

# Applying ecological thresholds to inform conservation and restoration efforts for stream fishes

Received: 13 August 2025

Accepted: 19 June 2026

Published online: 27 June 2026

Cite this article as: Brumm, K.J., Schinegger, R., Schürz, M. *et al.* Applying ecological thresholds to inform conservation and restoration efforts for stream fishes. *npj biodiversity* (2026). <https://doi.org/10.1038/s44185-026-00144-7>

Kyle J. Brumm, Rafaela Schinegger, Marlene Schürz, Georg Gruber, Florian Borgwardt, Carina Seliger & Dana M. Infante

We are providing an unedited version of this manuscript to give early access to its findings. Before final publication, the manuscript will undergo further editing. Please note there may be errors present which affect the content, and all legal disclaimers apply.

If this paper is publishing under a Transparent Peer Review model then Peer Review reports will publish with the final article.

**Manuscript Title:** Applying ecological thresholds to inform conservation and restoration efforts for stream fishes

**Authors' Full Names (E-mail Addresses):** Kyle J. Brumm<sup>a,b,\*</sup> (brummkyl@msu.edu), Rafaela Schinegger<sup>c</sup> (rafaela.schinegger@boku.ac.at), Marlene Schürz<sup>d,e,f</sup> (marlene.schuerz@boku.ac.at), Georg Gruber<sup>c</sup> (georg.gruber@boku.ac.at), Florian Borgwardt<sup>e</sup> (florian.borgwardt@boku.ac.at), Carina Seliger<sup>e</sup> (carina.seliger@boku.ac.at), Dana M. Infante<sup>a</sup> (infanted@msu.edu)

**Authors' Institutional Affiliations:** <sup>a</sup>Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, United States; <sup>b</sup>Biodiversity, Ecology, and Conservation Research Group, International Institute for Applied Systems Analysis, Laxenburg, Austria; <sup>c</sup>Institute of Landscape Development, Recreation and Conservation Planning, Department of Landscape, Water and Infrastructure, University of Natural Resources and Life Sciences, Vienna, Austria; <sup>d</sup>Department of Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany; <sup>e</sup>Institute of Hydrobiology and Aquatic Ecosystem Management, Department of Ecosystem Management, Climate and Biodiversity, University of Natural Resources and Life Science, Vienna, Austria; <sup>f</sup>Department of Biology, Chemistry, and Pharmacy, Institute of Biology, Free University Berlin, Berlin, Germany; \*corresponding author

**Corresponding Author:** Kyle J. Brumm (brumm@iiasa.ac.at): Biodiversity, Ecology, and Conservation Research Group, International Institute for Applied Systems Analysis, Schlossplatz 1, 2361 Laxenburg, Austria

**Keywords:** decision-support framework; functional traits; freshwater restoration; land use change; protected area coverage; spatial planning; vulnerability assessment

**Abstract**

Understanding stream fish responses to landscape stressors is fundamental to designing management strategies to conserve and restore fluvial ecosystems. Landscape stressors, including agricultural, pasture, and urban land use, often elicit threshold responses in stream fishes, causing rapid declines in abundance with comparatively small increases in stressor intensity. However, the use of thresholds to inform conservation and restoration decision-making remains limited, particularly when targeting entire stream fish assemblages at continental spatial extents. Here, we apply known threshold values to characterize the vulnerability of stream fishes across approximately 1.73 million stream reaches in the United States and Europe. We develop a decision-support framework that integrates threshold status indices with network catchment summaries of protected area coverage to prioritize (a) conservation actions in poorly protected catchments approaching land use thresholds, and (b) restoration actions in catchments that have exceeded thresholds despite high protected area coverage. Our findings highlight the vulnerability of stream fishes to landscape stressors across two continents and demonstrate how integrating threshold-based vulnerability assessments with protected area summaries can support management decision-making and help address the freshwater biodiversity crisis.

## Introduction

Freshwater fishes are threatened by human activities, including factors operating at the landscape scale<sup>1,2,3,4</sup>. Stressors associated with agricultural production and urban development are ubiquitous throughout the world, and they contribute to the freshwater biodiversity crisis<sup>5</sup> by altering natural hydrological regimes, changing physical characteristics of streams (e.g., fragmentation, sedimentation), and reducing water quality (e.g., nutrient enrichment)<sup>6,7,8,9</sup>. To address the freshwater biodiversity crisis, management efforts must account for complex responses of fish assemblages to multiple landscape stressors<sup>10,11</sup>, and they must also consider underlying social and economic drivers that influence conservation potential and restoration feasibility<sup>12,13</sup>.

Understanding how fish assemblages respond to landscape stressors is fundamental to designing effective management strategies to conserve and restore stream habitats<sup>14,15</sup>. Landscape stressors are known to elicit continuous but non-linear responses in stream fishes, characterized by points at which stream fish metrics decline rapidly with comparatively small increases in stressor intensity<sup>1,16,17</sup>. Such patterns can be identified using statistical analyses that quantify relationships between fish metrics (e.g., abundance of rheophilic fishes) and environmental factors (e.g., percent of urban land use within catchments). In applied contexts, these relationships may be expressed as threshold values, serving as empirical benchmarks that can readily be communicated to inform policy and management. These benchmarks can inform proactive conservation strategies to prevent landscape stressors from exceeding thresholds, while also guiding restoration efforts in degraded systems<sup>18,19,20</sup>. Although thresholds have considerable potential to inform conservation and restoration priorities<sup>21,22,23,24</sup>, efforts to incorporate them into the management of stream fishes remain limited<sup>25</sup>.

