)	1155 (0.06)	16,395 (0.85)
Southern Appalachians (SAP)	25,083	8.95%	636 (0.03)	624 (0.02)	319 (0.01)	308 (0.01)	23,823 (0.95)
Southern Plains (SPL)	25,176	8.98%	568 (0.02)	239 (0.01)	312 (0.01)	69 (<0.01)	24,369 (0.97)
Temperate Plains (TPL)	39,731	14.18%	3350 (0.08)	899 (0.02)	1275 (0.03)	274 (<0.01)	35,482 (0.89)
Upper Midwest (UMW)	41,415	14.78%	5928 (0.14)	6430 (0.16)	4433 (0.11)	4925 (0.12)	29,057 (0.70)
Western Mountains (WMT)	18,289	6.53%	8143 (0.45)	4666 (0.26)	7804 (0.43)	4053 (0.22)	5480 (0.30)
Xeric (XER)	9147	3.26%	1004 (0.11)	1577 (0.17)	670 (0.07)	940 (0.10)	6566 (0.72)
Lake connectivity class	Lakes ≥ 1 ha*	% of total	Strict, center	Multiuse, center	Strict, 80%	Multiuse, 80%	Unprotected
Drainage, lake/stream	16,263	7.90%	2725 (0.17)	1755 (0.11)	1871 (0.12)	975 (0.06)	11,783 (0.72)
Drainage, stream	90,725	44.08%	8156 (0.09)	6496 (0.07)	6265 (0.07)	4330 (0.05)	76,073 (0.84)
Headwater	29,865	14.51%	3139 (0.11)	2099 (0.07)	2583 (0.09)	1617 (0.05)	24,627 (0.82)
Isolated	68,944	33.50%	6781 (0.10)	5434 (0.08)	4546 (0.07)	3844 (0.06)	56,729 (0.82)

*73% of all lakes; includes only those that matched with connectivity classes.

southern, and central U.S. had $\leq 10\%$ (and often $< 5\%$) of lakes protected for all four lake protection groups, including the Coastal Plains, which had the highest percent of lakes in the U.S. (28.4%). The one exception was the Upper Midwest, which had 14.3% and 15.5% of lake centers under strict and multiuse protection, respectively. The Upper Midwest was the only relatively lake-rich ecoregion to exceed the CBD target, but only based on combined strict and multiuse protection for lake centers (29.8% of lakes protected). The Xeric and Upper Midwest ecoregions also exceeded the CBD target for combined strict and multiuse protection (17.6% and 22.6% of lakes, respectively) based on 80% catchment protection. However, the Western Mountains was the only ecoregion to exceed the CBD target based on the narrowest lake protection group (42.7% of lakes under strict, 80% catchment protection).

Lake protection was also geographically uneven across U.S. states: states with fewer lakes generally had greater percentages of lakes protected (Supporting Information Table S2, Fig. S4). Based on lake centers, 22 of 48 states met or exceeded the CBD target, whereas only 14 states did so based on 80% catchment protection (combined strict and multiuse). California, Delaware, Idaho, Oregon, Utah, Washington, and Wyoming were the only states to exceed the CBD target based on strict, 80% catchment protection. Across all lake protection groups, lake protection was relatively low in lake-rich southeastern and central states, but with some exceptions. Florida, Michigan, Minnesota, and Wisconsin, which were in the top 10 states by number of

lakes, all exceeded the CBD target based on lake center protection (combined strict and multiuse), and Minnesota did based on 80% catchment protection (Supporting Information Table S2, Fig. S4).

In addition to geographical location, examination of lake and catchment characteristics supported the idea that protected lakes are not ecologically representative. Across the U.S., protected lake catchments generally had greater wetland cover than nonprotected lake catchments and tended to be cooler and slightly drier, but characteristics of protected lake catchments also differed among regions (Fig. 4, Supporting Information Fig. S5). Protected lake catchments contained disproportionate amounts of wetland cover in most regions, but protected catchments had less wetland cover than unprotected catchments in the Western Mountains. Also, although higher elevation lakes were more likely to be protected in the Western Mountains, in many other regions, especially the Coastal Plains, unprotected lakes were more likely to be located at higher elevations. Finally, the definition of lake protection clearly affected conclusions regarding the ecological representativeness of protected lakes: higher elevation and more forested catchments were associated with multiuse protection, but wetland cover was more strongly associated with strict protection in most regions. Few lake-level characteristics were strongly associated with protection, indicating that characteristics of protected lakes themselves did not differ markedly from unprotected lakes, although their catchments can differ in significant ways (Fig. 4, Supporting Information Fig. S5).

