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# Multi-Scale Threat Assessment of Riverine Ecosystems in the Colorado River Basin

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# Multi-scale threat assessment of riverine ecosystems in the Colorado River Basin

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A R T I C L E I N F O

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A B S T R A C T

Freshwater ecosystems are facing a deepening biodiversity crisis. Developing robust indicators to assess ecological integrity across large spatial scales and identifying the specific threats and pathways of impairment are thus critically needed if we are to inform freshwater conservation strategies. Here we present the first comprehensive threat assessment across the Colorado River Basin – one of the largest and most endangered river basins in North America – using a spatial framework accounting for the wide range of human activities (land uses, transportation infrastructure, exploitative activities, water withdrawals), pathways (local footprint, overland runoff, upstream cumulative effects), and spatial extent of influence (valley bottom, catchment and river network) known to affect the ecological integrity of riverine ecosystems. We quantified and mapped 69 individual threat indices with geospatial tools for each permanent, ephemeral, and intermittent stream segment within the Basin, encompassing a total of >1,067,700 river kilometers. We further aggregated these indices into components of water quality (diffuse and point-source pollution), hydrology (flow regulation/uses and climate change), and physical system (connectivity and geomorphology). To demonstrate the potential of our framework to inform spatial planning decision processes, we examined the typical combinations of threats experienced by different hydrologic areas and stream segment types, identified candidate watersheds for habitat restoration and enhancement where hotspots of biodiversity and threat overlapped, and assessed the associations between threat indices and *in situ* measurements of ecological integrity describing a suite of biological (benthic macroinvertebrate, fish), chemical (total nitrogen load, water conductivity), hydrological (flow alteration) and physical indicators (streambed stability, instream habitat complexity). Our assessment highlights clear disparities in term of overall degree of threat that result from different combinations and contributions of individual stressors, with different priorities emerging for perennial versus intermittent or ephemeral stream segments, and between the upper and lower parts of the Basin. Importantly, we showed that our threat indices were generally correlated with biological, chemical, hydrological and physical indicators of ecological integrity they were intended to capture. In addition to its implications for the conservation and management of the highly imperiled Colorado River Basin, our case study illustrates how multi-faceted threat mapping can be used to assess the ecological integrity of riverine ecosystems in the absence of spatially extensive *in situ* measurements.

## 1. Introduction

Fresh waters represent a small fraction of all ecosystems on Earth but sustain a disproportionate diversity of biological life and ecosystems services that support human societies (Strayer & Dudgeon, 2010). Yet, despite their critical value, freshwater – and notably streams and rivers – ecosystems are facing a growing crisis (Reid et al., 2019; Tickner et al., 2020). The unprecedented scale of environmental degradation and biodiversity loss in these ecosystems, both past and present, is the result of numerous human activities accompanying population and economic growth. Threats including widespread land use conversion, resource extraction, waste disposal, fragmentation by transportation infrastructures, and water withdrawal or storage in reservoirs collectively exacerbate pollutant and sediment fluxes, alter hydrology and disturb

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fluvial geomorphological processes (Allan, 2004; Grill et al., 2019; Chen & Olden, 2020). There are also clear signs that riverine ecosystems are affected by recent climate change, posing additional challenges to aquatic communities and human water or food security (Seager et al., 2013; Ficklin et al., 2018). In this context, this study sought to develop a blueprint for mapping the threats of ecological integrity in riverine ecosystems, that could be used to identify and prioritize conservation actions.

Large rivers constitute complex hydrological, ecological, economic, political and social systems, providing myriad ecosystem services to human society (Johnson et al., 1995; Campbell et al., 2013; Erős et al., 2019). The iconic Colorado River Basin is no exception and is emblematic of the conservation challenges facing freshwater ecosystems across the world. Combined, the Upper and Lower sub-basins of the Colorado River (covering approximately 628,000 km$^2$) display inestimable ecological and cultural value, encompass many of the fastest growing cities in the United States, and are the most critical source of water in the American West (MacDonald, 2010; Sabo et al., 2010). Water supplies in the Colorado River Basin are increasingly over-allocated, largely driven by growing demands associated with population growth (Tidwell et al., 2014) and more frequent and extreme droughts caused by climate change (Seager et al., 2013). As a result, the Colorado River has appeared on the infamous list of American River's Most Endangered Rivers® regularly over the last decade (https://www.americanrivers.org/about-mer/).

Understanding the patterns and drivers of ecosystem change and developing tools to rank threats and prioritize management actions, whilst having mechanistic knowledge of pathways and interactions among threats, remains a critical priority for riverine conservation (Mattson & Angermeier, 2007; Falcone et al., 2010; Linke et al., 2011; Panlasigui et al., 2018). Monitoring and achieving ecological integrity have been widely adopted as a management directive by natural resource agencies across the world, and supported by legal mandates such as the Clean Water Act in the United States and the Water Framework Directive in the European Union (Wurtzebach & Schultz, 2016; Kuehne et al., 2017). In this context, spatial representation of human-induced threats or 'threat maps' have been increasingly used in conservation planning as a surrogate for field-based ecological integrity assessments (Stein et al., 2002; Vörösmarty et al., 2010; Esselman et al., 2011; Paukert et al., 2011; Tulloch et al., 2015; Kuehne et al., 2017). These maps provide a cost-effective means to represent the extent and relationships among different threats across large spatial scales, in place of extensive, costly and often impractical field-based assessments of integrity (Revenga et al., 2005; Mattson & Angermeier, 2007; Lessmann et al., 2019).

Yet, these spatial approaches can be ineffective and ecologically misleading if the complex spatial structure of hydrologic networks and the range of spatial extents over which human activities affect the ecological integrity of riverine ecosystems are not considered (Van Sickle & Burch Johnson, 2008; Peterson et al., 2011; Sheldon et al., 2012; Staponites et al., 2019). Although the issue of scale is critical to all ecological studies, this is especially so for rivers because ecological integrity is intimately linked to the surrounding terrestrial landscape and impacts propagate from upstream to downstream catchments (Allan, 2004; Peterson et al., 2013). An additional consideration is that from a management perspective, focusing on only a subset of threats may not have the desired outcomes on freshwater conservation targets if other threats remain unaddressed (Tulloch et al., 2015; Craig et al., 2017). As such, there is a growing interest in assessing the relative contribution of multiple, potentially correlated threats, as well as developing indices that best capture their joint effect (Mattson & Angermeier, 2007; Falcone et al., 2010; Lessmann et al., 2019; Bowler et al., 2020). For these reasons, approaches that include multiple indices reflecting a range of local, but also watershed-wide processes, may be a foundation for more reliable assessments of ecological integrity, as well as the specific pathways of impairment.

Here we develop the first comprehensive assessment of the ecological integrity of the Colorado River Basin at a hierarchy of nested spatial scales, from stream segments to watersheds and hydrographic regions. Our spatially explicit framework integrates a fine-scale hydrographic network with geospatial tools to trace hydrological connectivity (reach- and drainage-scale upstream–downstream linkages) and account for the different pathways (local footprint, overland runoff, upstream cumulative effects) and spatial extent of influence (valley bottom, catchment, and river network) by which human modification activities impair riverine ecosystems. We considered an array of 69 individual threats associated with diffuse and point-source pollution, recent climate change, flow regulation/uses, connectivity and geomorphologic constraints for > 1,067,700 river kilometers of the Basin, including perennial, intermittent and ephemeral flow regimes. Next, we quantified the strengths of the spatial relationships among the different threat indices, as well as their contribution to the overall degree of threat, and explored similarities and differences in the typical combination of threats found across the Basin. To test the ability of our 'desktop assessment' to provide a reliable representation of the local ecological integrity (and conservation priorities) of streams and rivers (Kuehne et al., 2017), we also evaluated associations between the threat indices and *in situ* measurements of ecological integrity describing a suite of biological (benthic macroinvertebrate, fish), chemical (total nitrogen load, water conductivity), hydrological (flow alteration) and physical (streambed stability, instream habitat complexity) indicators. Finally, we provided an illustration of how this framework can be used to identify conservation priority watersheds where hotspots of biodiversity and threat overlapped. Our approach provides a blueprint for multi-scale threat assessments that account for the complex spatial structure and numerous ways by which human activities affect freshwater ecosystems, in order to more reliably estimate ecological integrity and support conservation and management needs in these ecosystems.

## 2. Methods

### 2.1. Threat index development

The selection of individual threat indices was informed by a structured process and discussions held during an expert workshop on February 18, 2019 (see *Acknowledgments*). The experts were invited based on relevance of current research and interests in riverine ecosystems across the Colorado River Basin, as well as demonstrated research history in applying science to conservation planning, especially in the context of ecosystem integrity assessments. The workshop involved a mix of presentation and discussion-based activities focused on the ecosystem integrity assessment framework. Experts were asked to provide feedback on (i) the selection of human modification activities, (ii) spatial scales of assessment, (iii) aggregation (weighting) among threat indices, and (iv) validation of the treat indices. The participants had been provided with relevant materials and information about the aims of the meeting, including a briefing document and agenda before the meeting and a list of potentially relevant datasets of human modification activities during the meeting. Discussions were facilitated through a process of active dialogue among the full group and included directed and open questions.

