



# US cities can manage national hydrology and biodiversity using local infrastructure policy

Ryan A. McManamay<sup>a,1</sup>, Sujithkumar Surendran Nair<sup>a</sup>, Christopher R. DeRolph<sup>a</sup>, Benjamin L. Ruddell<sup>b</sup>, April M. Morton<sup>a</sup>, Robert N. Stewart<sup>a</sup>, Matthew J. Troia<sup>c</sup>, Liem Tran<sup>d</sup>, Hyun Kim<sup>d</sup>, and Budhendra L. Bhaduri<sup>a</sup>

<sup>a</sup>Urban Dynamics Institute, Oak Ridge National Laboratory, Oak Ridge, TN 37831; <sup>b</sup>School of Informatics, Computing, and Cyber Systems, Northern Arizona University, Flagstaff, AZ 86011; <sup>c</sup>Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN 37831; and <sup>d</sup>Department of Geography, University of Tennessee, Knoxville, TN 37996

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**Cities are concentrations of sociopolitical power and prime architects of land transformation, while also serving as consumption hubs of “hard” water and energy infrastructures. These infrastructures extend well outside metropolitan boundaries and impact distal river ecosystems. We used a comprehensive model to quantify the roles of anthropogenic stressors on hydrologic alteration and biodiversity in US streams and isolate the impacts stemming from hard infrastructure developments in cities. Across the contiguous United States, cities’ hard infrastructures have significantly altered at least 7% of streams, which influence habitats for over 60% of North America’s fish, mussel, and crayfish species. Additionally, city infrastructures have contributed to local extinctions in 260 species and currently influence 970 indigenous species, 27% of which are in jeopardy. We find that ecosystem impacts do not scale with city size but are instead proportionate to infrastructure decisions. For example, Atlanta’s impacts by hard infrastructures extend across four major river basins, 12,500 stream km, and contribute to 100 local extinctions of aquatic species. In contrast, Las Vegas, a similar size city, impacts <1,000 stream km, leading to only seven local extinctions. So, cities have local policy choices that can reduce future impacts to regional aquatic ecosystems as they grow. By coordinating policy and communication between hard infrastructure sectors, local city governments and utilities can directly improve environmental quality in a significant fraction of the nation’s streams reaching far beyond their city boundaries.**

urban ecology | energy–water nexus | electricity | urban sustainability | hydrologic alteration

Cities are the modern world’s epicenters of sociopolitical power and economic production, but also among the primary drivers of land transformation and resource consumption across the globe. Within the United States, almost 95% of the population and household income occurs within metropolitan statistical areas (*SI Methods*). The world’s growing urban populations will continue to extend commodity supply chains well beyond municipal boundaries, inducing environmental stress in distal geographies (1). As they grow, global cities are shifting toward reliance on expansive infrastructure and supply chain networks (2), which are controlled through a multitude of social institutions and disparate policies (3). Historically, local government policy was typically shaped by the immediate socioeconomic context within municipal boundaries, and externalities beyond that boundary were generally ignored (4, 5). However, city leaders are increasingly taking the initiative to transform regional social and environmental issues, reflecting a desire to leverage a city’s power to improve sustainability and welfare in the city’s area of influence.

Cities’ demand for goods and services are met through consumer supply chains (soft networks) or land, energy, water infrastructures (hard networks). A city’s external soft infrastructure and supply chain (1, 6) involves shipping of commodities, and is controlled by the diffuse individual purchasing decisions of private citizens and businesses; these soft networks are naturally resistant to government policy and control. By contrast, some of a city’s hard infrastructure systems (6, 7), such as land use practices within the municipal boundary (8), water and wastewater systems, and “EnergySheds”

(i.e., a region of transmission structures balancing electricity production at power plants with intense consumption in cities) collectively comprise a city’s land/energy/water (LEW) network and tend to be directly controlled by local city governments and utilities (Fig. 1). These infrastructures have wide-ranging direct and indirect impacts on natural resources, particularly aquatic ecosystems. The urban transformation of land to impervious surfaces induces dramatic storm flows (8), displacing water from natural infiltration to downstream communities (9). EnergySheds can be extensive, overlap with other cities’ EnergySheds, and be composed of many different energy production technologies with varying water use (10). Finally, public drinking water supplies can be highly extractive and require infrastructure that transports water beyond natural watershed boundaries. Thus, these hard infrastructures can in principle create pathways by which local governments and utilities can manage ecosystem integrity beyond the municipal boundary.