Ecosystem management must contend with financial constraints and limited institutional capacities, requiring spatial planning to guide the strategic allocation of conservation and restoration actions and to maximize cost-effectiveness<sup>26,27,28</sup>. Such approaches typically consider the distributions of

priority species and rare habitat types, but they may also incorporate vulnerability assessments to mitigate risk associated with landscape stressors<sup>29</sup>. The irreplaceability-condition-vulnerability (ICV) framework, for instance, integrates measures of conservation potential and stressor exposure, thereby incorporating risk into the decision-making process<sup>30,31,32,33</sup>. Related approaches have incorporated thresholds into spatial planning, although such applications have mostly been limited to relatively small regions<sup>34</sup>. For example, Ettinger et al.<sup>35</sup> used urban land use thresholds to develop an index of pre-spawn mortality risk for coho and Chinook salmon in the Puget Sound basin, identifying priorities for the preservation and restoration of critical habitats. Comparable frameworks applicable to entire stream fish assemblages across broader regional extents are lacking, highlighting the need to account for regional variation in the responses of stream fishes to landscape stressors<sup>24</sup>.

In addition to using thresholds to characterize vulnerability of stream fishes to multiple landscape stressors, spatial planning and decision-support frameworks can be strengthened by considering the distribution and effectiveness of protected areas, defined as locations dedicated to the long-term conservation of nature through legal or other effective means<sup>36</sup>. Catchments with a higher degree of upstream protection may support better outcomes for stream fishes by mitigating effects of landscape stressors<sup>37,38</sup>, while increases in institutional infrastructure often associated with protected areas may be used as a general proxy of restoration feasibility<sup>39,40,41</sup>. For example, conserving landscapes that are most vulnerable to human activities is more cost-effective than protecting landscapes with a relatively low risk of degradation<sup>33,42</sup>, whereas restoration may be more feasible in moderately disturbed landscapes<sup>43,44</sup>. Therefore, integrating threshold-based vulnerability and protected area assessments could inform policies such as the Kunming-Montreal Global Biodiversity Framework, United Nations Decade on Ecosystem Restoration, and European Union's Nature Restoration Regulation<sup>15,23,45,46</sup>.

The primary goal of this study is to develop a decision-support framework for identifying conservation and restoration priorities in fluvial ecosystems across a broad, continental spatial extent. To

achieve this, we first calculate threshold status indices to assess the vulnerability of stream fishes to agricultural, pasture, and urban land use in catchments of approximately 1.73 million stream reaches across the United States (US) and Europe – regions that offer contrasting case studies given their distinct land use histories and regulatory frameworks<sup>47</sup>. Second, we test empirical associations between percentages of protected land area within network catchments and measures of stream fish abundance to assess the potential benefits of landscape protection for stream fishes. We then integrate threshold status indices with protected area summaries to prioritize conservation and restoration efforts for stream fishes, and include two case studies to demonstrate how the same framework can be applied to inform management of fluvial ecosystems across different social-ecological contexts.

## Results

### *Summarizing threshold status indices across the conterminous United States and Europe*

In total, we calculated 44 threshold status indices to characterize vulnerability of stream fishes to agricultural, pasture, and urban land use within 19 ecoregions, including 14 ecoregions in the US and 5 ecoregions in Europe (Table 1; Figure S1). Thresholds for agricultural land use ranged from 0.10% for rivers in the Middle Missouri ecoregion to 40.06% for creeks in the Western Iberia ecoregion. Thresholds for pasture land use ranged from 1.52% for creeks in the Upper Mississippi ecoregion to 15.43% for rivers in the Colorado ecoregion. Lastly, urban land use thresholds ranged from 0.08% for rivers in the Western Iberia ecoregion to 12.30% for creeks in the Laurentian Great Lakes ecoregion (Table 1).

### *Evaluating the effectiveness of protected areas for supporting stream fishes*

All four fish metrics showed a significant positive association with protected area coverage, including the relative abundances of intolerant (Kruskal-Wallis chi-squared ( $\chi^2$ ) = 2425.7;  $p < 0.001$ ), migratory ( $\chi^2$  = 2005.7;  $p < 0.001$ ), lithophilic ( $\chi^2$  = 1176.3;  $p < 0.001$ ), and rheophilic ( $\chi^2$  = 1125.9;  $p < 0.001$ ) fishes (Figure 2). For each fish metric, pairwise Wilcoxon rank sum tests revealed significant differences among all protected area categories (i.e., *low*, *medium*, and *high* protection; all  $p$  values <

0.001). These findings, which were based on thousands of records of stream fishes sampled across two continents, support the inclusion of protected area coverage as a complementary dimension in the decision-support framework.