We selected a total of 69 individual threat indices intended to capture the diverse ways by which human modification activities affect the ecological integrity of riverine ecosystems (Table 1). Each threat index was calculated for each stream segment (spatial grain) based on their expected influence at the valley bottom, catchment, and river network extents. Whereas valley bottom threat indices sought to capture local ecological alterations, catchment and river network threat indices were designed to reflect catchment- (overland runoff) and river network-wide (upstream–downstream) cumulative effects. Threat indices were then aggregated into different threat categories using a weighted mean approach where each individual threat was assigned a relative weight

**Table 1**
Threat indices grouped into six main categories defined with respect to their expected effects on different components of ecological integrity. *Weight* indicates the relative weights used to aggregate the individual threats into their respective threat category and *Source* the source of the datasets.

| Component of ecological integrity | Threat category<br>Individual threat | Spatial extent | Weight | Source |
|---|---|---|---|---|
| **Water quality** | **Diffuse pollution** | | | |
| | Urban development - high intensity | Catchment | 1.0 | [1] |
| | Urban development - medium intensity | Catchment | 0.8 | [1] |
| | Urban development - low intensity | Catchment | 0.6 | [1] |
| | Urban development - open spaces | Catchment | 0.1 | [1] |
| | Cultivated crops | Catchment | 1.0 | [1] |
| | Pasture/Hay | Catchment | 0.8 | [1] |
| | Livestock ranching | Catchment | 0.8 | [2] |
| | Timber production | Catchment | 0.3 | [3] |
| | Fertilizer application | Catchment | 1.0 | [4] |
| | Railways | Catchment | 0.4 | [5] |
| | Primary roads | Catchment | 0.5 | [5] |
| | Secondary roads | Catchment | 0.4 | [5] |
| | Local roads | Catchment | 0.3 | [5] |
| | Service roads | Catchment | 0.2 | [5] |
| | Undeveloped (4WD) roads | Catchment | 0.1 | [5] |
| | Recreational trails | Catchment | 0.01 | [5] |
| | **Point-source pollution** | | | |
| | Coal mines (active surface) | Catchment | 1.0 | [2] |
| | Energy mines (excluding coal) | Catchment | 1.0 | [6] |
| | Metal mines | Catchment | 1.0 | [6] |
| | Nonmetallic mines (sand & gravel) | Catchment | 0.4 | [6] |
| | Abandoned mines (coal) | Catchment | 0.2 | [7] |
| | Oil & gas wells | Catchment | 0.4 | [2] |
| | Oil & gas pipelines | Catchment | 0.1 | [8] |
| | Wastewater treatment facilities | Catchment | 1.0 | [9] |
| | NPDES-permitted facilities | Catchment | 1.0 | [10] |
| | Solar farms | Catchment | 0.1 | [2] |
| **Hydrology** | **Flow regulation/use** | | | |
| | Instream water storage | River network | 1.0 | [11; 12] |
| | Water withdrawals | Catchment | 1.0 | [13] |
| | Water pipelines | River network | 0.2 | [12] |
| | **Climate change (past trends)** | | | |
| | Annual precipitation | Valley bottom | 1.0 | [14] |
| | Annual temperature | Valley bottom | 1.0 | [14] |
| **Physical system** | **Connectivity** | | | |
| | Railways | River network | 0.8 | [5] |
| | Primary roads | River network | 1.0 | [5] |
| | Secondary roads | River network | 0.8 | [5] |
| | Local roads | River network | 0.6 | [5] |
| | Service roads | River network | 0.4 | [5] |
| | Undeveloped (4WD) roads | River network | 0.2 | [5] |

**Table 1** (*continued*)

| Component of ecological integrity | Threat category<br>Individual threat | Spatial extent | Weight | Source |
|---|---|---|---|---|
| | Recreational trails | River network | 0.01 | [5] |
| | Oil & gas pipelines | River network | 0.1 | [8] |
| | Water pipelines | River network | 0.6 | [13] |
| | Major dams | River network | 1.0 | [11] |
| | Minor dams | River network | 0.3 | [11] |
| | **Geomorphology** | | | |
| | Urban development - high intensity | Valley bottom | 1.0 | [1] |
| | Urban development - medium intensity | Valley bottom | 0.8 | [1] |
| | Urban development - low intensity | Valley bottom | 0.6 | [1] |
| | Urban development - open spaces | Valley bottom | 0.1 | [1] |
| | Cultivated crops | Valley bottom | 1.0 | [1] |
| | Pasture/Hay | Valley bottom | 0.8 | [1] |
| | Livestock ranching | Valley bottom | 0.8 | [2] |
| | Timber production | Valley bottom | 0.3 | [3] |
| | Railways | Valley bottom | 0.6 | [5] |
| | Primary roads | Valley bottom | 1.0 | [5] |
| | Secondary roads | Valley bottom | 0.6 | [5] |
| | Local roads | Valley bottom | 0.4 | [5] |
| | Service roads | Valley bottom | 0.2 | [5] |
| | Undeveloped (4WD) roads | Valley bottom | 0.1 | [5] |
| | Recreational trails | Valley bottom | 0.01 | [5] |
| | Coal mines (active surface) | Valley bottom | 1.0 | [2] |
| | Energy mines (excluding coal) | Valley bottom | 1.0 | [6] |
| | Metal mines | Valley bottom | 1.0 | [6] |
| | Nonmetalic mines (sand & gravel) | Valley bottom | 0.4 | [6] |
| | Abandoned mines (coal) | Valley bottom | 0.2 | [7] |
| | Oil & gas wells | Valley bottom | 0.4 | [2] |
| | Oil & gas pipelines | Valley bottom | 0.1 | [8] |
| | Water pipelines | Valley bottom | 0.2 | [13] |
| | Wastewater treatment facilities | Valley bottom | 0.2 | [9] |
| | NPDES-permitted facilities | Valley bottom | 0.2 | [10] |
| | Solar farms | Valley bottom | 0.2 | [2] |
| | Nonnative vegetation | Valley bottom | 1.0 | [15] |

[1] National Land Cover Database (Dewitz, 2019); [2] Conservation Science Partners (2019); [3] FSGeodata Clearinghouse (U.S. Forest Service, 2020); [4] Falcone & LaMotte (2016); [5] TIGER (U.S. Census Bureau, 2019); [6] Mineral Resources Data System (U.S. Geological Survey, 2005); [7] Abandoned Mine Land Inventory System e-AMLIS (Office of Surface Mining Reclamation and Enforcement, 2020); [8] U.S. Energy Mapping System (U.S. Energy Information Administration, 2019); [9] National US EPA Clean Watershed Needs Survey

(Ivahnenko, 2017); [10] EPA Facility Registry System (U.S. Environmental Protection Agency, 2020a); [11] National Inventory of dams (U.S. Army Corps of Engineers, 2019); [12] National Hydrography Dataset Plus High Resolution (U.S. Geological Survey, 2019b); [13] Falcone (2016); [14] NEX Downscaled Climate Projections at 30 arc-seconds NEX-DCP30 (Thrasher et al., 2013); [15] LANDFIRE Remap 2016 (LANDFIRE et al., 2020).

according to its expected contribution to the main components of ecological integrity. We considered six threat categories: diffuse and point-source pollution (component of water quality), flow regulation/uses and recent climate change (component of hydrology), as well as connectivity and geomorphology (component of physical system). Relative weights were estimated based on a combination of peer-reviewed literature and expert opinion of the authors. We note that due to the lack of information regarding the expected contributions of different human modification activities across spatial extents, previous assessments (e.g., Stein et al., 2002; Paukert et al., 2011; Theobald, 2013) were used to derive a first estimation of the matrix of weights, which was subsequently completed and adjusted by the authors. Details regarding the choice of the individual threat indices, study area, and threat index computation, including information regarding cumulative effects and threat aggregation are detailed in the following sections and in **Appendix A**.

### 2.1.1. *Choice of human modification activities and threat categories*

The choice of the threat indices was informed by published ecological integrity assessments (reviewed in Kuehne et al., 2017) and captured a trade-off between the state of science regarding known or perceived major sources of threats in the Colorado River Basin and both the availability and quality of primary data sources for human modification activities (e.g., housing & urban areas; livestock farming & ranching; mining & quarrying; dams & water management/use; see Table A1). Briefly, the *diffuse pollution* category sought to capture the diffuse effect of human activities across the upstream catchments, including urban land use, agriculture, timber production, livestock ranching and transportation corridors on water quality. The *point-source pollution* category encapsulated the potential array of human activities producing point-sources of pollution (i.e., source of pollution of negligible extent) across the upstream catchments, including mining of coal, metallic and mineral resources, oil and gas extraction/transportation, wastewater treatment plans, National Pollutant Discharge Elimination System (NPDES) permitted-facilities and solar farms. The *flow regulation/uses* category aimed to capture alterations of the natural flow regime resulting from the management and uses of freshwater resources by humans, notably instream water storage in reservoirs, water withdrawals (e.g., from urban, agriculture, and mining land uses), and the presence of diversion structures (e.g., water pipelines for irrigation, drainage and water supply purposes). The *climate change* category was intended to reflect various alterations to hydrological regimes resulting from recent (1950–2005) changes in air temperature and precipitation. The *connectivity* category was designed to capture the disruption of river network connectivity resulting from the intersection with human-made structures, including transportation or services corridors (i.e., roads, railways, oil and gas pipelines), and the presence of impoundments (i.e., major and minor dams). The *geomorphology* category sought to represent the degree of human-induced geomorphic changes to floodplain integrity, estimated through the spatial footprint of various threats (e.g., urban development, agricultural land use, transportation infrastructures, mines, nonnative vegetation) occurring within valley bottoms.

### 2.1.2. *Study area and spatial grain*

Individual threat indices were calculated for each stream segment (spatial grain) of the Colorado River Basin as defined by the most current version of the National Hydrography Dataset, the NHDPlus High Resolution (U.S. Geological Survey, 2019a), composed of 16 main hydrographic regions (i.e., 4-digits Hydrologic Unit Code [HUC]) and totaling > 1,067,700 km of river network (Fig. 1**a**). Perennial, ephemeral and intermittent stream segments represent 14%, 50% and 36% of the total river network, respectively, and show marked spatial patterns between the upper and lower parts of the Basin (Fig. 1**b**).

### 2.1.3. *Threat index calculations*

The workflow for the threat index calculations followed a seven-step procedure as illustrated in Fig. 2. We considered three different spatial extents to estimate the individual threat indices: valley bottom (areas adjacent to streams and rivers as delineated by the valley bottom edges; mean area = 0.04 km$^2$), catchment (upstream contributing catchment area that drain to each stream segment, mean area = 0.31 km$^2$), and river network (river channel, mean length = 0.57 km) (Fig. 1**c**). We did not consider smaller hierarchical scales (e.g., pool/riffle or microhabitat subsystems, Frissell et al., 1986) due to the lack of available data across the entire Colorado River Basin.

*2.1.3.1. Valley bottom-level threat indices.* The *valley bottom* extent was intended to capture the local footprint of human activities occurring in areas adjacent to streams and rivers. Valley bottoms were delineated using the Valley Bottom Extraction Tool (V-BET; Gilbert et al., 2016) and further split into polygons attributed to each stream segment. Valley bottom-level threat indices were then estimated for each stream segment as the proportional area of its valley bottom affected by a particular threat, calculated as the sum of threat intensity (represented by either binary or continuous values varying between 0 and 1) divided by the total area (number of cells) of the valley bottom (Fig. A2).