The health of aquatic ecosystems is of general interest to the public at large, and of special interest to cities that are located along streams. Understanding the major contributors of hydrologic alteration (9) and biodiversity loss (5) reveals the predominant pathways in which city planners can minimize future impacts to aquatic ecosystems (2). Furthermore, clean and hydrologically intact streams provide water supply, stormwater management, and recreational services to cities. At the same time, cities incur large costs to meet federally regulated goals for stormwater quality and wastewater quality management costs that can be mitigated or exacerbated depending on the ecological

## Significance

**We introduce a unique and detailed data-driven approach that links cities’ hard infrastructures to their distal ecological impacts on streams. Although US cities concentrate most of the nation’s population, wealth, and consumption in roughly 5% of the land area, we find that city infrastructures influence habitats for over 60% of North America’s fish, mussel, and crayfish species and have contributed to local and complete extinctions in 260 species. We also demonstrate that city impacts are not proportionate to city size but reflect infrastructure decisions; thus, as US urbanization trends continue, local government and utility companies have opportunities to improve regional aquatic ecosystem conditions outside city boundaries through their hard infrastructure policies.**

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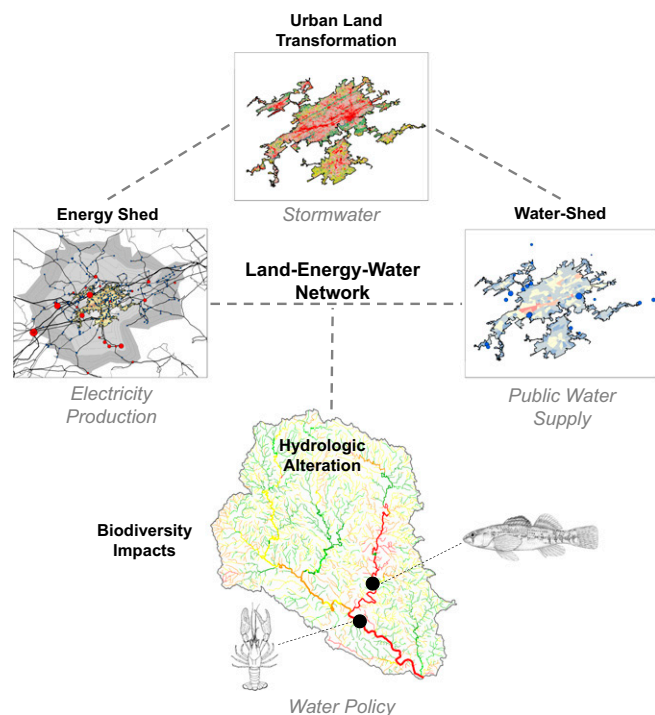
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Data deposition: Data underlying our analysis are available on figshare at <https://doi.org/10.6084/m9.figshare.5257936.v1>.

<sup>1</sup>To whom correspondence should be addressed. Email: [mcmmanamayra@ornl.gov](mailto:mcmmanamayra@ornl.gov).

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**Fig. 1.** Mapping a city's LEW network as impacts to hydrologic and biodiversity impacts in river networks enables communication among disparate policy sectors.

health of the stream. Moreover, although municipal boundaries are mutually exclusive, the impacts of cities' external supply infrastructures overlap with other cities (1), so the hundreds of cities in the United States should be concerned about cooperation and competition on ecosystem and water supply concerns (2).

This study is the first application of a data-driven model to map hydrologic flow alteration and biodiversity impacts on all US streams and attribute these impacts to their anthropogenic causes, specifically those relevant to city infrastructures. Once predominant anthropogenic stressors of hydrology and biodiversity are identified, the study then employs a detailed analysis of five cities varying in geography, population size, and LEW infrastructure to quantify the impact of their hard infrastructures and visualize the pathways by which these cities can directly manage regional aquatic ecosystems using local policy. Herein, we answer the question, What is the extent of a city's impact on hydrology and biodiversity in rivers when evaluated through its hard infrastructure network (Fig. 1)?

## Results and Discussion

### US Urban Land Transformation and Electricity Production Impacts.

Streams with hydrology departing from natural or reference conditions are termed hydrologically altered, which we represent as changes in any one of 12 different hydrologic indices (*Methods* and *SI Methods*). Using a presumptive threshold of 20% hydrologic alteration (11), we estimate that almost 31% of streams ( $1.56 \times 10^6$  km) in the contiguous United States are hydrologically altered based on our cumulative hydrologic alteration index (Fig. 2A and *SI Methods*). These estimates are congruent with other national assessments depicting hydrologic alteration in stream gages (25%) (12) or characterizing streams habitats using surrogates of hydrologic alteration (39%) (13). However, a more conservative threshold of 10% suggests that almost 80% of streams show some sign of hydrologic alteration. Our results suggested that the most influential anthropogenic drivers of hydrologic alteration in the United States were urban land cover and reservoir storage, whereas other variables related to city infrastructure, such as waste water discharges, were not as significant

(Fig. S1). Thus, for the entire United States, we subsequently focused on impacts of urban land transformation (ULT) and electricity production (EP), i.e., indices representing the combined effects of multiple variables related to those sectors (*SI Methods*).