#### *Case Study 1 - Central and Western Europe ecoregion*

Our first case study focused on the Central and Western Europe ecoregion, which consisted of 141,132 catchments, including 107,597 creeks and 33,535 rivers. According to our threshold status indices, 45.1% of creeks and 67.4% of rivers had exceeded the agricultural land use threshold, whereas 34.4% of creeks and 75.2% of rivers had exceeded the threshold for urban land use (Figure 3a, b; Table S1). Most catchments were poorly protected, with 59.0% of creeks and 59.7% of rivers falling in the *low* protection category. In contrast, 13.8% of catchments had *medium* protection and 27.1% had *high* protection. Our investigation of multiple stressor configurations indicated that 30.5% of catchments had exceeded both the agricultural and urban land use thresholds, whereas 36.0% of catchments had not exceeded either threshold (Figure 4a). Additionally, 19.9% of catchments had exceeded the agricultural but not the urban land use threshold, and 13.6% had exceeded the urban but not the agricultural land use threshold (Figure 4a).

Using the framework shown in Figure 5, we identified conservation and restoration priorities for 35.1% of creeks and 45.9% of rivers within the Central and Western Europe ecoregion (Figure S2a). For creeks, 32.7% of priorities were associated with urban conservation, followed by 25.3% for agricultural conservation, and 16.6% for agricultural restoration. For rivers, the top priorities were associated with agricultural (24.0%) and urban restoration (18.3%).

#### *Case Study 2 - Middle Missouri ecoregion*

Our second case study focused on the Middle Missouri ecoregion, which consisted of 181,176 catchments, including 138,993 creeks and 42,183 rivers. According to our threshold status indices, 82.8% of creeks and 90.8% of rivers had exceeded the agricultural land use threshold, whereas 65.6% of creeks

and 65.3% of rivers had exceeded the threshold for urban land use (Figure 3c, d; Table S1). Consistent with our findings in the Central and Western Europe ecoregion, most catchments in the Middle Missouri ecoregion were poorly protected, with 97.8% of creeks and 97.6% of rivers falling in the *low* protection category. In contrast, just 1.1% of catchments had *medium* protection and 1.2% had *high* protection. Our investigation of multiple stressor configurations indicated that 63.0% of catchments had exceeded both the agricultural and urban land use thresholds, whereas 12.8% had not exceeded either threshold (Figure 4b). Additionally, 21.7% of catchments had exceeded the agricultural but not the urban land use threshold, and 2.6% had exceeded the urban but not the agricultural land use threshold (Figure 4b).

Using the framework shown in Figure 5, we identified conservation and restoration priorities for 16.7% of creeks and 22.1% of rivers within the Middle Missouri ecoregion (Figure S2b). For creeks, 91.8% of priorities were associated with urban conservation, followed by 3.0% for agricultural restoration. Similarly for rivers, the top priorities were associated with urban conservation (86.0%) and agricultural conservation (7.4%).

#### *Applying the framework across spatial scales*

To illustrate how the framework can be applied across spatial scales, we aggregated priorities identified at the catchment scale and considered implications for conservation and restoration in subbasins of the Vistula River watershed, Poland (Figure 6). Compared to other subbasins in the Vistula River watershed, the Bug River had a relatively low coverage of protected areas but had not yet exceeded the agricultural or urban land use thresholds, suggesting that proactive conservation actions could prevent further degradation. In contrast, contiguous sections of the Narew River were either moderately or highly protected but had marginally exceeded both the agricultural and urban land use thresholds, making the Narew River a high priority for agricultural and urban restoration efforts (e.g., riparian rewilding, regulating pesticide and fertilizer application rates, addressing hydrologic alteration). The mainstem Vistula River was identified as a high priority for agricultural restoration (Figure 6c), whereas the Wkra

River was identified as a high priority for urban restoration (Figure 6d). Together, these examples demonstrate how the framework can inform conservation and restoration priorities within subbasins and across entire watersheds.

## Discussion

Characterizing responses of stream fishes to landscape stressors is fundamental for informing conservation and restoration efforts targeting the maintenance and recovery of stream habitats<sup>48,49</sup>. To prioritize management actions in catchments throughout the conterminous United States and Europe, we developed a decision-support framework that integrates threshold responses of stream fishes to landscape stressors and summaries of protected area coverage within network catchments. In addition to demonstrating an empirical association between the percentage of upstream protection and stream fish abundance, we present two case studies in Central and Western Europe and Middle Missouri ecoregions to showcase how this framework can be applied similarly to inform management across different regional contexts. Below, we address practical considerations regarding its use and continued development.

Vulnerability assessments are useful for determining where management strategies can best be applied to proactively conserve or retroactively restore stream habitats. The threshold status indices developed here are unique in that they quantify how far catchments are from exceeding land use thresholds known to elicit rapid declines in the abundance of stream fishes, providing opportunities to investigate patterns in the relative vulnerability of stream fishes across several large, heterogeneous ecoregions. This builds upon previous examples in which individual land use thresholds have been applied to inform management of focal species within specific local contexts<sup>35</sup>, extending their applicability to entire stream fish assemblages across multiple spatial scales<sup>17</sup>. Because our basic unit of analysis was the network catchment, our indices can be used in local applications or scaled up to draw inferences about the relative vulnerability of subbasins, watersheds, or administrative units, making our approach relevant to a variety

of research and management activities including local stakeholder engagements, regional planning exercises, and even national assessments<sup>27,50,51,52</sup>.