*2.1.3.2. Catchment-level threat indices.* The *catchment* extent was intended to capture threats resulting from human activities occurring across the entire upstream contributing catchment area (including the valley bottom) that drain to each stream segment. Except for water withdrawals, catchment-level threat indices were calculated using an inverse-distance weighting function accounting for preferential flow pathways within catchments where greater amounts of overland flow are expected to occur (Peterson et al., 2011; Staponites et al., 2019). To do so, we calculated for each cell of the catchment the inverse distance to the closest stream that we multiplied by the log-number of cells expected to contribute flow into this particular cell as estimated using an overland flow accumulation analysis. In this case, a threat located close to the stream segment or on hydrologically 'active' overland flow paths (preferential flow pathways as identified using the flow direction raster layers) is weighted more heavily than a threat located farther away or on hydrologically 'inactive' overland flow paths (non-preferential flow pathways). The threat index for a given catchment was then obtained by summing the adjusted weights across all cells where the threat was present, divided by the sum of weights across all cells in the catchment, thus representing the distance-weighted proportion (e.g., land use) or frequency (e.g., point-source pollution) of occurrence of a given threat within the catchment (Fig. A3). Water withdrawals were estimated directly using the sum of the annual volume of surface water withdrawn for consumptive use (e.g., irrigation, human consumption, mining activities) across all cells in each catchment.

*2.1.3.3. River network-level threat indices.* The *river network* extent was intended to capture threats located on the river channel, thus measuring the degree to which human activities interrupt the continuum of a river network. Except for instream water storage, river network-level threats were estimated using the density of intersections between the stream segments and various human-made structures, including roads, dams, and oil or water pipelines (Fig. A4). The degree of instream water storage was then estimated for each stream segment based on the normal storage capacity of the dams located on the particular stream segment (if any).

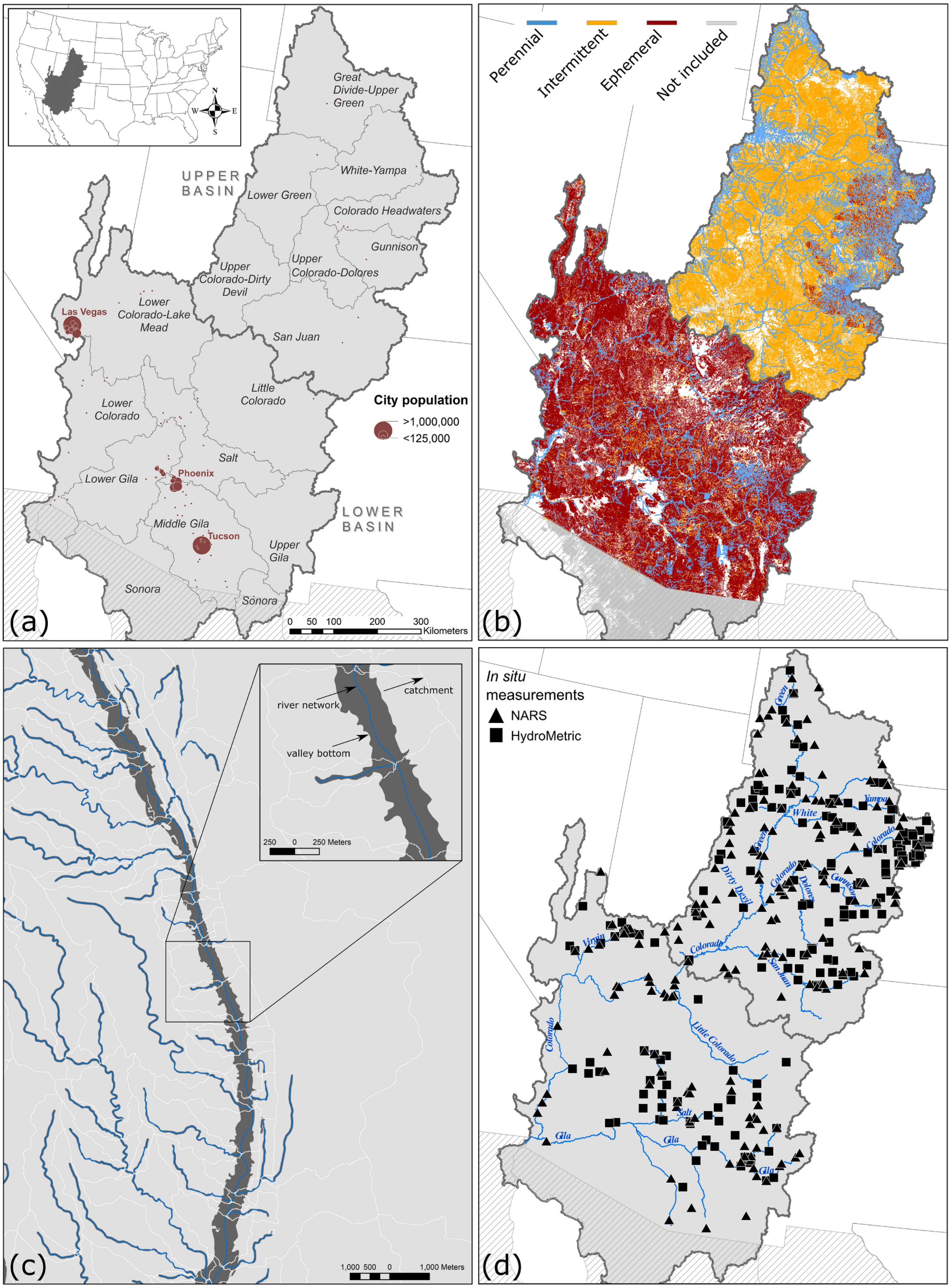


**Fig. 1.** Map of the Colorado River Basin showing (a) the main hydrographic regions, (b) the stream segments colored by hydrologic type, (c) the spatial extents used for the individual threat index computations, and (d) the locations used to assess the relationships between the threat indices and *in situ* metrics of ecological integrity.

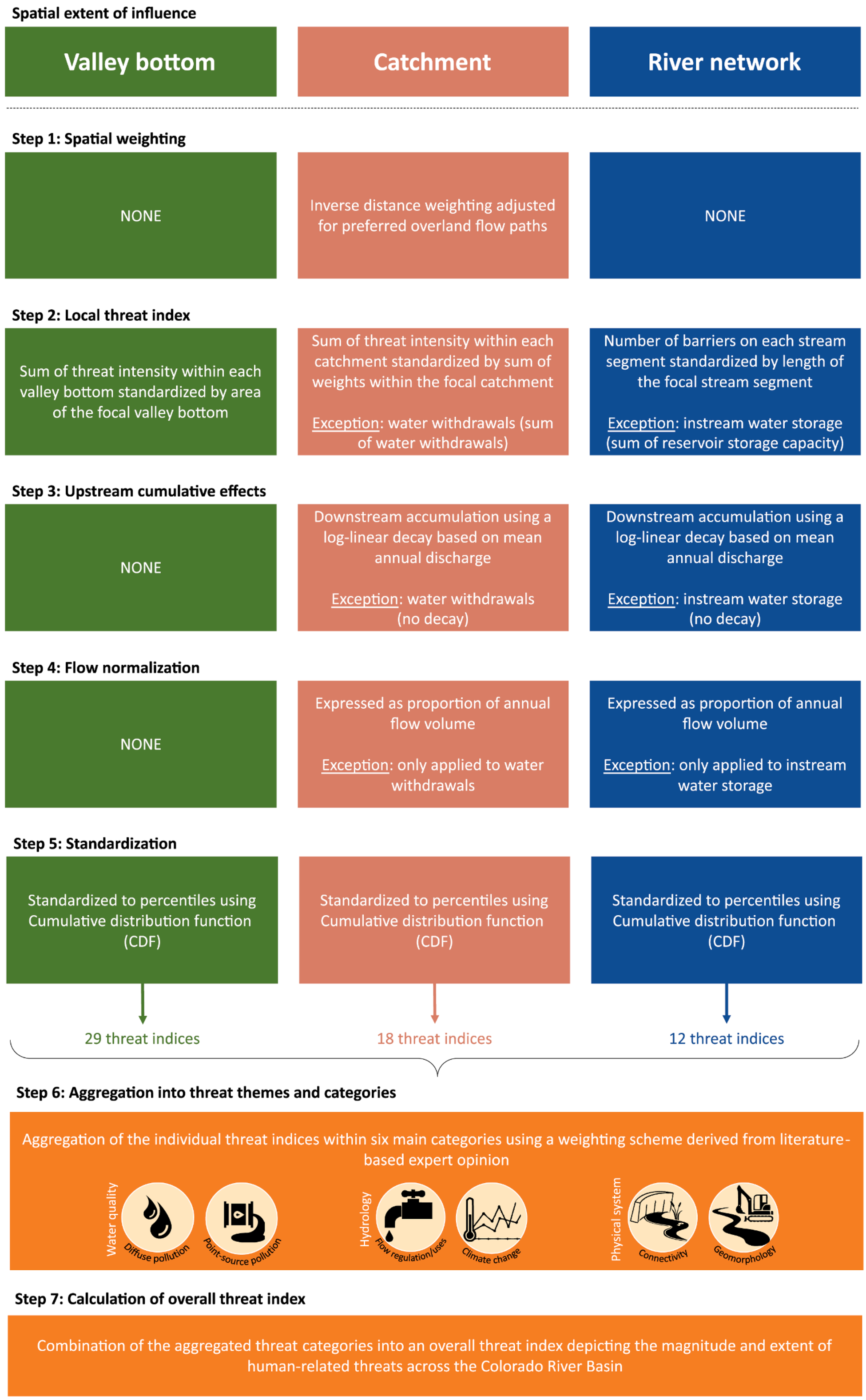


**Fig. 2.** Schematic diagram illustrating the steps of the workflow for threat index calculations according to the three spatial extents of influence.

*2.1.3.4. Upstream cumulative effects.* The threat indices measured at both the catchment and river network extents further accounted for upstream–downstream propagation of threats within drainage basins (Stein et al., 2002; Vörösmarty et al., 2010; Grill et al., 2019). Upstream cumulative effects were estimated using a flow accumulation analysis across the whole Colorado River Basin and a log-linear decay function based on mean annual discharge (Fig. A5). Discharge in this context was thus used as a proxy for distance along the network in the 'environmental' sense, where the cumulative effects gradually diminish in the absence of additional threat as stream segments become increasingly dissimilar in terms of annual mean discharge in the downstream direction (e.g., Grill et al., 2019). The upstream cumulative threat index was further constrained to never exceed the maximum potential local threat value such that all threat indices were bounded between 0 and 1. We note that upstream cumulative effects were estimated separately for each individual threat index, and did not account for joint effects among threats (e.g. considering both secondary road crossings and major dams). In addition, within the flow regulation/uses category, the degree of hydrologic alteration resulting from water withdrawals (or water loss sensu Vörösmarty et al., 2010; calculated at the catchment extent) and instream water storage (or flow regulation sensu Grill et al., 2014 calculated at the river network extent) were estimated such that the water diverted from upstream areas directly reduces the amount of water available to downstream areas (with no decay). However, both threat indices were further normalized according to the mean annual flow volume estimated for each stream segment in the absence of human activities. Normalized indices thus represent the proportion of the natural flow volume withdrawn or stored in upstream catchments and range between 0 (no upstream water withdrawal or dam storage) and 1 (the volume of upstream water withdrawals or dam storage is equal to or exceeds the mean annual flow volume expected for this given stream segment in the absence of human activities).