Impacts from ULT include ~6.2% of streams ( $3.14 \times 10^5$  km), whereas 1.3% of streams ( $6.58 \times 10^4$  km) are impacted from EP (Fig. 2B–D). When considered jointly, ULT and EP impact 7% of US streams. Although these estimates may not seem extensive, they result in very large biodiversity impacts. In total, ULT and EP have impacted 1,223 fish, mussel, or crayfish species, 260 of which are locally extinct and 970 of which are currently extant. Of the extant species, 27% are imperiled or vulnerable to extinction (Fig. 2E). On an individual basis, ULT impacts 1,118 fish, mussel, or crayfish species (current or locally extinct), whereas EP impacts 938 species (Fig. 2E). This suggests ULT and EP impact 59% and 50% of all freshwater species found in North America, respectively (*SI Methods*). Additionally, as much as 192 (20%) species and 216 (19%) species are estimated to be locally extinct due to EP and ULT impacts, respectively. Although ULT impacts occupy far more of the nation's stream mileage, EP tends to impact far larger systems, with average upstream drainage areas and mean annual flows, 5.6 and 6.7 times greater, respectively, than ULT-impacted streams (Fig. 2D). Likewise, EP impacts 14.2 species per 1,000 km of stream compared with 3.56 species per 1,000 km impacted by ULT (Fig. 2E). As a result, cumulative biodiversity impacts of EP in the United States approximate that of ULT.

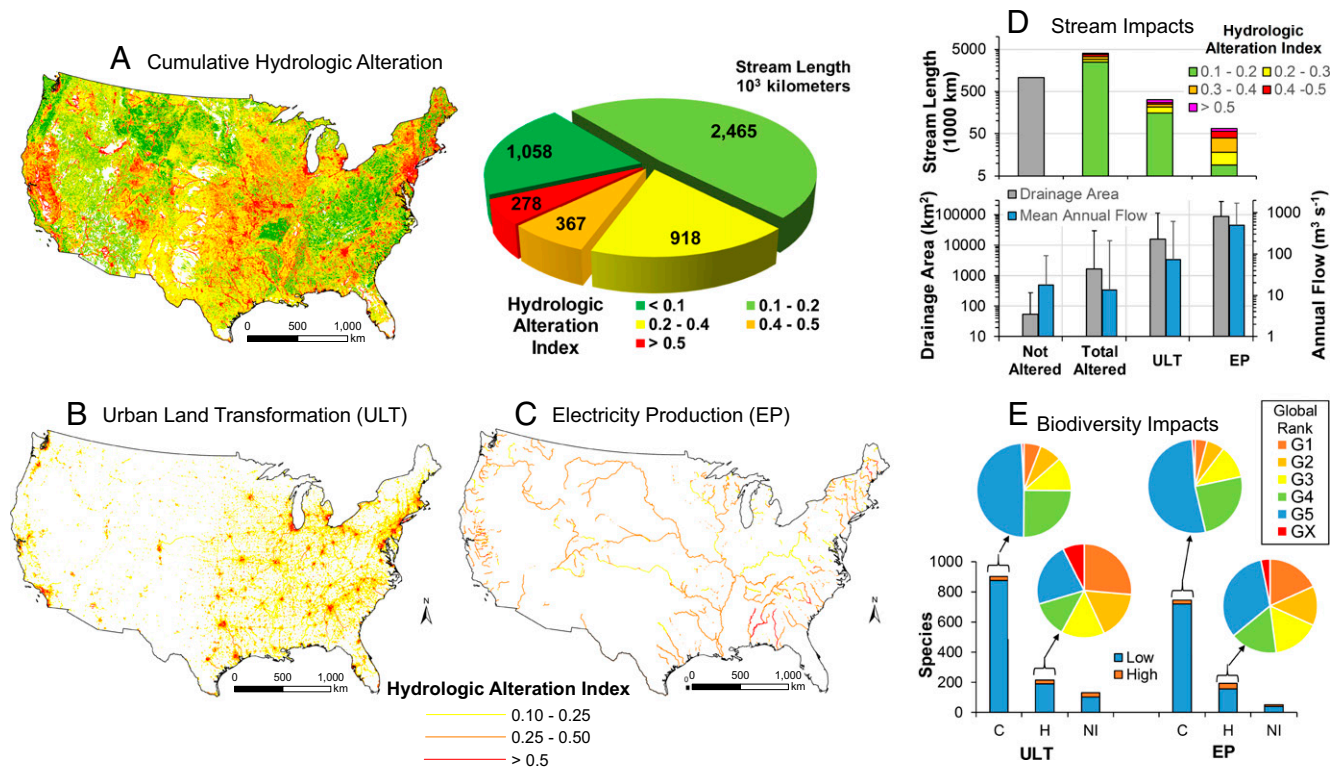
Our results clearly display that EP propagates hydrologic impacts within most large river systems in the United States. Electricity production, especially related to reservoir operation, can alter hydrology for extensive river distances (e.g.,  $>10^2$  km) (14). In contrast, ULT is typically compact, intensive, and inherently tied with population density, which suggests urban impacts are localized and transformative of river environments proximate to impervious surfaces (9). Although our results suggest this is true to an extent, the map of ULT hydrologic impacts extend well beyond urban boundaries in many cases (Fig. 2B) and is likely dependent upon the nature and extent of impervious surfaces and exceedance of hydraulic thresholds (9).