While we considered changes in the relative abundance of stream fishes, our framework is not limited to this choice of indicator. Any biodiversity metric for which meaningful response relationships or thresholds can be quantified – such as species richness, functional diversity, or rarity – could be incorporated, assuming the requisite data are available. This is an important consideration because biodiversity is inherently multidimensional and different metrics may respond differently to environmental factors across different regional contexts<sup>53,54,55</sup>. Accordingly, metric selection should be aligned with specific management objectives, with explicit consideration of how variation among metrics shapes ecological interpretation and influences management priorities<sup>8,15</sup>.

Whether protected areas are an effective means for conserving biodiversity is a topic that has been debated in both the terrestrial and marine realms<sup>56,57</sup>. Because the criteria for a protected area to be considered effective are likely to vary based on specific management objectives, such assessments should be included as a component of any spatial planning effort<sup>36</sup>. Recent assessments conducted in freshwater ecosystems have provided evidence that protected areas can, in some cases, be effective for supporting freshwater biodiversity<sup>58</sup>. Consistent with these findings, we demonstrate a positive association between the percentage of protected land area within network catchments and the relative abundances of intolerant, migratory, lithophilic, and rheophilic fishes across the conterminous United States and Europe. However, we also show that most catchments in Central and Western Europe and Middle Missouri ecoregions were poorly protected. In the Iberian peninsula, Hermoso et al.<sup>59</sup> showed that Natura 2000 sites, which are designated to safeguard threatened species and habitats in Europe, failed to provide adequate coverage for several freshwater taxa, and similar findings have been observed for stream fishes in the Brazilian Amazon<sup>60</sup> and in the conterminous United States<sup>61</sup>. Together, these findings indicate that protected areas

can benefit stream fishes, while underscoring the need to explicitly incorporate freshwater ecosystems in the design of future protected areas to help close gaps in representation<sup>62,63</sup>.

Here, we summarized the percentage of protected land area within network catchments and used this as a proxy of restoration feasibility. Upstream protection is expected to benefit freshwater ecosystems by mitigating cumulative effects of landscape pressures, particularly in cases where in-stream protection has not explicitly been mandated<sup>38</sup>. In this context, restoration may occur both within protected areas and in the surrounding landscape matrix, consistent with integrated approaches to river basin management<sup>64,65</sup> (see below). This proxy could be refined by accounting for variation in IUCN protected area management categories (e.g., strict protection), or adapted to represent additional spatial configurations (e.g., riparian or headwater protection). Nonetheless, protected area coverage provides complementary, policy-relevant information that, in conjunction with threshold-based vulnerability assessments, helps to identify where conservation and restoration efforts may be most cost-effective<sup>66</sup>.

While our decision-support framework identifies management priorities based on the proximity of catchments to known land use thresholds, the management decision-making process is complex and must be informed by additional data inputs that account for synergies and trade-offs among measures of cultural, economic, and social relevance<sup>36,67,68</sup>. This framework was designed to inform regional priorities by identifying catchments most vulnerable to landscape stressors, but local management decisions must ultimately be made in collaboration with local stakeholders<sup>69,70</sup>. Although stakeholder engagement is a significant determinant of the success of conservation programs<sup>71</sup>, stakeholder feedback is rarely considered in spatial planning processes<sup>27</sup>.

Our results provide a basis for engaging policymakers, natural resource managers, and local stakeholders in planning and implementing on-the-ground management actions. In the context of the DPSIR (Driver-Pressure-State-Impact-Response) framework, targeted local assessments are needed to better understand how agricultural and urban land use contribute to site-specific pressures that modify the

physical or chemical state of local habitats<sup>72</sup>. Local insights into how human pressures – such as fragmentation, hydrologic alteration, sedimentation, and nutrient enrichment – impact stream habitats and the fishes they support are crucial for identifying appropriate mitigation strategies and shaping societal responses<sup>73</sup>. Proactive conservation strategies, including the establishment of protected areas and conservation easements, are essential to limit further degradation of stream habitats in catchments where land use thresholds have not yet been exceeded. Conversely, restoration efforts should seek to promote recovery of species and ecological processes within freshwater ecosystems<sup>40,44,74,75</sup>. In urban settings, this may include building green infrastructure to minimize hydrological change and contain nutrient runoff<sup>76</sup>, while in agricultural settings, improved land use practices – such as reduced pesticide and fertilizer application, or riparian rewilding – can help mitigate non-point source pressures<sup>77</sup>. In both contexts, conservation and restoration efforts will require local habitat condition assessments to characterize specific mechanisms of impairment.

One limitation of our approach is that while network catchments account for cumulative upstream influences, downstream interactions are not explicitly represented, potentially influencing prioritization outcomes in systems with varying degrees of fragmentation. Future work could address this limitation by integrating river network connectivity and longitudinal processes into the decision-support framework<sup>15,78,79,80</sup>.

A second limitation is that we identified restoration priorities based on the assumption that habitat degradation is inherently reversible. However, the literature suggests that most restoration projects fall short of attaining pre-disturbance conditions<sup>44</sup>. In part, the effectiveness of restoration projects is limited by uncertainties in the conditions under which a degraded system can be fully restored to a reference state<sup>20</sup> (i.e., hysteresis). Under high levels of uncertainty, an alternative strategy may be to intentionally direct the transformation of a degraded ecosystem toward a new, desirable state<sup>81</sup> – a process that must ultimately be shaped by local stakeholders.