*2.1.3.5. Threat standardization and aggregation.* The 69 individual threat indices were first standardized based on an empirical cumulative distribution function applied independently to each index (Fig. A6). This standardization procedure replaced each value of a given threat index by its percentile within the distribution of values across all stream segments (after excluding the stream segments where no threat was detected). This allowed us to account for different numerical ranges among individual threat indices as well as to moderate the influence of extreme values (e.g., Vörösmarty et al., 2010). The standardized threat indices were then aggregated into their respective threat category using a weighting scheme derived from literature-based expert opinion into a *diffuse pollution index*, *point-source pollution index*, *flow regulation/uses index*, *climate change index*, *connectivity index* and *geomorphology index*. This weighting procedure is common in freshwater threat assessments (e.g., Stein et al., 2002; Mattson & Angermeier, 2007; Paukert et al., 2011), and recognizes the fact that it is not always possible to calibrate weights using the fitted relationship between threat indices and ecological responses of interest (e.g., Esselman et al., 2011). However, we note that by doing so, the aggregation procedure only accounts for additive effects among threats, and not synergetic (e.g., the fact that the cumulative effects of different threats may be greater than the sum of their single effects) or antagonistic (e.g., the fact that the cumulative effects of different threats may be less than the sum of their single effects) effects. Relative weights were defined on a 0–1 scale common to all indices and subsequently normalized to sum 1 within each threat category (see Tables S2-S7 and Appendix A ‘Aggregation into threat categories’ for more detailed justifications regarding the matrix of weights). The aggregated threat indices were finally combined into an *overall threat index* using an equal-weighting scheme (i.e., relative weight of 1/6 for each aggregated index), depicting the extent and magnitude of human-related threats across the Colorado River Basin.

#### *2.1.4. Web application*

To ensure transparency and promote sharing of information, we developed an interactive web application where all the threat assessment indices can be visualized and downloaded. Among the different features of the web application, we note that the user can define custom weights to calculate the overall threat index. The web application can be accessed at https://wff-rivers.gitlab.io/mapping/.

### *2.2. Quantifying the geography of threat across the Colorado River Basin*

To characterize the spatial distribution and main sources of human-related ecological impairment across the Colorado River Basin, we first mapped the values of the aggregated threat indices among stream segments according to their respective percentile bins. To assess spatial covariation among threats and identify potential anthropogenic threat complexes (sensu Bowler et al., 2020), we calculated the Spearman’s rank correlation coefficients among pairs of individual threat indices, both within and between threat categories. To more formally assess the spatial contributions of different human modification activities to the different threat categories, we removed one individual threat index at a time and recalculated the aggregated threat indices each time (i.e., jackknifed aggregated indices). The relative contributions of each individual threat to its respective threat category for each stream segment were then computed as the differences between the original aggregated index and the jackknifed index multiplied by 100, where 0 indicates a null contribution and 100 indicates an exclusive contribution. Note that the relative contribution *per se* does not reflect the degree of threat as a stream segment can be exposed to multiple threats simultaneously, resulting in a modest decrease in the aggregated index when an individual threat index was removed from the computation, even if it displayed a high threat value. Hence, this analysis was designed to help reveal the spatial patterns of exposure to different threats and assess the extent to which they are likely to act in isolation or in combination to influence ecological integrity. To further assess if the degree of threat and anthropogenic threat complexes vary across space and/or among habitat types (e.g., socio-economic and ecological contexts), we performed these analyses across all stream segments and then separately per main hydrographic region and hydrologic type (i.e., perennial, intermittent and ephemeral).

### *2.3. Identifying conservation priority watersheds*

We assessed the biological implications of our results by overlaying the overall threat index with a biodiversity index from EnviroAtlas (U.S. Environmental Protection Agency, 2019) that represents a combined measure of rarity and the count of threatened and endangered species among 1,510 amphibians, decapods, fishes, mollusks, and turtles across the conterminous U.S. Briefly, the native species distributions were compiled by reallocating ranges from the International Union for Conservation of Nature (IUCN) Red List spatial database to watersheds (12-digit Hydrologic Unit Codes; HUC12). The number of threatened species was then calculated as the number of species that are listed as “vulnerable”, “endangered”, or “critically endangered” according to the IUCN Red List (2016). The measure of rarity was computed using the average of the rarity weights of each species present in a given watershed based on relative range size, where species with range sizes below the lowest quartile are considered “rare”. The biodiversity index was finally estimated by normalizing and averaging these two metrics (see Panlasigui et al., 2018 for more details).

To match the spatial grain of the biodiversity index, we computed the mean overall threat index value per watershed (HUC12) among all the stream segments included in the assessment, weighted by the length of the stream segments. However, to ensure that the assessment conducted at the watershed scale was representative of the variety of habitats present, we excluded watersheds if more than 25% of the stream segments displayed missing threat index values (e.g., segments located outside of U.S. borders or with no discharge estimates), and considered only flowing water habitats (i.e., after excluding lake- and wetland-type habitats). This selection resulted in the examination of 6,938 out of the 7,552 watersheds in the Colorado River Basin. Spatial overlap among watersheds was visualized by categorizing the overall threat index and native biodiversity index based on three percentile bins. We then explored the nature and complexity of interactions between individual threat indices for an exemplar watershed identified as a potential candidate for habitat restoration and enhancement efforts (i.e., displaying both a high degree of overall threat and native biodiversity).

### 2.4. Testing the robustness of the threat assessment

#### 2.4.1. Sensitivity analysis

We assessed the uncertainty introduced by the choice of the weighting scheme used to aggregate the individual threat indices by comparing the overall threat index to the same index obtained using alternative matrices of weights. More specifically, we computed a 'randomized' version of the overall threat index in which the weights among individual threat indices were assigned randomly by permuting the rows of the matrix of weights 999 times and recalculating the overall threat index each time. The sensitivity of our results was estimated using the correlations between the 'original' overall threat index values and the 'randomized' values. We also implemented an intermediate scenario in which each weight was modified using a value randomly drawn from a uniform distribution ranging between ± 25% of the original weight value bounded between 0 and 1 (hereafter referred to as 'modified' weights). As before, we recalculated the overall threat index 999 times and assessed the correlation between the 'original' overall threat index values and the index values calculated using the 'modified' weights.

#### 2.4.2. Relationship with ecological integrity metrics

To evaluate the ability of the threat assessment to provide a reliable representation of the local ecological integrity of streams and rivers, we regressed the threat indices developed as part of this assessment against *in situ* measurements of ecological integrity throughout the Colorado River Basin (Table 2; Fig. 1**d**). To do so, we selected a suite of biological, chemical, and physical indicators developed as part of the National Aquatic Resource Surveys (NARS, U.S. Environmental Protection Agency, 2016, 2020b), as well as additional hydrological indicators developed by Eng (2018) (hereafter referred as HydroMetric).

First, we assessed the relationships between the overall threat index and metrics of biological integrity for: (a) benthic macroinvertebrate using an observed-to-expected (O/E) condition score comparing the actual number of macroinvertebrate taxa observed at each site with the number expected to be found based on the sum of the taxon occurrence probabilities predicted from a model using natural environmental features as predictor variables (n = 181 sites from NARS); and (b) fish using a regional multi-metric condition index (MMI) aggregating several metrics representing different dimensions of assemblage structure and function such as percentage of taxa tolerant to disturbance or benthic invertivores and adjusted for natural variability (n = 134 sites from NARS). Given their high sensitivity and predictable responses to a wide range of environmental stressors (Karr, 1991; Pont et al., 2006; Li et al., 2010), we expected both benthic macroinvertebrate and fish indicators to show a strong negative association with the overall threat index.

Next, we assessed relationships between the aggregated threat indices and selected water quality, hydrological and physical indicators, as dictated by the expected threat-specific impairment pathways and data availability. For the water quality indices (diffuse and point-source pollution indices), we focused on total nitrogen load (TNL; n = 181 sites from NARS) and conductivity (COND; n = 181 sites from NARS). Whereas TNL is an indicator of eutrophication, COND provides a more general measure of water quality (particularly with regards to salinity) based on the quantity of dissolved solids present in the water. We therefore expected both indicators to associate positively with the diffuse and point-source pollution indices. We note that we did not include total phosphorus load due to its strong correlation with TNL (r = 0.70).

For the flow regulation/uses index, we focused on indicators of hydrologic alteration pertaining to the magnitude of low (AMLF; n = 194 sites from HydroMetric) and high (AMHF; n = 194 sites from HydroMetric) flows, quantified as the ratios of observed-to-expected 1st and 99th percentile streamflows (O/E) for the period 1980 to 2014 divided by the drainage area. We focused on magnitude instead of other aspects of flow regime (variability, frequency, duration, timing and rate of change), expecting that the most common consequence of flow regulation and uses will be to decrease the magnitude of downstream peak flows (Poff et al., 2007). We expected a negative relationship between the degree of flow regulation/uses and the two indicators of hydrological alteration (such as a high degree of threat correlates with low O/E streamflows), especially with regards to the magnitude of high flow. No meaningful indicator was available to evaluate the climate change index based on the specific and recent nature of the threat, and therefore we did not assess any relationship with ecological integrity metrics for this index.

For the physical system indices (connectivity and geomorphology indices), we focused on indicators of relative streambed stability (RBS; n = 172 sites from NARS) and of instream habitat complexity (IHC; n = 173 sites from NARS). Whereas RBS measures the interplay between sediment supply and transport with lower-than-expected values indicating excess fine sediments. IHC represents a holistic measure of habitat complexity based on a variety of fish concealment features (undercut banks, boulders, live trees and roots, large pieces of wood, brush, and cover from overhanging vegetation) within a meter of the water surface. We therefore expected both indicators to associate negatively with the connectivity and geomorphology indices. All the predicted relationships were tested using ordinary least squares regressions after log-transforming the response variables (ecological integrity metrics) to better approximate normality when necessary. The assumption of homoscedasticity and normality in the model residuals were assessed using the Breusch-Pagan and Kolmogorov-Smirnov tests, respectively.