We estimate that 92% of US residential and commercial electricity consumption occurs in urban areas (*SI Methods*). Additionally, more than one third of the streams regulated by power plants ( $1.9 \times 10^4$  km) in the contiguous United States are also recipients of hydrologically modified stream flows from upstream urbanization. This suggests cities not only offset their resource burdens on distal ecosystems (1), but they also compound stress on external regulations. For example, US power plant operations must be responsive to power load demands while minimizing environmental impacts and serving other purposes (e.g., flood control). Hence, irregular flows from urbanization are likely to place additional stress on energy operations, yet there is no federal regulation of storm flows beyond pollution control (15).

### Quantifying City Infrastructure Impacts.

The national-scale analysis yielded important insights into the primary drivers of hydrologic alteration relevant to city infrastructures. Here, we transition to assessing the individual impacts of cities on regional hydrology and biodiversity by linking cities, their utilities, and surrounding resources via hard infrastructure mapping. We selected five rapidly growing cities in two groups representing the water-stressed southeastern and southwestern United States, eastern and western power grid interconnections, and "old" (eastern United States) and "new" (western United States) ages and styles of infrastructure and institutions. Due to rapid population growth combined with water stress, cities in these regions have strong potential to cease increased ecosystem impacts and to create cross-competition between cities' hinterlands via the water and power infrastructure. Cities were similar in that large federal water managers were present in all regions. Capturing city LEW infrastructures requires establishing the city as the hub of networks linking energy demand, water demand, and associated resources in the surrounding landscape. From these





**Fig. 2.** Hydrologic and biodiversity impacts of ULT and EP in the contiguous United States. (A) Cumulative hydrologic alteration mapped to stream reaches and distribution of stream length by degree of alteration. (B) ULT and (C) EP impacts on hydrologic alteration in the nation's streams. (D) Stream distance and size characteristics impacted by ULT and EP sectors. (E) Biodiversity impacts (fish, crayfish, and bivalves) of each sector consider current (C), historically present (H) but locally extinct, and nonindigenous (NI) species and global conservation ranking (*SI Methods*). Low (blue bars) and high (red bars) estimates generated by accounting for detection probability.

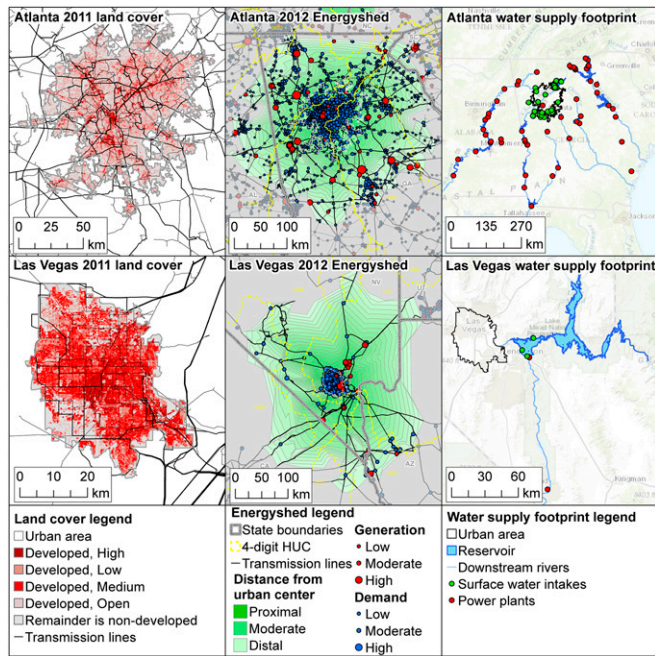
interdependent relationships, we derived geospatial data relevant to capturing hydrologic alteration among the ULT, EP, and water supply (WS) infrastructures (Fig. 3). For instance, we identified power plants and water intakes (and associated water use and reservoirs) contributing to each city's EnergyShed and water supply network, respectively (Table 1). Collectively, we term a city's ULT, EP, and WS infrastructure the LEW network.