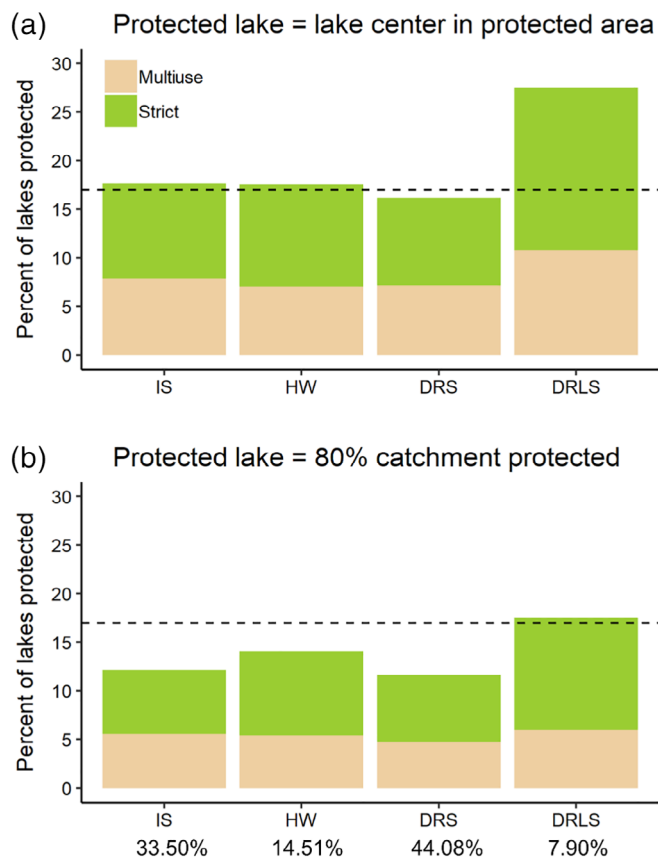


Fig. 2. Percent of lakes protected defined by (a) occurrence of lake centers in protected areas and (b) 80% catchment protection by lake connectivity class (arranged from least to most connected). Dashed lines represent 17% CBD conservation target for freshwaters. IS, isolated; HW, headwater; DRS, drainage stream; DRLS, drainage lake/stream. Numbers beneath connectivity classes are the percent of U.S. lakes in each class. See Table 1 for number of lakes in each connectivity class.

Discussion

Catchment if you can: What is a protected lake?

Our study represents the first assessment of the extent to which existing U.S. protected areas meet the 17% CBD conservation target for lakes. Based on lake center protection and combined strict and multiuse protection, 17.8% of lakes are protected, meeting the CBD target. However, this percentage is below the target based on other more protective definitions of lake protection. When limited to strictly protected areas, just 10.2% of lakes are protected (based on lake centers), and if one defines lake protection based on the more ecologically relevant 80% catchment protection, only 12.7% and 7.5% of lakes are protected (combined strict/multiuse and strict protection only, respectively). Therefore, definitions of lake protection determine protected lake assessments and U.S. lakes may be insufficiently protected.

Based on decades of research on the importance of catchments to freshwater ecosystem services and functioning, we