## 3. Results

### 3.1. Geography of threat across the Colorado River Basin

Assessing > 1,067,700 km of river network across the Colorado River Basin, we found that human-related threats display a complex

**Table 2**
Expected positive (+) or negative (−) relationships between the threat indices and ecological integrity metrics. *Nsites* represents the number of locations (sample size) in each dataset and *Source* the source of the datasets.

| Ecological integrity metric | Abbreviation | Expected relationship with threat indices | Nsites | Source |
|---|---|---|---|---|
| Biotic | | | | |
| *Benthic macroinvertebrate O/E score* | Macroinvertebrate condition | Overall threat index (-) | 181 | [1] |
| *Fish MMI* | Fish condition | Overall threat index (-) | 134 | [1] |
| Water quality | | | | |
| *Total nitrogen load* | TNL | Diffuse pollution index (+); Point-source pollution index (+) | 181 | [1] |
| *Conductivity* | COND | Diffuse pollution index (+); Point-source pollution index (+) | 181 | [1] |
| Hydrological | | | | |
| *Alteration in low flow magnitude* | AMLF | Flow regulation/uses index (-) | 194 | [2] |
| *Alteration in high flow magnitude* | AMHF | Flow regulation/uses index (-) | 194 | [2] |
| Physical | | | | |
| *Relative bed stability* | RBS | Connectivity index (-); Geomorphology index (-) | 172 | [1] |
| *Instream habitat complexity* | IHC | Connectivity index (-); Geomorphology index (-) | 173 | [1] |

[1] NARS (U.S. Environmental Protection Agency, 2016, 2020b); [2] HydroMetric (Eng, 2018).

geography. We observed a large range of variability in the distribution of values, indicating that the degree of threat ranges from very low to very high within each hydrologic region and stream segment type (Fig. 3). Overall, we found that perennial stream segments, despite representing<15% of the overall river network, are the most exposed to the deleterious effects of human activities. Among non-perennial stream segments, intermittent streams showed the highest degree of threat. Among hydrologic regions, the northern (Upper and Lower Green River) and southwestern parts of the Basin (lower sections of the Colorado River) tended to show a higher degree of threat, whereas the San Juan, Little Colorado and numerous tributaries in the Gila hydrographic regions displayed a comparatively lower degree of threat. However, all the major river Basins showed marked spatial gradients, with stream segments located on the main river stems (e.g., Colorado, San Juan, Green, Virgin, White, Salt, Gila, and Little Colorado Rivers) or around large urban centers (e.g., Las Vegas, Phoenix, Tucson) usually displaying a higher degree of threat.

Examining the different components of ecological integrity, the diffuse pollution index indicated widespread water quality alterations across both the Upper and Lower Colorado River sub-basins (Fig. 4**a**). The degree of threat was particularly high along the downstream sections of the Colorado and Gila Rivers or around the cities of Las Vegas and Phoenix, and decreased from perennial to ephemeral stream segments. Major hydrographic regions displaying a higher degree of threat included the Upper and Lower Green, White-Yampa, and Upper Colorado-Dolores for the Upper Colorado sub-basin and the Salt and Upper Gila for the Lower Colorado sub-basin. This somewhat contrasted with the point-source pollution index showing a concentration of threats on the main river stems irrespective of the hydrological region considered (Fig. 4**b**). The flow regulation/uses index identified a higher degree of threat along most of the perennial main river stems, notably on the Lower Green, Gunnison, San Juan, Lower Gila and lower sections of the Colorado River but also on smaller order streams located across the White-Yampa, Upper Green and San Juan hydrographic regions (Fig. 4**c**). The degree of hydrologic threat around the cities of Las Vegas, Phoenix and Tucson appeared particularly high. The climate change index showed a clear spatial structuring, with the northern portion of the Basin (Green and White-Yampa Rivers) and the Upper Colorado-Dirty Devil and Lower Colorado-Lake Mead regions being the most exposed to recent climatic changes (Fig. 4**d**). The connectivity index indicated a significant threat posed by barriers on most medium to large rivers located in the Basin, and notably for perennial stream segments, around large urban centers (e.g., Phoenix, Las Vegas, Tucson), and downstream of the Hoover Dam on the Lower Colorado River (Fig. 4**e**). The geomorphology index also highlighted a widespread threat posed by floodplain development across most of the Basin with the relative exception of large portions of the San Juan, Little and Lower Colorado regions (Fig. 4**f**). In contrast with other threat categories the highest degree of threat was found (on average) for intermittent stream segment, although we note a large range of variability within each hydrologic type. Again, the Upper Colorado sub-basin (Green, White-Yampa, Upper Colorado-Dolores), downstream sections of the Gila and Colorado Rivers, as well as areas around large urban centers (Las Vegas, Phoenix and Tucson) were identified as presenting the highest degree of threat.

We found a relatively low degree of association between threats, both within (mean Spearman's $\rho = 0.15$) and between (mean Spearman's $\rho = 0.13$) threat categories (as represented by the links on Fig. 5; see also **Fig A7** in **Appendix B** for an alternative representation of the network of threats). This indicated that the selected indices effectively captured different facets of human-related threats within their respective threat categories. A notable exception to this pattern was found

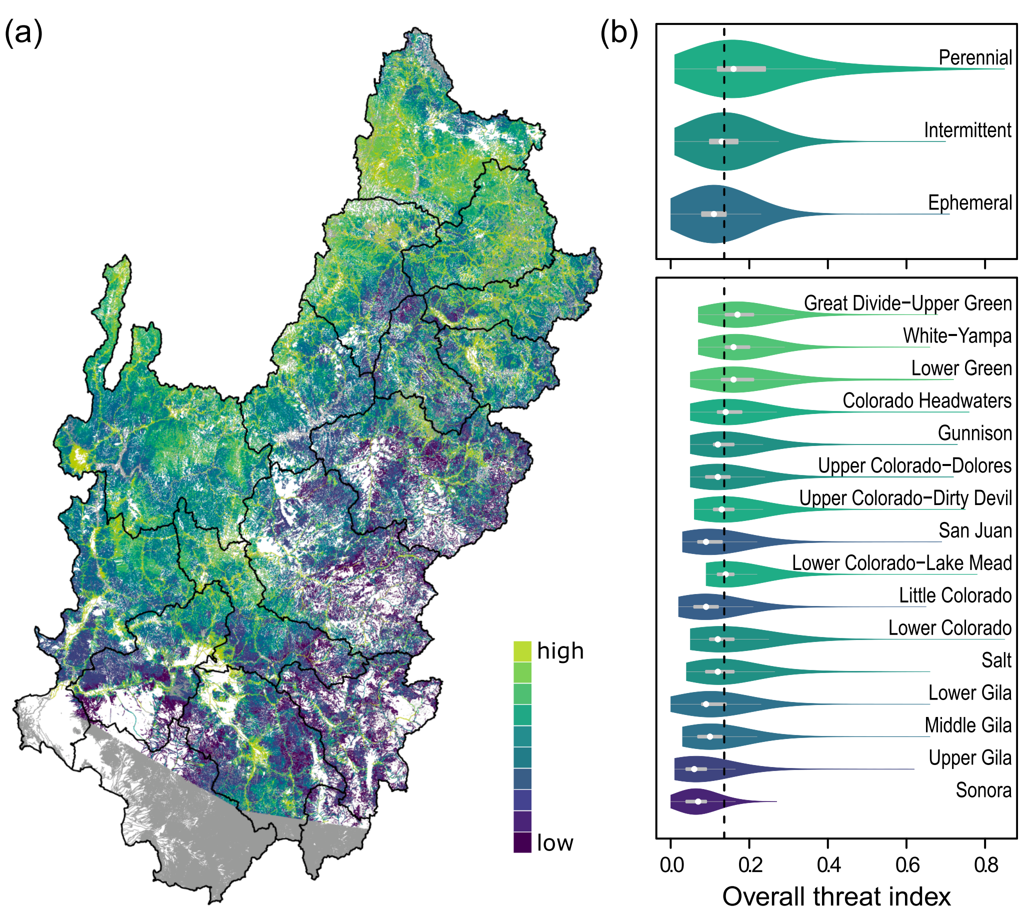


**Fig. 3.** Overall threat index across the Colorado River Basin: (a) Map showing the distribution of values among stream segments divided into percentile bins where purple indicates a low degree of threat (0-10th percentile) and light green a high degree of threat (90-100th percentile); (b) violin plot showing the distribution of values per hydrologic type and hydrologic region where the dotted line indicates the mean value among all stream segments included in the assessment and the color the mean percentile value for each category.