Stream mileage and associated biodiversity impacted from altered hydrology was not strongly related to population size (Fig. S2), per-capita energy demand, or energy efficiency (Table 1), but generally reflected an east-to-west pattern, primarily driven by regional differences in water availability and faunal richness. After accounting for stream network density, we found that relationships between impacts and city population size remained weak (Fig. S2). LEW impacts ranged from 867 km for Tucson to almost 12,500 km for Atlanta (Figs. 4 and 5), and biodiversity impacts included 523 indigenous species for Atlanta but only 2 for Tucson (Fig. 5 and Fig. S3). Streams impacted by western cities had biological communities dominated by non-indigenous species relative to eastern cities (Fig. 5 and Fig. S3) (16). Hydrologic impacts for individual infrastructures also ranged dramatically. For all cities, ULT consistently impacted more stream length than EP and WS sectors; however, EP impacted the most species in Knoxville, Atlanta, and Phoenix (Fig. 5). In comparison with eastern cities, WS impacts approximated those of EP in Phoenix and Las Vegas, a likely result of energy production and water supply infrastructure using the same reservoirs (Figs. 3 and 5).

**Competing Cities and Sectors.** Mapping systemic impacts on river environments reveals competition among cities and the potential to develop cooperative transbasin agreements between local city governments. Undoubtedly, urban geography has considerable relevance to aquatic ecosystem impacts (9, 17) and subsequent

city competition. For instance, Atlanta's ULT extends across the headwaters of three major basins and propagates hydrologic impacts for almost 9,600 river km, which intersect 21 other cities (Fig. 4). In other cases, human-environmental infrastructure results in complex and unexpected water competition without respect to geography. For example, Phoenix and Tucson are geographically proximate to one another, yet share no ecologically relevant overlap in each other's impacts (Fig. 4). However, Phoenix and Tucson coordinate management of water supplies through the Central Arizona Project (CAP) (18). Las Vegas, however, occurs over 480 km from Phoenix, but exerts hydrologic impacts on 474 km of the lower Colorado River, which directly competes with public water supplies of the CAP. Natural hydrography also plays a large role in urban-generated hydrologic alteration (17). In comparison with water-rich eastern US cities, sparse dendritic stream networks in the western United States promote competition via more intensive water abstraction at fewer locations (Table 1).

Irrespective of geography, cities can impact far reaching areas due to the sheer intensity of resource demands. Atlanta's EnergyShed impacts 569 km of the Savannah River Basin and 982 km of the Tennessee River Basin (Fig. 4). These impacts only compound the hydrologic alteration resulting from cities more proximate to those watersheds. Additionally, Georgia legislature is renegotiating their state boundary with Tennessee to claim part of the Tennessee River to support Atlanta's water demand (19). Our framework challenges the prevailing viewpoints of city-to-city water competition and policy governance in two main ways. First, we suggest that city competition does not necessarily follow the traditional upstream-to-downstream model. Indeed, cities occurring downstream or in adjacent basins can inflict just as much, if not more, water competition on other cities than if they had occurred upstream. Second, the only monetary compensation for water use relates to the physical



**Fig. 3.** Examples of geographic data used to isolate the relative roles of different city infrastructure sectors in altering hydrology in stream networks for Atlanta (Upper) and Las Vegas (Lower). (Left) Developed land cover is summarized within urban areas to represent urban land transformation. (Center) EnergySheds are developed as utility network regions along the electric grid and balance energy demand with production from power plants. (Right) Water supply intakes and power plants supporting city demands are associated with reservoirs and summarized for cities. Sources of data are provided in Table S3.

movement of water through interbasin transfers and not virtual water movement, i.e., electricity production. For example, in 2009, Georgia proposed purchasing 379 million L·d<sup>-1</sup> from South Carolina in the upper Savannah River to support Atlanta (19). Our analysis suggests, however, that Atlanta is already impacting the Savannah River and its tributaries, because the basin provides over 20% of Atlanta's electricity demand.