Initiatives such as the Kunming-Montreal Global Biodiversity Framework, United Nations Decade on Ecosystem Restoration, and the European Union's Nature Restoration Regulation<sup>46</sup> represent formal commitments to addressing the freshwater biodiversity crisis<sup>23,82,83</sup>. To help achieve the ambitious conservation and restoration targets set forth by such initiatives, spatial planning efforts conducted at broad spatial extents must account for complex responses of fish assemblages to multiple landscape stressors<sup>11</sup>. By characterizing vulnerability of stream fishes to multiple landscape stressors, our decision-support framework promotes the use of ecological thresholds in decision-making applications throughout the conterminous United States and Europe. More broadly, our decision-support framework provides a transferable approach for incorporating thresholds into conservation and restoration planning for freshwater ecosystems throughout the world.

## **Methods**

### *Defining our study region and spatial framework*

This study was conducted in streams located throughout the conterminous United States (US) and Europe. Stream networks were defined using the National Hydrography Dataset<sup>84</sup> (NHDPlusV2) and the Catchment Characterization and Modelling Database<sup>85</sup> (CCM2). Using these established hydrographic datasets, we delineated network catchments – the total upstream land area draining to a given stream reach<sup>86</sup> – to account for integrated and directional influences of landscape stressors on stream habitats and the fishes they support. To account for natural biogeographic differences in climate, geology, and physiography, analyses were conducted within freshwater ecoregions (Freshwater Ecoregions of the World<sup>87</sup> (FEOW); Figure S1) and further stratified by stream size (hereafter, strata). Stream reaches were assigned to one of two strata: those with a network catchment area larger than 100 km<sup>2</sup> were classified as rivers (R), and all others were classified as creeks<sup>86,88</sup> (C).

### *Identifying threshold responses of fishes to human landscape stressors*

Thresholds characterizing responses of fish assemblages to landscape stressors were sourced from<sup>17</sup>, who identified thresholds by testing responses of four fish metrics – representing abundances of intolerant, migratory, lithophilic, and rheophilic fishes – to percentages of agricultural, pasture, and urban land use summarized within both local and network catchments. These fish metrics are commonly used in vulnerability assessments because they are sensitive to factors such as chemical pollution, fragmentation, sedimentation, and hydrologic alteration<sup>9,89</sup>. Thresholds were identified using piecewise linear regression and verified using a combination of change-point analysis and visual confirmation<sup>17</sup>. Within each ecoregion, analyses were repeated for each combination of fish metric, land use type, catchment unit, and stratum, yielding up to 48 thresholds per ecoregion<sup>17</sup>. For this study, we extracted thresholds for network catchments and retained the lowest threshold value across all four fish metrics – for each land use type and stratum – to represent the minimum land use intensity at which changes in fish assemblages were expected to occur (e.g., a single threshold characterizing influences of urban land use on fish assemblages in creeks). A summary of these stratum-specific threshold values is provided in Table 1.

#### *Calculating threshold status indices*

To address our first objective (Figure 1), we summarized the percentage of agricultural, pasture, and urban land use within network catchments<sup>90</sup>. Land use data were sourced from the 2019 National Land Cover Database<sup>91</sup> (NLCD; US), and from the 2018 Coordination of Information on the Environment Land Cover Dataset<sup>92</sup> (CORINE; Europe). Agricultural land use includes areas dedicated to the production of cultivated crops, including orchards and vineyards (NLCD class 82; CORINE classes 2.1, 2.2, and 2.4); pasture is defined separately to include areas planted for livestock grazing and fodder production (NLCD class 81; CORINE class 2.3).

For each ecoregion, we calculated a threshold status index for each catchment by dividing network catchment land use summaries by stratum-specific threshold values. Index values greater than 1 indicate

that a catchment has exceeded a given land use threshold (higher disturbance), whereas values of 1 or less indicate the threshold has not yet been exceeded (lower disturbance). To facilitate interpretation, we used a quantile classification to assign these index values to one of four categories, designating whether each catchment was *far above*, *just above*, *just below*, or *far below* each land use threshold.

#### *Summarizing protected area coverage within network catchments*

To address our second objective and justify inclusion of protected areas in the decision-support framework, we investigated associations between stream fish metrics and protected area coverage (Figure 1). Protected area data were sourced from the World Database of Protected Areas<sup>93</sup> (WDPA), processed using a dissolve operation in ArcGIS Pro<sup>94</sup>, and summarized as the percentage of protected land area within each network catchment. While protected area coverage and human land use are related, they are not mutually exclusive measures as catchments often include semi-natural or low-intensity lands that lack formal protection. To facilitate interpretation, catchments were assigned to one of three equal interval categories corresponding to classes of *low* ( $\leq 33.3\%$ ), *medium* ( $> 33.3\%$  and  $\leq 66.6\%$ ), and *high* ( $> 66.6\%$ ) protection. We then used Kruskal-Wallis and Wilcoxon rank sum tests ( $\alpha = 0.017$ , Bonferroni correction) to assess differences among protection categories for each of the four fish metrics described above<sup>95,96</sup>.