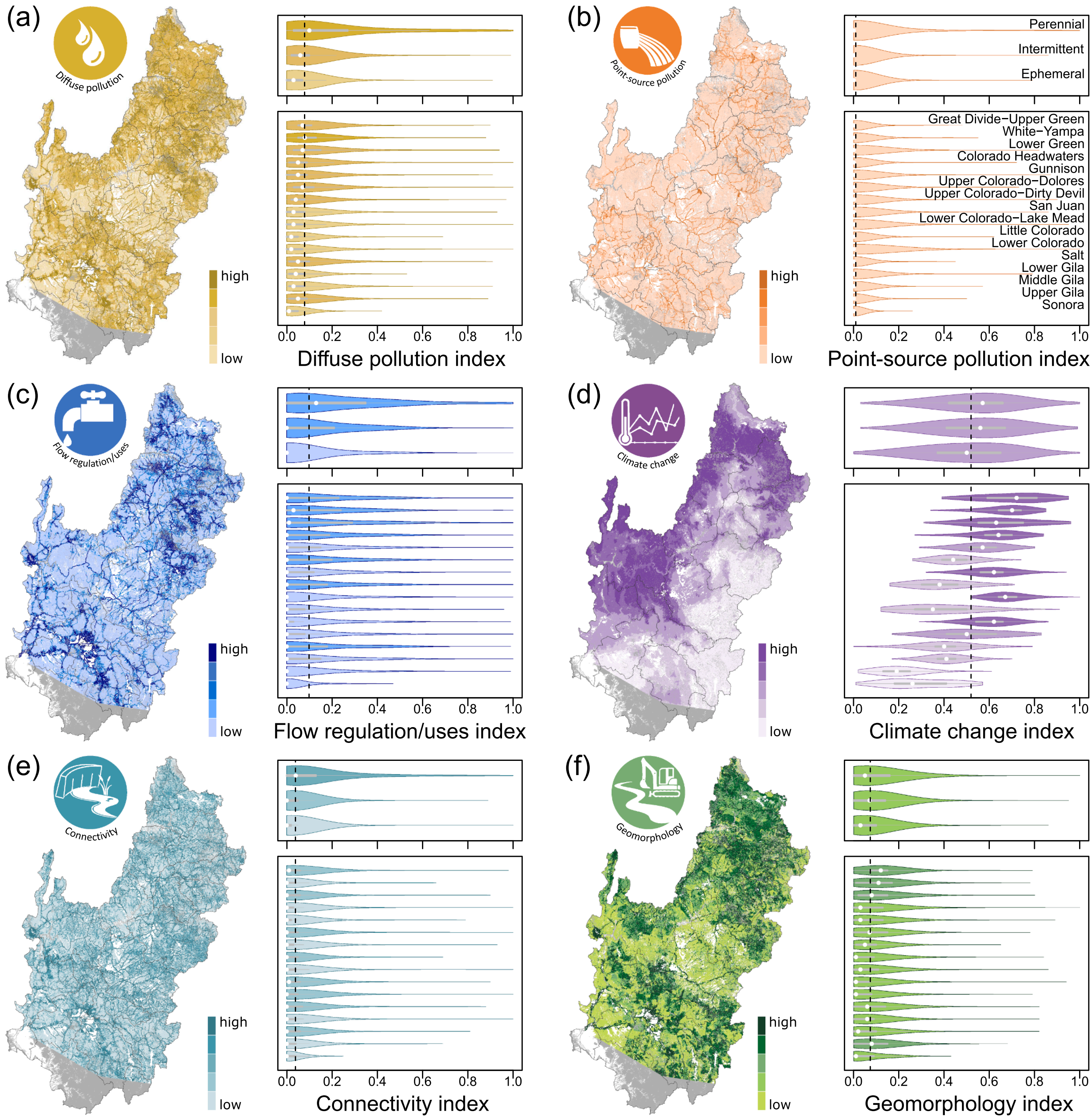


**Fig. 4.** Aggregated threat indices across the Colorado River Basin: distribution of values among stream segments divided into percentile bins where light colors indicate a low degree of threat (0-20th percentile) and dark colors a high degree of threat (80-100th percentile), together with violin plots showing the distribution of values per hydrologic type and hydrologic region where the dotted line indicates the mean value among all stream segments included in the assessment and the color the mean percentile value for each category: (a) Diffuse pollution, (b) Point-source pollution, (c) Flow regulation/uses, (d) Climate change, (e) Connectivity, (f) Geomorphology.

between the different development intensities included within the diffuse pollution index, which showed correlations > 0.80. The individual threat indices were also more strongly correlated within than between threat categories (*t*-test; $P < 0.05$), indicating that they are likely good indicators of the different threat categories they were selected for. Despite this pattern, the threats associated with the same human modification activities tended to correlate positively across spatial extents (e.g., oil & gas or water pipelines, local or undeveloped 4WD roads), although the correlations were usually lower when they involved threats estimated at the valley bottom extent (included in the geomorphology index). This suggested that the covariations identified between threat categories were likely to arise at least partly through upstream cumulative effects along the main river stems. Yet, we found that the correlations between the aggregated threat indices were all < 0.70, indicating that even if upstream cumulative effects are to be expected in the downstream sections of the Basin, the overall geography of threat largely reflects spatial variations in the patterns of human modification activities. Notably, recent climatic changes, together with geomorphological threats related to mining activities within valley bottoms emerged as largely spatially distinct threats, showing only very weak covariations with other threats.

All individual threat indices contributed, at least in part, to patterns

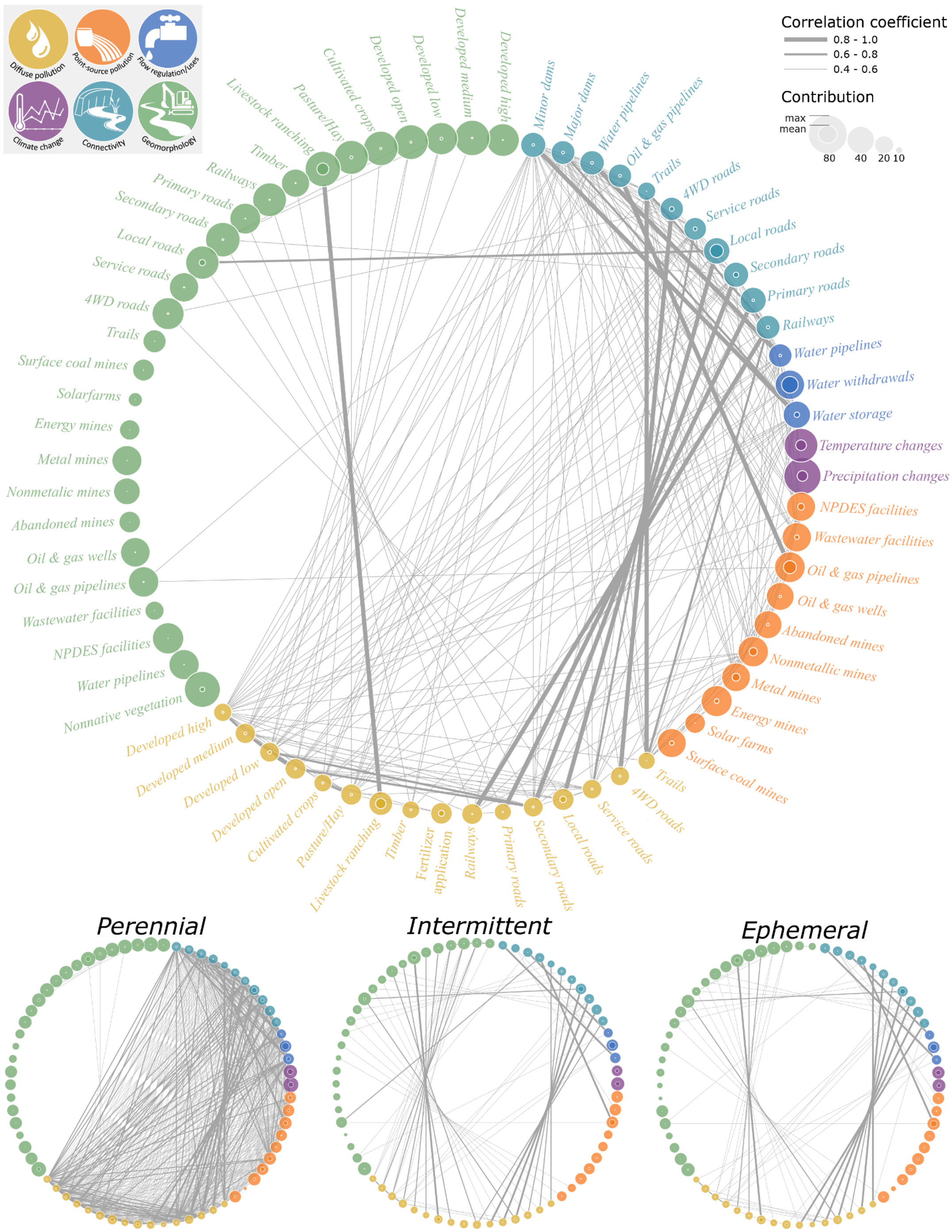


**Fig. 5.** Network representing the contributions (maximum and mean; nodes) to the aggregated threat indices and spatial correlations (Spearman's $\rho > 0.4$; links) between the individual threat indices across the Colorado River Basin and by hydrologic type. Individual threats are colored according to their respective threat category: Diffuse pollution, Point-source pollution, Flow regulation/uses, Climate change, Connectivity, Geomorphology.

of overall threat demonstrated in the Colorado River Basin. Maximum contribution values recorded for a given stream segment varied between 12.1 and 83.3 among individual threat indices (mean value = 43.6; as represented by the nodes on Fig. 5 & **Fig. A7**). The diffuse pollution index appeared particularly sensitive to agricultural practices such as livestock ranching and fertilizer application, as well as minor transportation infrastructure (i.e., local roads). This reflects the widespread presence of these threats across the Basin, as well as their tendency to occur in isolation from other threats. Urban land use also appeared influential, although the comparatively lower mean contributions of the different development categories indicated that urbanization is more likely to overlap with other threats. The point-source pollution index appeared particularly sensitive to the presence of oil and gas pipelines, but also to various mining and industrial activities. This suggests that the different sources of point-source pollution across the Colorado River Basin are largely decoupled from each other, rendering their specific influence easier to detect. The flow regulation/uses index appeared disproportionately influenced by water withdrawals, which largely reflects the high pressure resulting from the direct consumption of freshwater resources across most of the Basin, including headwater streams. In comparison, the pressures resulting from instream water storage in upstream reservoirs or the presence of water pipelines are more likely to arise and co-occur on higher order streams, which also account for a lesser proportion of the river network. This resulted in a comparatively lower overall contribution to the aggregated index for these two individual threat indices. By contrast, the climate change index appeared equally influenced by recent changes in both temperature and precipitation. Nonetheless, the fact that both indices showed maximum contributions > 50 (precipitation changes = 83.3, temperature changes = 68.9) also reflects a complex geography of recent climatic changes with decoupled trends in temperature and precipitation in parts of the Basin. The connectivity index displayed a high sensitivity to minor transportation infrastructure (notably local roads), again reflecting their widespread presence despite having lower relative weights than other threats. Last, the geomorphology index was sensitive to agricultural activities (livestock ranching, pasture/hay), transportation infrastructure (local roads), nonnative vegetation, and, to a lesser extent, urban land use. Despite the large number of individual threats included in the aggregated index, the maximum contributions were > 50 for most of them, which not only reflects the ubiquitous use of floodplains for various human activities, but also the fact that many of these threats are likely to act in isolation from each other in large portions of the Basin.

The nature and complexity of interactions between threats also varied greatly among hydrological types (bottom panels Fig. 5 & **Figs. A8-A10**). Perennial stream segments were more likely to be exposed to multiple, cumulative threats originating in upstream catchments, thus simultaneously affecting water quality, hydrology, and connectivity. Perennial streams also displayed limited covariation between threats occurring within valley bottom, despite important local contributions. By contrast, intermittent and ephemeral stream segments showed an overall lower degree of covariation between threats but appeared particularly sensitive to a cluster of threats associated with urbanization (e.g., development intensity, local roads, water withdrawals), particularly within valley bottoms.