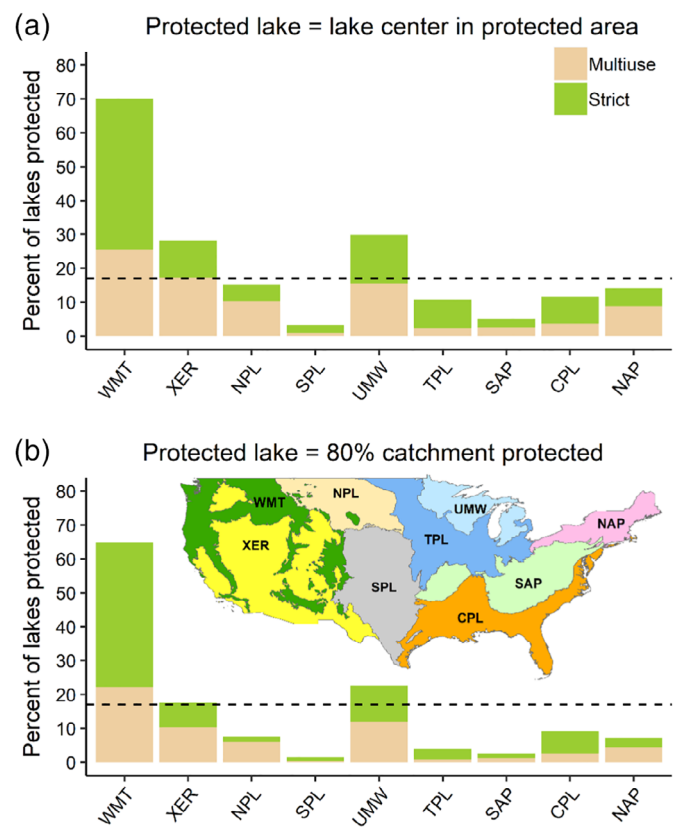


Fig. 3. Percent of lakes protected by ecoregion defined by (a) lake centers occurring within protected areas and (b) 80% catchment protection. Dashed lines represent 17% CBD conservation target for freshwaters. WMT, Western Mountains; XER, Xeric; NPL, Northern Plains; SPL, Southern Plains; UMW, Upper Midwest; TPL, Temperate Plains; SAP, Southern Appalachians; CPL, Coastal Plains; NAP, Northern Appalachians. See Table 1 for number of lakes in each ecoregion.

propose that lakes should only be considered protected when their catchments are also protected. However, catchments are not typically considered in protected area design and there are currently no guidelines for the appropriate amount of catchment protection. Requiring 80% catchment protection represents an ambitious standard and may be impractical in some landscapes. However, more achievable standards and other strategies may still protect biodiversity and ecosystem services. One strategy that has been proposed is zone-based catchment management.

Abell et al. (2007) proposed such an approach with varying levels of protection and use restrictions across freshwaters and their catchments. This zoning approach affords the most protection to “freshwater focal areas” (important freshwater features such as spawning areas or biodiversity hotspots), but generally does not prohibit responsibly managed human land and water use throughout catchments. For example, riparian areas surrounding or directly upstream from freshwater focal areas may be designated as “critical management zones”