Translating LEW networks into metrics of hydrologic alteration offers a template to examine sector-to-sector competition and provide clarity to complex disagreements over water. The 30-y water conflict between Florida and Georgia over flows in the Apalachicola Chattahoochee Flint (ACF) River reached a

climax in 2013 with Florida requesting the US Supreme Court create an equitable apportionment of water between the two states (19). Florida's suit claims that Georgia overuses water for Atlanta's public water supply and Georgia's agriculture industry (19). Although withdrawals undoubtedly impact flows in the ACF, our analysis suggests that, by far, the largest hydrologic and biodiversity impacts of Atlanta stem from ULT and EP, not WS (Figs. 4 and 5). Unless the sectors exerting the largest influence on hydrology are abated, we suggest there is little hope to expect drastic improvements in water sustainability in the ACF. To our knowledge, the water conflict has remained tangential to EP impacts.

Mapping competition among sectors also reveals vulnerabilities in a city's LEW network. Las Vegas's public water supply impacts are spatially synonymous with its energy impacts because the primary source of hydrologic alteration is withdrawals and operations within Lake Mead, located on the Colorado River (Fig. 3). Las Vegas relies heavily on Lake Mead for both public water supply and hydropower generation. With persistent drought conditions (16), water levels in Lake Mead have remained >70% below full pool (20), and Las Vegas recently completed the construction of a third intake extending deeper into the reservoir (21). Increases in water abstractions from increasing demands come at the expense of losses in hydroelectric generation at Hoover Dam (20). Additionally, limited storage in Lake Mead reduces the flexibility to support environmental flows for protection of endangered species and preventing native species replacement by nonindigenous species (16). Assuming no changes in water allocation strategies, Lake Mead has a 50% probability of losing all usable storage in the next 4 y, which would lead to complete collapse of the agricultural industry and public water supply for the entire region (20).

### Conclusions

Where state, federal, or global regulations have failed to ensure future water sustainability, cities provide alternative platforms to make the necessary changes, including implementing local regulations and energy taxes, incentivizing renewable investments, and coordinating policies among cities and utilities (22) (SI Discussion). Our analysis shows that holistic impacts of cities on the water cycle are also not implicitly tied to population size, as others have found for land expansion (23). This suggests that growing cities have a choice in attaining water sustainability by adopting strategies to minimize reliance on infrastructures imposing significant hydrologic alterations to rivers, such as reducing thermoelectric power, or remediation alterations, such as properly managing storm flows (SI Discussion). Attaining future water sustainability for cities will require large-scale, transformative, and expensive solutions (24). This includes novel policy considerations, such as creating new basin treaties merging city governance of hard infrastructures with external institutions managing water infrastructure (SI Discussion).

**Table 1. Characteristics of urban, energy, and water supply sectors for each city used to isolate sector-specific roles in hydrologic alteration models**

Characteristic	Knoxville	Atlanta	Las Vegas	Phoenix	Tucson
Population (10 <sup>3</sup> )	559	4,515	1,886	3,629	843
Developed land (km <sup>2</sup> )	704	3,979	827	2,286	584
Public water demand (10 <sup>6</sup> L·d <sup>-1</sup> )	201	1,548	1,416	2,025	19
Per capita water demand (L·d <sup>-1</sup> ·ind <sup>-1</sup> )	360	344	750	556	23
Number of intakes	22	87	3	43	16
Reservoir storage public water supply (10 <sup>3</sup> megaliters)	3,424	4,055	37,297	322	0
Energy demand (GWh·y <sup>-1</sup> )	11,717	69,792	17,435	35,633	8,098
EnergyShed area (km <sup>2</sup> )	18,354	67,922	61,704	23,766	47,391
Per capita energy demand (MWh y <sup>-1</sup> ·ind <sup>-1</sup> )	21	15	9	10	10
Number of power plants	25	142	44	43	30
Reservoir storage power plants (10 <sup>3</sup> megaliters)	9,609	21,443	37,297	4,886	0
Energy Efficiency Score (city rank)*	48.5 (-)	51.5 (18)	33.5 (32)	57 (14)	-(-)

Data used to map city infrastructures are provided in Table S3. Ind, individual.

\*2017 Energy Efficiency Scorecard, American Council for an Energy-Efficient Economy ([aceee.org/local-policy/city-scorecard](http://aceee.org/local-policy/city-scorecard)). Scores out of 100. Higher scores and lower ranking indicate superior energy efficiency.