### 3.2. Conservation priority watersheds

We found contrasting patterns of overlap between the native aquatic biodiversity index and overall degree of threat throughout the Basin, suggesting differing management approaches would be warranted to address threats to integrity identified by the assessment (Fig. 6**a**). The southeastern part of the Basin (Upper Gila, Sonora) supports a high degree of biodiversity but a low overall degree of threat, helping to identify potential candidate watersheds for conservation and protection. For instance, large portions of these areas drain lands outside of current protected areas, which highlights potential opportunities to expand the conservation areas in the future. By contrast, the central (parts of the White-Yampa, Colorado Headwaters, Lower Green, Salt, Middle Gila) and southwestern (Lower Colorado-Lake Mead, Lower Colorado) parts of the Basin present both a high degree of native biodiversity and overall

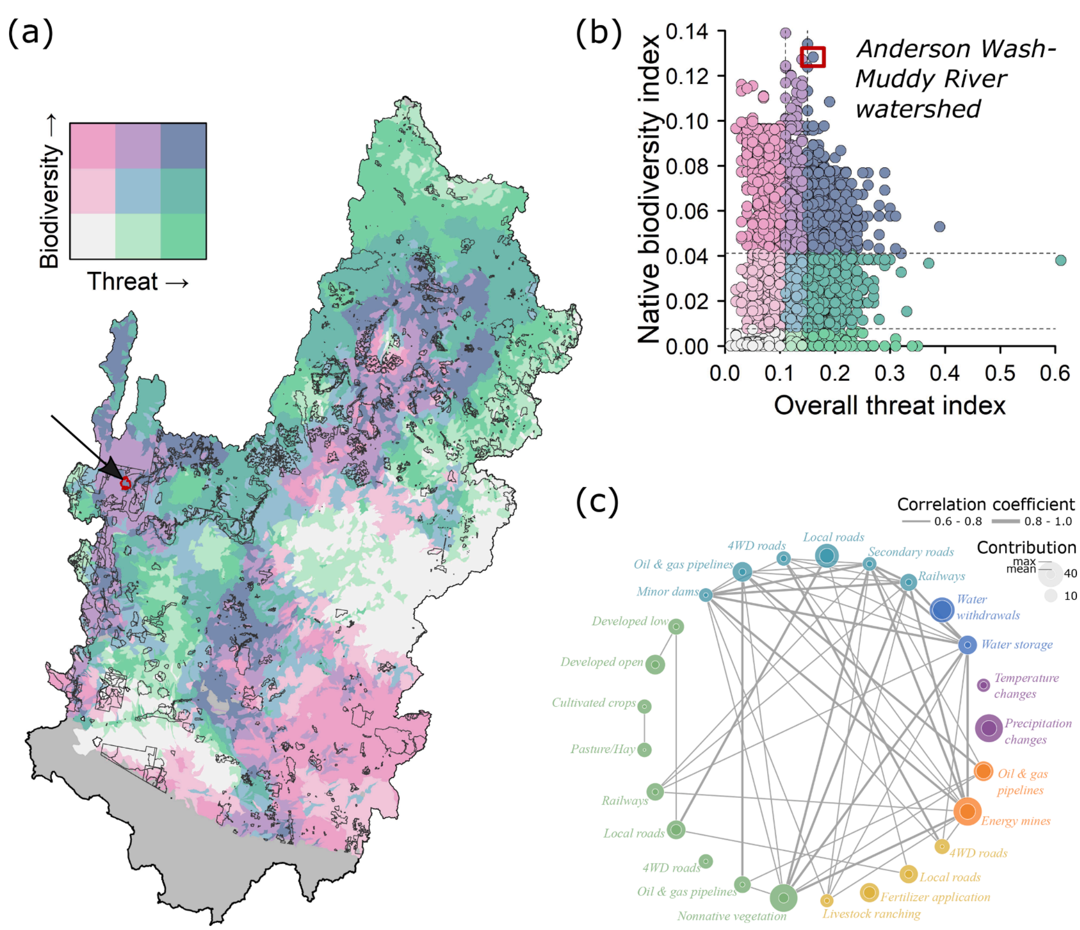


**Fig. 6.** Management opportunities across the Colorado River Basin watersheds. (a) Map showing the overlap between the overall threat index and the native biodiversity index classified into three classes (low, moderate, high based on their respective percentiles). Black polygons on the map indicate current protected areas throughout the Basin (GAP Status Code 1 and 2; U.S. Geological Survey, 2020). (b) This overlap can be used to identify candidate watersheds for conservation and protection efforts (upper left quadrant) or habitat restoration and enhancement (upper right quadrant) efforts, such as the Anderson Wash-Muddy River watershed displaying a high degree of threat and high native biodiversity (also highlighted in red on the map). (c) Network representing the contributions (maximum and mean; nodes) to the overall threat index and spatial correlations (Spearman's ρ; links) between the individual threat indices for the Anderson Wash-Muddy River watershed. For clarity individual threats with a contribution < 10 for any stream segments within the watershed and spatial correlations between individual threats < 0.6 are not displayed.

threat, suggesting candidate watersheds for habitat restoration and enhancement. Such efforts would facilitate persistence and recovery of native populations in these biodiverse areas, although we note that our approach does not explicitly account for recent biodiversity trends.

As an illustration of a priority watershed for restoration, we selected the Anderson Wash-Muddy River (located in the Lower Colorado-Lake Mead hydrographic region) because of its exceptional degree of biodiversity and high degree of threat (Fig. 6**b**). We found that this watershed is currently facing an array of threats captured by all the ecological integrity components simultaneously (Fig. 6**c**; see also **Fig. A11**). Among them, we identified two largely independent clusters of threats. The first one was related to the effects of residential development and characterized by the effects of different development intensities on fluvial geomorphology together with the effects of local roads on water quality and connectivity. The second one was related to exploitative activities through the effects of mining and drilling on fluvial geomorphology and water quality, also covarying with a decrease in connectivity due to the presence of transportation infrastructures (railways and undeveloped roads), the presence of nonnative vegetation and high instream water storage in upstream reservoirs. Despite being important threat contributors, recent changes in annual precipitation and water withdrawals appeared largely decoupled from other threats.

### 3.3. *Robustness of the threat assessment*

Our threat assessment was robust to the specification of the weighting scheme used to aggregate the individual threat indices, and captured the degree of impairment with respect to several components of ecological integrity measured *in situ* throughout the Colorado River Basin. In particular, we found a strong degree of correlation between the original overall threat index and the indices computed using alternative matrices of weights (**Fig. A12** in **Appendix C**). Not surprisingly, the overall threat index was more sensitive to 'randomized' than to 'modified' weights. The correlation coefficients varied between 0.79 and 1.00 when the relative weights were randomized, compared with 0.996 to 1.000 when the relative weights were modified within ± 25% of their

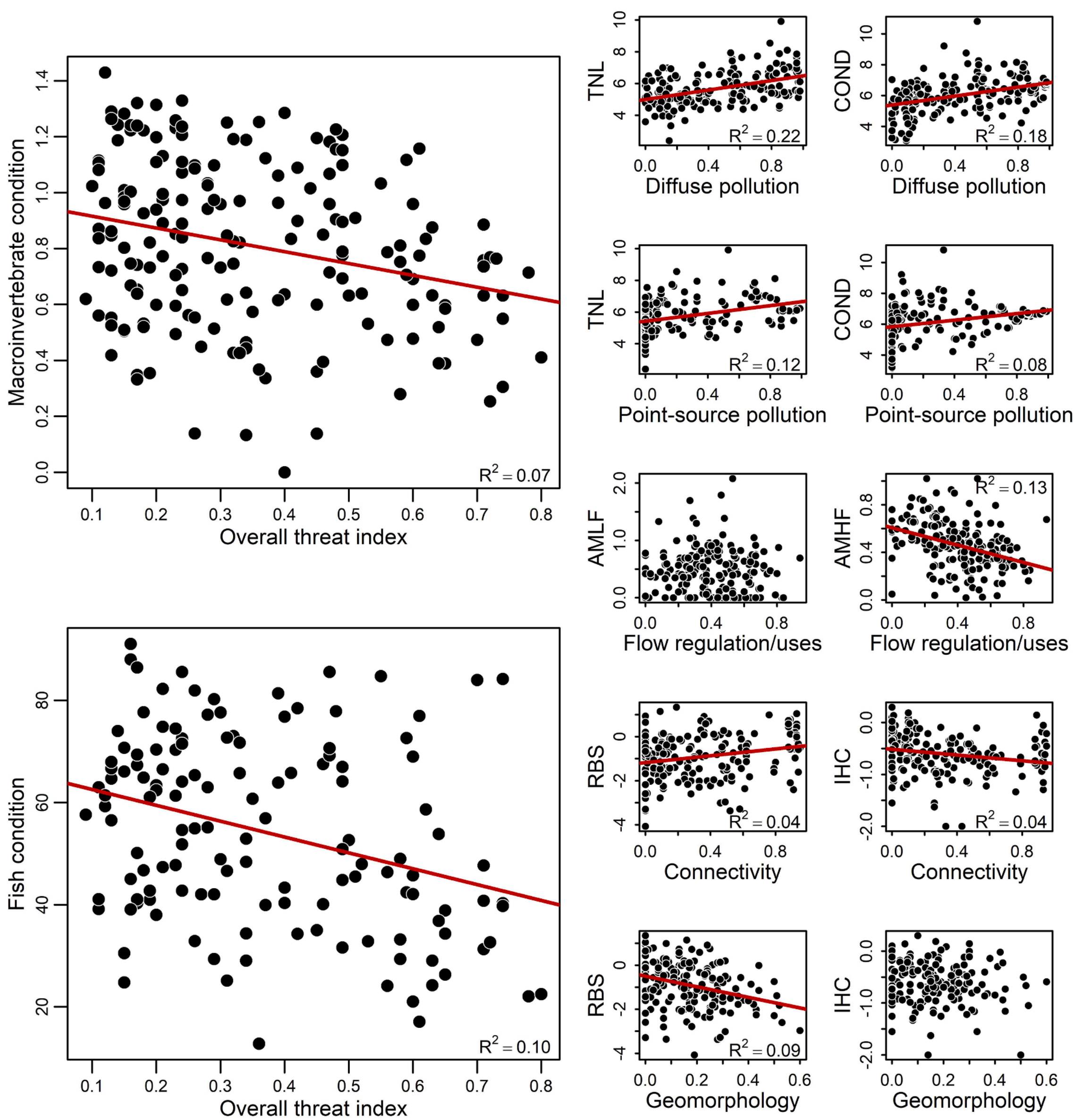


**Fig. 7.** Relationships between the overall or aggregated threat indices and biotic, chemical, hydrologic and physical indicators of ecological integrity. Red lines and $R^2$ indicate significant relationships ($P < 0.05$). Codes for the ecological integrity indicators are as follows: total nitrogen load (TNL); Conductivity (COND); alteration magnitude of low flow (AMLF); alteration magnitude of high flow (AMHF); relative bed stability (RBS); instream habitat complexity (IHC). See Table 1 for more information.

original values. The coefficient of variations (CV, calculated as a measure of variability across the 999 iterations) also indicated limited variability, notably when using 'modified' weights (CV $< 1\%$). Given that the scenario based on 'modified' weights was likely to be more ecologically meaningful than the one based on randomized weights (e.g., it is reasonable to assume that primary roads exert a stronger influence on ecological integrity than recreational trails), these results indicate that the uncertainty arising from the formulation of the matrix of weights was reduced when using a range of values informed by expert opinion and not likely to alter the major findings.