#### *Developing the decision-support framework*

To address the primary goal of this study, we integrated insights from both the threshold status and protected area assessments to develop a decision-support framework for prioritizing conservation and restoration efforts (Figure 1). In this framework, catchments with *low* protection that were *just below* a given land use threshold were considered high priority for conservation. These catchments are particularly vulnerable to crossing a land use threshold and would likely benefit from implementing proactive conservation efforts to limit degradation of stream habitats. In contrast, catchments with *medium* or *high* protection that were *just above* a given land use threshold were considered high priority for restoration. Despite being relatively well-protected, these catchments have marginally exceeded one or more land use

thresholds and are expected to be more amenable to restoration than catchments draining highly disturbed or unprotected landscapes.

### *Case studies*

To illustrate the utility of this framework, we mapped results for each recommended management action and summarized their frequency by ecoregion and stratum (e.g., percentage of catchments identified as high priority for urban conservation). Because stream catchments support multiple human activities that degrade stream habitats and contribute to biodiversity loss, we demonstrated how threshold status indices can be combined to identify catchments that have exceeded multiple thresholds<sup>97,98,99</sup>. Lastly, using the Vistula River watershed, Poland as an example, we show how the framework can be applied across scales, from identifying opportunities within individual catchments to drawing broader inferences about subbasins and entire watersheds.

### **Data Availability**

The data supporting the findings of this study are publicly available in Zenodo (<https://doi.org/10.5281/zenodo.20326525>). Fish abundance data were provided by the NFHP in the US and the EFI+ consortium in Europe and may be available upon request to the respective data owners.

### **Code Availability**

The code supporting the findings of this study are publicly available in Zenodo (<https://doi.org/10.5281/zenodo.20326525>).

### **Acknowledgements**

We thank all partners who contributed to the database of the European Fish Index Plus project (EFI+) and the United States National Fish Habitat Partnership (NFHP) for providing fish sampling data. We also thank the Fulbright Austria Foundation and the European Union ERASMUS+ program for supporting exchanges of K.J.B. and D.M.I. at the University of Natural Resources and Life Sciences, Vienna (BOKU) and R.S. and M.S. at Michigan State University (MSU), which enriched the development of this project.

K.J.B. and D.M.I. were supported by the U.S. Geological Survey Aquatic Gap Project (agreement no. G21AC00013) and Michigan State University. F.B. and M.S. were supported by the Horizon Europe project DANUBELifelines (contract no. 101213836).

### **Author Contributions**

K.J.B., R.S., F.B., and D.M.I. conceived the methodology. K.J.B. led on data curation and formal analysis, with support from M.S., G.G., and C.S. K.J.B. and D.M.I. wrote the original draft of the manuscript which was reviewed, edited, and approved by all authors.

### **Competing Interests**

The authors declare no competing financial or non-financial interests.

ARTICLE IN PRESS

## References

1. Allan, J.D. Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annu. Rev. Ecol. Evol. Syst.* **35**, 257-284 (2004).
2. Dudgeon, D. Multiple threats imperil freshwater biodiversity in the Anthropocene. *Curr. Biol.* **29**, R960-R967 (2019).
3. Schürings, C. et al. River ecological status is shaped by agricultural land use intensity across Europe. *Water Res.* **251**, 121136 (2024).
4. Sayer, C.A. et al. One-quarter of freshwater fauna threatened with extinction. *Nature.* **638**, 138-145 (2025).
5. Dudgeon, D. & Strayer, D.L. Bending the curve of global freshwater biodiversity loss: what are the prospects? *Biol. Rev.* **100**, 205-226 (2025).
6. Booth, D.B. et al. Reviving urban streams: land use, hydrology, biology, and human behavior. *J. Am. Water Resour. Assoc.* **40**, 1129-1388 (2004).
7. Riseng, C.M., Wiley, M.J., Black, R.W. & Munn, M.D. Impacts of agricultural land use on biological integrity: a causal analysis. *Ecol. Appl.* **21**, 3128-3146 (2011).
8. Feio, M.J. et al. Fish and macroinvertebrate assemblages reveal extensive degradation of the world's rivers. *Global Change Biol.* **29**, 355-374 (2023).
9. Brumm, K.J. et al. Relationships between environmental variables and fish functional groups in impounded reaches of the Upper Mississippi and Yangtze Rivers. *Water Biol. Secur.* **3**, 100291 (2024).
10. Schinegger, R., Palt, M., Segurado, P. & Schmutz, S. Untangling the effects of multiple human stressors and their impacts on fish assemblages in European running waters. *Sci. Total Environ.* **573**, 1079-1088 (2016).
11. van Rees, C.B. et al. Safeguarding freshwater life beyond 2020: recommendations for the new global biodiversity framework from the European experience. *Conserv. Lett.* **14**, e12771 (2021).
12. Domisch, S. et al. Social equity shapes zone-selection: balancing aquatic biodiversity conservation and ecosystem services delivery in the transboundary Danube River Basin. *Sci. Total Environ.* **656**, 797-807 (2019).
13. Logez, M., Bouraï, L., Hette-Tronquart, N. & Argillier, C. Ecological vulnerability of aquatic ecosystems – a review. *Environ. Manage.* **75**, 192-204 (2025).
14. Schlosser, I.J. Stream fish ecology: a landscape perspective. *BioScience.* **41**, 704-712 (1991).
15. Stoffers, T. et al. A collaborative research agenda for restoring free-flowing rivers. *Commun. Earth Environ.* **7**, 303 (2026).
16. Baker, M.E. & King, R.S. A new method for detecting and interpreting biodiversity and ecological community thresholds. *Methods Ecol. Evol.* **1**, 25-37 (2010).
17. Üblacker, M.M. et al. Cross-continental evaluation of landscape-scale drivers and their impacts to fluvial fishes: understanding frequency and severity to improve fish conservation in Europe and the United States. *Sci. Total Environ.* **897**, 165101 (2023).
18. Foley, M.M. et al. Using ecological thresholds to inform resource management: current options and future possibilities. *Fronti. Mar. Sci.* **2**, 95 (2015).
19. Kelly, R.P. et al. Embracing thresholds for better environmental management. *Phil. Trans. R. Soc. B.* **370**, 20130276 (2015).