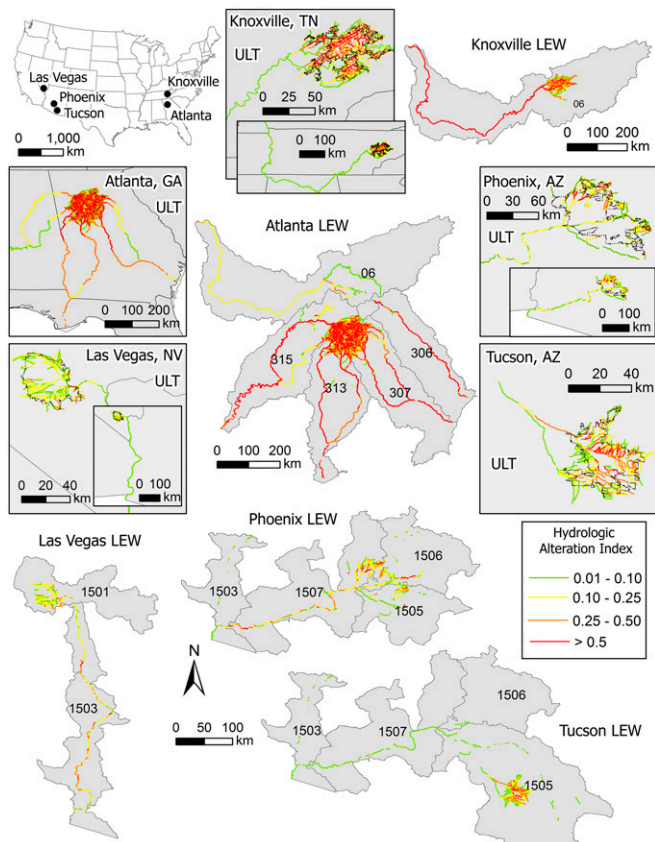


Fig. 4. Hydrologic impacts of each city based solely on the ULT sector (in panels) vs. the entire LEW (not in panels).

Holistic and integrated approaches to understand and manage urban systems as complex human–environmental systems are desperately needed (2). The fundamental challenges of translating energy–water nexus science into practice include identifying practical solutions to sustainable water management from the minutia of complex interactions and enabling communication across disparate policy sectors (SI Discussion). Because water is the media by which we measure impacts of the LEW network, city and utility communication should be centralized around the scale at which the water policy operates. Apportioning city- and infrastructure-level environmental impacts, such as biodiversity loss, provides a platform to quantify relative responsibility of different entities in managing shared, but limited, resources.

**Methods**

Mapping hydrologic alteration across the United States required developing hydrologic alteration models (25) and extrapolating estimates of hydrologic alteration to stream reaches (26). Hydrologic alteration models were constructed using streamflow information from 7,088 US Geological Survey (USGS) stream gages partitioned into reference and nonreference condition (25). Estimates of natural hydrologic conditions were generated for non-reference gages (25), and measures of hydrologic alteration were quantified for 12 hydrologic metrics (SI Methods). Negative and positive changes for all metrics were scaled from 0 to 1 to represent probability of alteration (26). Fifty-two variables that influence the water cycle were assembled for basins contributing to USGS stream gages and for entire networks draining all US NHDPlusV1 stream reaches (SI Methods). Random forests (27) were used to predict measures of hydrologic alteration (Table S1) and extrapolated estimates to 2.6 million stream reaches within the United States.

Random forest models considered a comprehensive and diverse set of variables (Table S2) allowing us to isolate specific anthropogenic causes, such as ULT and EP (SI Methods). Isolating the relative roles of ULT and EP on hydrologic alteration required (i) identifying the individual effects of model variables on hydrologic alteration and (ii) summarizing hydrologic impacts

for entire sectors (e.g., ULT and EP). For example, ULT and EP indices were comprised of eight and seven individual anthropogenic stressors, respectively. To identify individual roles of variables in hydrologic alteration (HA), partial dependency predictions (PDPs) were extracted from random forests by holding all other variables constant in the forest, and then predicting responses by varying values for only the variable under consideration. Data from PDPs were scaled from 0 to 1 and then used to develop partial dependency functions (PDFs) using locally adaptive polynomial regressions. PDFs represent the relative direction and magnitude of changes in HA-based values of a given disturbance variable, but this does not yield a measure of relative importance (RI) of variables on HA. RIs were derived from random forest models and scaled from 0 to 1. To calculate the relative hydrologic impacts of a given metric (M) for an entire sector, s, for the j<sup>th</sup> stream segment, we used the following equation:

$$M_{sj} = \frac{\sum_i PDF_{ij} * RI_i * \overline{HA}_j}{\sum_i RI_i}$$

where hydrologic impacts for i to n individual variables are summed within the respective infrastructure (e.g., ULT, EP) (SI Methods).  $\overline{HA}_j$  represents estimated hydrologic alteration metric for each stream segment based on predictions from hydrologic alteration models. We then extrapolated estimated impacts of ULT and EP on hydrologic across all streams in the United States.