The aggregated indices demonstrated significant – albeit moderate – associations with the *in situ* measurements of ecological integrity they were designed to capture (Fig. 7). The overall threat was negatively associated with both macroinvertebrate ($R^2 = 0.07$; $P < 0.001$) and fish assemblage condition ($R^2 = 0.10$; $P < 0.001$), suggesting that sites displaying an overall high degree of human-related threats were also characterized by impaired species assemblages. In agreement with our expectations, the indices of diffuse and point-source pollution were positively associated with total nitrogen load (TNL: $R^2 = 0.12 – 0.22$; $P < 0.001$) and conductivity (COND: $R^2 = 0.08 – 0.018$; $P < 0.001$) with high values signaling water quality impairments. The index of flow regulation/uses was also negatively associated with an indicator of hydrologic alteration in the magnitude of high flow (AMHF: $R^2 = 0.13$; $P < 0.001$). This demonstrates that a high degree of hydrological threat translates into a lower-than-expected high flow, although no relationship was apparent with the magnitude of low flow (AMLF: $R^2 = 0.00$; $P = 0.572$). As expected, the index of connectivity was also negatively associated with instream habitat complexity (IHC: $R^2 = 0.09$; $P < 0.01$), and the index of geomorphology with relative bed stability (RBS: $R^2 = 0.04$; $P < 0.001$). This indicated that stream segments with highly fragmented upstream catchments or developed valley bottoms also display reduced habitat complexity and an excess of fine sediments, respectively. However, counter to our expectations, the index of connectivity was positively associated with RBS ($R^2 = 0.04$; $P < 0.01$), and the index of geomorphology showed little association with IHC ($P = 0.06$). The Breusch-Pagan tests indicated no evidence of heteroscedasticity (all $P \geq 0.05$), and the Kolmogorov-Smirnov tests no deviation from a normal distribution in the model residuals ($P \geq 0.05$), except for AMLF.

## 4. Discussion

We developed a robust spatial framework to assess the ecological integrity of riverine ecosystems, that combines multiple threat indices, varying local and watershed-scale processes, and capacity to reveal which human activities and impairment pathways contribute to overall impact. The result is a powerful tool that can be used to prioritize restoration and conservation efforts throughout the highly endangered Colorado River Basin.

We identified complex spatial threat associations throughout the Colorado River Basin, with an overall higher degree of threat around large urban centers, on the mainstem perennial rivers, and in the upper and southwestern parts of the Basin. The highest contributing threats are generally associated with urbanization (e.g., development intensity, local roads, water withdrawals), and tend to accumulate in downstream catchments - in line with previous investigations conducted in the Lower Colorado River sub-basin (Paukert et al., 2011). We also identified livestock ranching and exploitative activities (mining and drilling) as important sources of threat throughout the Basin. Importantly, the relatively low correlation between individual threat indices – especially those occurring within valley bottoms – indicates that the various human modification activities largely occur in different areas of the Basin. Therefore, the threat complexes identified among perennial stream segments likely result from the interplay of multiple pathways of influence rather than from the overlap between the various human modification activities (Craig et al., 2017). As a result, even if few threats contribute disproportionately to regional-scale ecological impairment (e.g., transportation corridors that covary with the incidence of other human modification activities related to development and resource extraction), indices composed of a combination of threats and pathways may be more relevant to capture ecological integrity at the local scale (Falcone et al., 2010; Lessmann et al., 2019). For instance, recent climate change appears as largely spatially distinct from other threats and high individual contributions were detected for most of the threat indices in at least part of the Basin. Although these examples suggest limited scope for widespread interactions between climate change and other human pressures (Bowler et al., 2020), it also indicates that even relatively undeveloped areas such as the most arid parts of the Basin are not out of reach from human influence.

Importantly, we showed that our threat indices were generally correlated with *in situ* measurements of ecological integrity. Notably, we found that a higher degree of overall threat was associated with impaired macroinvertebrate and fish assemblages, two taxonomic groups widely used in bioassessment of aquatic ecosystems and likely to respond to both local and regional environmental drivers (Karr, 1991; Li et al., 2010). The aggregated indices were also associated with several components of ecological integrity they were intended to capture and describe the chemical, hydrological and physical condition of the stream segments. However, the large range of variability in the strength of association with *in situ* measurements ($R^2 = 0.04–0.22$) suggests limited predictive power of threat maps to predict local-scale ecological integrity, as found by others (Thornbrugh et al., 2018; Lessmann et al., 2019). This may stem from the diversity of water bodies included in our assessment (i.e., from small ephemeral headwaters to major perennial tributaries, including the Colorado River), as well as the fact that interactions between threats were not explicitly accounted for by our method. Indeed, despite evidence that non-additive (including antagonistic) effects between threats are ubiquitous in freshwater ecosystems (Jackson et al., 2016), the lack of information about the direction and relative strengths of interactions for a large number of threat combinations and environmental contexts precluded their inclusion. Resolving whether threats interact or simply co-occur undoubtedly exemplifies a persistent and increasingly pressing conservation challenge in freshwater ecosystems (Reid et al., 2019).

Nonetheless, recognizing that the threat indices cannot be realistically validated for each stream segment across the Basin, and the fact that many knowledge gaps remain regarding the interactions between threats (Craig et al., 2017), our approach provides a reasonable picture of the fine-scale ecological state throughout one of the largest and most culturally significant river basins in North America. Our findings also confirm the minimal influence of the weighting scheme on the overall threat ranking among stream segments (e.g., Vörösmarty et al., 2010; Paukert et al., 2011), but show that informing the relative weight matrix using expert opinion reduce the uncertainty as compared to random choices. This demonstrates that combining spatial data with expert knowledge (i.e., relative weights estimated based on expert opinion rather than calibrated weights using the fitted relationship between threat indices and ecological responses of interest) can be an effective approach to assess the impact of anthropogenic threats in the absence of comprehensive scientific evidence. In particular, our spatial framework may help policy makers and managers to identify key threats or complexes of closely correlated threats and identify priority areas for habitat protection and restoration efforts. We provided an example of how combining the overall degree of threat with a biodiversity index could be used to identify management opportunities across watersheds, but note that the integration of complementary socio-economic and biodiversity variables (e.g., functional or phylogenetic diversity) could more effectively direct conservation and enhancement efforts (Dauwalter et al., 2011; Strecker et al., 2011).

The co-occurrence of multiple threats, such as seen in the Anderson Wash-Muddy River watershed and more generally among perennial stream segments, can be challenging for managers to address. First, different management goals are not always aligned such that potential conflicts may arise between efforts to protect or restore freshwater biodiversity and human demand for natural resources (van Rees et al., 2021). Methods have been developed to optimize allocation of limited resources to manage multiple threats simultaneously (e.g., Moore et al., 2021), which could be used in conjunction with our threat assessment to provide cost-effective management recommendations. Second, our study points out that the high degree of spatial overlap among threats on perennial stream segments partly arises through catchment-wide cumulative effects. The fact that most threats to freshwater systems are of terrestrial origin and accumulate along river networks has long been recognized (Ward et al., 2002), but is far from trivial when trying to protect freshwater habitats as it is seldom possible to conserve or restore entire upstream catchments (Abell et al., 2007). Prioritizing management efforts, therefore, requires a shift in management perspective to account for the connected nature of rivers in a more systematic way (Linke et al., 2011). Alternatively, the high contribution but low degree of spatial overlap among threats occurring within valley bottom and among ephemeral and intermittent stream segments (that compose the majority of the stream network throughout the Basin) suggests that there may be some threats that could be managed efficiently in isolation. For instance, the lower degree of threat clustering in the southeastern part of the Basin (e.g., Upper Gila), together with the fact that this region also has high fish diversity and representativeness (Strecker et al., 2011), suggest management opportunities for targeted restoration approaches in valley bottoms.

Identifying conservation priorities and management strategies involves not only considering ecological integrity from a present-day perspective but also potential changes in the importance and distribution of threats in the future (Reid et al., 2019). With many population centers predicted to grow by $>$ 50% in the coming decades in the Basin (e.g., Phoenix metropolitan area is predicted to double by 2040; Sabo et al., 2010), water withdrawals and threats associated with urbanization (habitat conversion, local roads) are likely to continue to represent the most pressing conservation challenges throughout the Colorado River Basin (Tidwell et al., 2014). Whereas it is also certain that temperature will continue to rise, recent models project a significant risk of decadal to multidecadal drought in the coming century, translating to flow reductions of at least 35% throughout the Basin (Seager et al., 2013; Udall & Overpeck, 2017). Such alarming trends will not only pose a direct threat to freshwater-dependent biodiversity but also strengthen the pressure from human activities on already scarce water resources, thereby further exacerbating the potential for water shortages, exposure to other threats (e.g., pollution) and subsequent biodiversity impacts (Jaeger et al., 2014; Whitney et al., 2017). The results from this study could therefore be combined with detailed climate and socio-economic data, including spatial information on trans-regional changes in water allocation policies (Schwabe et al., 2020), as a very important next step to aid in effective conservation planning now and in the future.

## *CRediT authorship contribution statement*

**Lise Comte:** Conceptualization, Data curation, Methodology, Formal analysis, Writing – original draft. **Julian D. Olden:** Conceptualization, Methodology, Funding acquisition, Supervision, Writing – review & editing. **Stacy Lischka:** Project administration, Writing – review & editing. **Brett G. Dickson:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108840.

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