20. Harper, M. et al. A multi-realm perspective on applying potential tipping points to environmental decision-making. *Environ. Rev.* **32**, 131-144 (2024).
21. Hastings, A. et al. Transient phenomena in ecology. *Science*. **361**, 6406 (2018).
22. Ross, J.A., Infante, D.M., Cooper, A.R., Whittier, J.B. & Daniel, W.M. Assessing impacts of human stressors on stream fish habitats across the Mississippi River basin. *Water*. **15**, 2400 (2023).
23. Stoffers, T. et al. Reviving Europe's rivers: Seven challenges in the implementation of the Nature Restoration Law to restore free-flowing rivers. *WIREs Water*. **11**, e1717 (2024).
24. van Rees, C.B., Geist, J. & Arthington, A.H. Grasping at water: a gap-oriented approach to bridging shortfalls in freshwater biodiversity conservation. *Biol. Rev.* **100**, 1970-1993 (2025).
25. Hernández Martínez de la Riva, A. et al. Tipping points in freshwater ecosystems: an evidence map. *Front. Freshw. Sci.* **1**, 1264427 (2023).
26. Kukkala, A.S. & Moilanen, A. Core concepts of spatial prioritization in systematic conservation planning. *Biol. Rev.* **88**, 443-464 (2013).
27. Jung, M. et al. An assessment of the state of conservation planning in Europe. *Phil. Trans. R. Soc. B.* **379**, 20230015 (2024).
28. Giakoumi, S. et al. Advances in systematic conservation planning to meet global biodiversity goals. *Trends Ecol. Evol.* **40**, 395-410 (2025).
29. Moilanen, A. et al. Novel methods for spatial prioritization with applications in conservation, land use planning and ecological impact avoidance. *Methods Ecol. Evol.* **13**, 1062-1072 (2022).
30. Lawler, J.J., White, D. & Master, L.L. Integrating representation and vulnerability: two approaches for prioritizing areas for conservation. *Ecol. Appl.* **13**, 1762-1772 (2003).
31. Linke, S., Pressey, R.L., Bailey, R.C. & Norris, R.H. Management options for river conservation planning: condition and conservation re-visited. *Freshwater Biol.* **52**, 918-938 (2007).
32. Mattson, K.M. & Angermeier, P.L. Integrating human impacts and ecological integrity into a risk-based protocol for conservation planning. *Environ. Manage.* **39**, 125-138 (2007).
33. Hansen, A.J. et al. Informing conservation decisions to target private lands of highest ecological value and risk of loss. *Ecol. Appl.* **32**, e2612 (2022).
34. Le Bagousse-Pinguet, Y. et al. Thresholds of functional trait diversity driven by land use intensification. *Nat. Ecol. Evol.* **9**, 1224-1233 (2025).
35. Ettinger, A.K. et al. Prioritizing conservation actions in urbanizing landscapes. *Sci. Rep.* **11**, 818 (2021).
36. Hermoso, V., Abell, R., Linke, S. & Boon, P. The role of protected areas for freshwater biodiversity conservation: challenges and opportunities in a rapidly changing world. *Aquat. Conserv. Mar. Freshwater Ecosyst.* **26**, 3-11 (2016).
37. Abell, R., Allan, J.D. & Lehner, B. Unlocking the potential of protected areas for freshwaters. *Biol. Conserv.* **134**, 48-63 (2007).
38. Abell, R., Lehner, B., Thieme, M. & Linke, S. Looking beyond the fence line: assessing protection gaps for the world's rivers. *Conserv. Lett.* **10**, 384-394 (2017).
39. Brancalion, P.H.S. et al. Global restoration opportunities in tropical rainforest landscapes. *Sci. Adv.* **5**, eaav3223 (2019).
40. Piczak, M.L. et al. Protecting and restoring habitats to benefit freshwater biodiversity. *Environ. Rev.* **32**, 438-456 (2024).