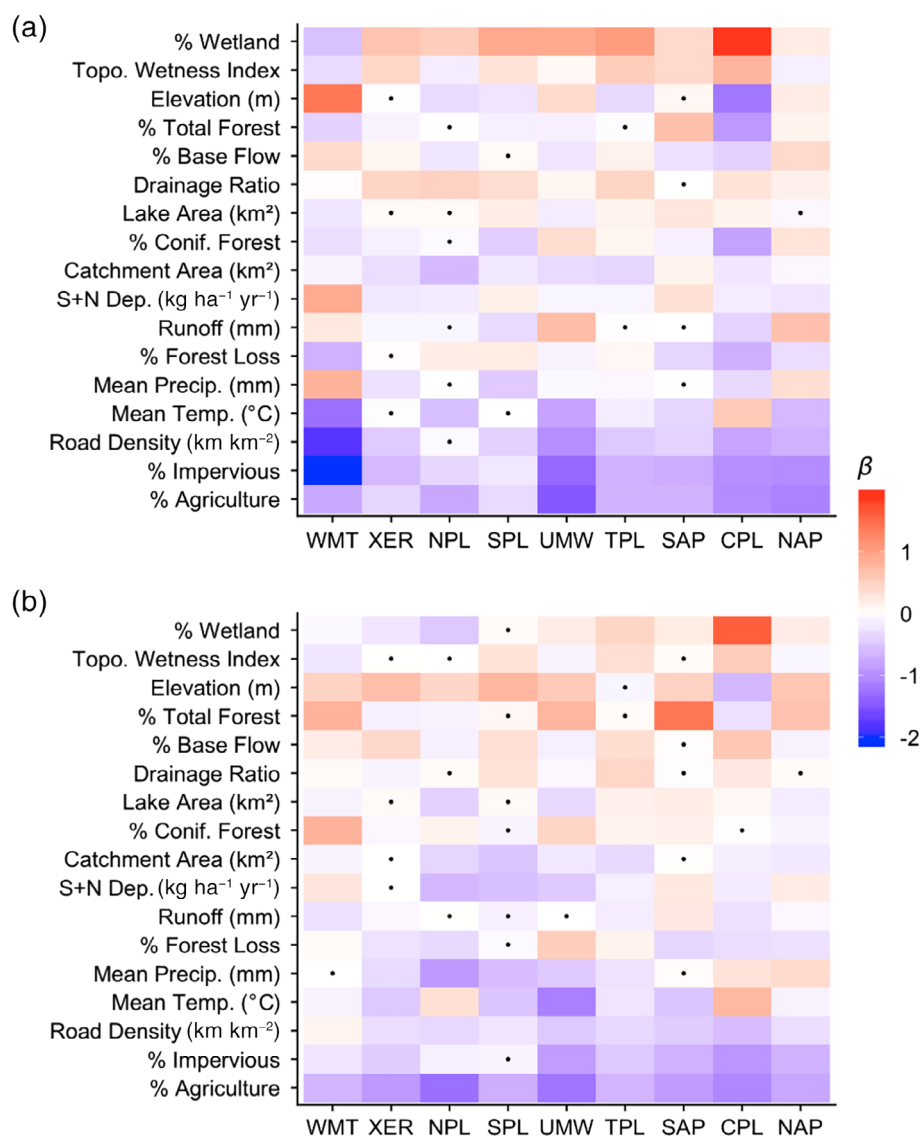


Fig. 4. Heatmap of logistic regression coefficients (β) representing the change in log odds of (a) strict and (b) multiuse 80% catchment protection for a one unit change in standardized covariate values. Coefficient estimates were generated separately by ecoregion (x-axis). Climate covariates (“mean temp.” and “mean precip.”) are 30-yr normals calculated from 1981 to 2010. Dots in panels identify nonstatistically significant coefficient estimates ($p \geq 0.05$). See Supporting Information Table S1 for full variable descriptions and Supporting Information Fig. S5 for corresponding analysis based on lake center protection.

managed specifically to maintain focal areas. Managers would then designate the remainder of the catchment as a “catchment management zone” and apply common standards such as restricted development on steep slopes and regulated use of pesticides and fertilizers (Abell et al. 2007). Such zone-based, multiuse catchment management approaches may be more practical than a one-size-fits all catchment protection threshold, may grant local managers more flexibility to tailor strategies to local conservation objectives, and therefore may be more likely to be implemented than strict protection

(Barmuta et al. 2011). Furthermore, zone-based approaches emphasize the spatial configuration of catchment protection as a way to increase the efficiency and effectiveness of conservation actions (Abell et al. 2007; Juffe-Bignoli et al. 2016). Spatial conservation planning frameworks applied to prioritize conservation actions in river basins have previously helped implement zone-based strategies (e.g., Thieme et al. 2016; Erős et al. 2018). Because lake, stream, and river catchments are often hydrologically integrated (i.e., riverscapes), there is likely future potential for achieving greater protection of lake

and freshwater biodiversity by explicitly considering these different types of freshwaters and their spatial configuration in regional conservation planning frameworks.

Moving toward an ecologically representative, well-connected set of protected lakes

Disproportionate protection of western U.S. lakes suggests that protected lakes are not ecologically representative of continental U.S. lakes. Overrepresentation in the Western Mountains indicates high levels of protection for mountain lakes, which tend to be cold and unproductive (Williamson et al. 2010). These findings are not unique to lakes. Owing to the prevalence of large protected areas in the western U.S., previous studies from both terrestrial and freshwater ecosystems have shown that unproductive locations with relatively low biodiversity are most often protected (Scott et al. 2001; Lawrence et al. 2011; Aycrigg et al. 2013), which signals that the most productive, biologically diverse ecosystems, including those that contain rare and endemic freshwater and terrestrial species, are often underprotected (Jenkins et al. 2015). In the case of lakes, an important example is prairie pothole lakes, which occur in the Northern and Temperate Plains and are important for biogeochemical cycling and migratory waterbird habitat (Gleason et al. 2011), but are underprotected based on all four groups of protection. Furthermore, the Coastal Plains and Southern Appalachians have the greatest diversity of fish, reptiles, and amphibians in the continental U.S. (Jenkins et al. 2015), but lake protection in these ecoregions is below the CBD target for all protection groups. Therefore, geographic congruence in conservation needs for both freshwater and terrestrial biodiversity suggests that protecting additional lakes and catchments across the continental U.S., particularly in lake-rich regions with high levels of freshwater biodiversity, would likely benefit both freshwater and terrestrial biodiversity.