Characterizing the hydrologic and biodiversity impacts of city LEW networks (ULT, EP, and WS) required that we develop spatial linkages between cities, their resource demands, and distal infrastructures, and then isolate these infrastructures from other unrelated anthropogenic impacts in the landscape (SI Methods). We first created separate hydrologic alteration models for the Tennessee River and South Atlantic Gulf Basins combined (Atlanta and Knoxville) and the Lower Colorado Basin (Las Vegas, Phoenix,

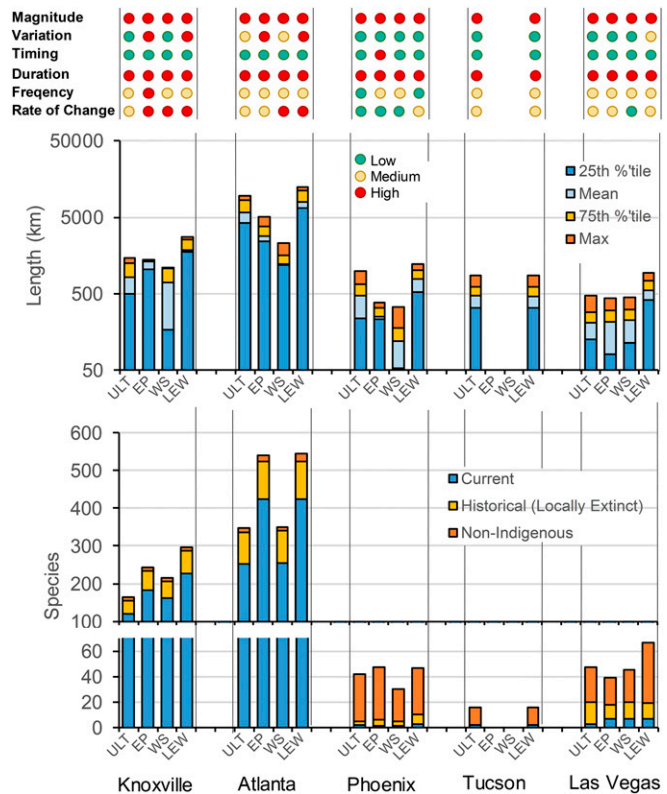


Fig. 5. Length of stream and number of fish, crayfish, and mussels species impacted by individual sectors and cumulative urban energy–water nexus footprints for each city. Dots above the bar plot represent relative stream mileage impacted depending upon which hydrologic metric was considered. Percentiles were calculated based on length of stream impacted across 12 different hydrologic metrics. Length of stream and number of species impacted is based on maximum values for the 12 metrics.

and Tucson) and extrapolated  $\overline{FA}$  to each stream reach. Establishing network connections between ULT, EP, and WS sectors required balancing resource demands in urban areas with surrounding electricity and water supply sources (*SI Methods*). Geographic features impacted only by a given city's LEW network were isolated from the remainder of the landscape (Table S3) and network path analysis was used to summarize those variables in river networks. Using hydrologic alteration models for a respective region, hydrologic impacts for all 12 metrics were calculated for each sector individually and for the entire LEW network. Mapping hydrologic impacts for cities required establishing ecologically relevant alteration thresholds. As little as 10% hydrologic alteration can result in significant ecological degradation (11); thus, streams with  $\geq 0.1$  values for hydrologic alteration were assumed to result in biological impacts.

Biodiversity impacts included indigenous and nonindigenous fish, bivalve, and crayfish species either currently present or locally extinct (i.e., historical) within reaches exceeding the hydrologic alteration threshold. Using a database on geographical locations of species presences (28), we spatially joined species occurrence records with stream reaches and partitioned records into historical (pre-1990) and current (post-1990), as justified elsewhere (29). For the entire United States and each city, historical and current species detections falling within water footprints for individual sectors were summarized into species lists along with their conservation status (*SI Methods*). Comparisons of historical and current species lists yielded the total number of indigenous or nonindigenous species detected in both historical and current records ( $R_c$  and  $NR_c$ , respectively), the number of

indigenous or nonindigenous species currently present but historically undetected ( $U_c$  and  $NU_c$ , respectively), and the number of indigenous species historically present but currently undetected ( $U_h$ ). For each taxon, we calculated detection probabilities for indigenous species ( $p_i$ ) and nonindigenous species ( $p_n$ ), where  $p_i = U_c/R_c$  and  $p_n = NU_c/NR_c$ . We then corrected for false absences by inflating species richness estimates for current indigenous species ( $\hat{R}_c$ ) and nonindigenous species ( $\hat{NR}_c$ ), but deflating locally extinct indigenous species richness ( $\hat{U}_h$ ) using the following:  $\hat{R}_c = U_c/p_i + (R_c - U_c)$ ,  $\hat{NR}_c = NU_c/p_n + (NR_c - NU_c)$ , and  $\hat{U}_h = U_h \times p_i$ .

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