Disproportionate protection of western U.S. lakes underscores the challenge of potentially conflicting societal priorities for biodiversity and ecosystem services, both of which the CBD emphasizes. Although lakes are not always considered when making land conservation decisions, prioritization of western U.S. lakes may suggest a societal interest in maintaining freshwater resources in regions that depend on lakes for drinking water and are most vulnerable to water scarcity. Most western U.S. lakes at low to moderate elevations are human-made reservoirs, many of which supply water to millions of people (e.g., Hetch Hetchy Reservoir in Yosemite National Park, California and the San Francisco metropolitan area). In contrast, water scarcity is a much smaller concern in the southeastern U.S. where there is considerably greater freshwater biodiversity and abundant freshwater resources (including thousands of human-made reservoirs). The relatively low level of lake protection in the southeastern U.S. may suggest that biodiversity is a lower societal priority than drinking water. However, these low levels of protection may expose many human communities to reduced water

quality and waterborne diseases (Pires 2004; Postel and Thompson 2005). Ultimately, protecting an ecologically representative set of U.S. lakes for long-term maintenance of freshwater biodiversity and ecosystem services depends on the recognition that the current system of protected areas is likely insufficient for meeting both of these priorities.

The CBD also recognizes the importance of protecting connectivity among freshwaters because connections play key roles in maintaining biodiversity and ecosystem services. We emphasize that ecologically representative protected lakes include lakes across the full range of connectivity classes. Disproportionate protection of highly connected lakes suggests that some freshwater structural connectivity is currently protected. However, isolated lakes are disproportionately unprotected and are important for semiaquatic species that rely on the integrated aquatic-terrestrial landscape (Erős et al. 2012; Hermoso et al. 2018). Although previous studies have recommended protecting headwaters for their ecosystem services, headwater lakes are no more likely to be protected than other lake connectivity classes. Therefore, protecting additional headwater lakes (and their catchments) could have large additional downstream benefits, particularly for reservoirs that represent an important drinking water source in regions with few natural lakes (e.g., southeastern and western U.S.). A key challenge, however, is the current lack of a national-scale classification distinguishing natural lakes and reservoirs, which complicates the goal of protecting lake ecosystem services across large geographic areas.

Ecoregions, connectivity classes, and catchment-scale ecological characteristics do not capture all of the variation in ecologically relevant lake characteristics (e.g., water quality, lake depth, and shoreline habitat characteristics) that directly influence biodiversity and ecosystem services. However, these lake-specific data are unavailable for all U.S. lakes and cannot be easily predicted from existing data sources. For example, lake water quality is more spatially heterogeneous than ex situ predictor variables such as catchment land use/cover, climate, and hydrology (Lapierre et al. 2018) and lake depth is not strongly correlated with surrounding topography (Oliver et al. 2016). Therefore, conservation gap analyses must rely on surrogate information that can be obtained for all or a representative sample of lakes, but are also appropriately scaled to represent spatial patterns of biodiversity and ecosystem services. Our analysis of lake and catchment characteristics based on a broad-scale ecological database (LakeCat) represents an important intermediate step between coarse, regional gap analyses, and those that incorporate in situ data.

Recommended changes to the CBD conservation target for lakes

We recommend revising the CBD conservation target for lakes to incorporate both waterbodies and catchments and more explicit consideration of freshwater connectivity. Although current emphasis on achieving conservation targets through ecologically representative, well-connected protected

areas are useful for terrestrial conservation, this approach is insufficient for lakes and other freshwaters. Not only does meeting current lake conservation targets require protecting thousands of additional lakes and their catchments across diverse ecological settings, but protecting an ecologically representative set of lakes cannot be achieved without protecting diverse forms of freshwater connectivity.

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