41. Zamorano-Elgueta, C. et al. Integrating ecological suitability and socioeconomic feasibility at landscape scale to restore biodiversity and ecosystem services in Southern Chile. *Environ. Manage.* **75**, 588-605 (2025).
42. Negret, P.J., Venegas, R., Sonter, L.J., Possingham, H.P. & Maron, M. Conservation planning for retention, not just protection. *Global Change Biol.* **30**, e17211 (2024).
43. Noss, R., Nielsen, S. & Vance-Borland, K. Prioritizing ecosystems, species, and sites for restoration (ed. Moilanen, A., Wilson, K.A. & Possingham, H.P.) Chapter 12 (Oxford University Press, 2009).
44. Palmer, M.A. & Stewart, G.A. Ecosystem restoration is risky... but we can change that. *One Earth.* **3**, 661-664 (2020).
45. Cooke, S.J. et al. A freshwater perspective on the United Nations decade for ecosystem restoration. *Conserv. Sci. Pract.* **4**, e12787 (2022).
46. European Union Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on nature restoration and amending Regulation (EU) 2022/869 (2024).
47. Davison, C.W., Rahbek, C. & Morueta-Holme, N. Land-use change and biodiversity: challenges for assembling evidence on the greatest threat to nature. *Global Change Biol.* **27**, 5414-5429 (2021).
48. Brumm, K.J., Infante, D.M. & Cooper, A.R. Functional biogeography of fluvial fishes across the conterminous U.S.A.: assessing the generalizability of trait-environment relationships over large regions. *Freshwater Biol.* **68**, 790-805 (2023).
49. Biggs, J. et al. Building the freshwater network: a new approach to the identification of freshwater biodiversity hotspots and restoration opportunities in England and Wales. *Ecol. Solutions and Evidence.* **6**, e70089 (2025).
50. Leonard, P.B., Baldwin, R.F. & Hanks, R.D. Landscape-scale conservation design across biotic realms: sequential integration of aquatic and terrestrial landscapes. *Sci. Rep.* **7**, 14556 (2017).
51. Robinson, K.F., Fuller, A.K., Stedman, R.C., Siemer, W.F. & Decker, D.J. Integration of social and ecological sciences for natural resource decision making: challenges and opportunities. *Environ. Manage.* **63**, 565-573 (2019).
52. Lees, C.M., Rutschmann, A., Santure, A.W. & Beggs, J.R. Science-based, stakeholder-inclusive and participatory conservation planning helps reverse the decline of threatened species. *Biol. Conserv.* **260**, 109194 (2021).
53. Villéger, S., Miranda, J.R., Hernández, D.F. & Mouillot, D. Contrasting changes in taxonomic vs. functional diversity of tropical fish communities after habitat degradation. *Ecol. Appl.* **20**, 1512-1522 (2010).
54. Chen, K. & Olden, J.D. Threshold responses of riverine fish communities to land use conversion across regions of the world. *Global Change Biol.* **26**, 4952-4965 (2020).
55. Su, G. et al. Human impacts on global freshwater fish biodiversity. *Science.* **371**, 835-838 (2021).
56. Watson, J.E.M., Dudley, N., Segan, D.B. & Hockings, M. The performance and potential of protected areas. *Nature.* **515**, 67-73 (2014).
57. Pressey, R.L. et al. The mismeasure of conservation. *Trends Ecol. Evol.* **36**, 808-821 (2021).
58. Acreman, M., Hughes, K.A., Arthington, A.H., Tickner, D. & Dueñas, M.A. Protected areas and freshwater biodiversity: a novel systematic review distils eight lessons for effective conservation. *Conserv. Lett.* **13**, e12684 (2020).
59. Hermoso, V., Filipe, A.F., Segurado, P. & Beja, P. Effectiveness of a large reserve network in protecting freshwater biodiversity: a test for the Iberian Peninsula. *Freshwater Biol.* **60**, 698-710 (2015).

60. Frederico, R.G., Zuanon, J. & de Marco Jr., P. Amazon protected areas and its ability to protect stream-dwelling fish fauna. *Biol. Conserv.* **219**, 12-19 (2018).
61. Cooper, A.R. et al. Protected areas lacking for many common fluvial fishes of the conterminous USA. *Divers. Distrib.* **25**, 1289-1303 (2019).
62. Kail, J., Januschke, K. & Hering, D. Freshwater-related species richness in Natura 2000 sites strongly depends on the surrounding land use besides local habitat conditions. *Journal of Environ. Manage.* **340**, 118025 (2023).
63. Baattrup-Pedersen, A. et al. Freshwater habitats within the Natura 2000 network. *Ecol. Appl.* **36**, e70241 (2026).
64. Spray, C. et al. Strategic design and delivery of integrated catchment restoration monitoring: emerging lessons from a 12-year study in the UK. *Water.* **14**, 2305 (2022).
65. Riato, L., Leibowitz, S.G., Weber, M.H. & Hill, R.A. A multiscale landscape approach for prioritizing river and stream protection and restoration actions. *Ecosphere.* **14**, e4350 (2023).
66. Visconti, P. et al. Protected area targets post-2020. *Science.* **364**, 239-241 (2019).
67. Margules, C.R. & Pressey, R.L. Systematic conservation planning. *Nature.* **405**, 243-253 (2000).
68. Mace, G.M. Whose conservation? *Science.* **345**, 1558-1560 (2014).
69. Doyle-Capitman, C.E. & Decker, D.J. Facilitating local stakeholder participation in collaborative landscape conservation planning: a practitioners' guide. Human Dimensions Research Unit Publication Series 17-12. Department of Natural Resources, College of Agriculture and Life Sciences, Cornell University, Ithaca, New York, United States (2018).
70. Mori, A.S. & Isbell, F. Untangling the threads of conservation: a closer look at restoration and preservation. *J. Appl. Ecol.* **61**, 215-222 (2024).
71. Farwig, N. et al. Identifying major factors for success and failure of conservation programs in Europe. *Environ. Manage.* **75**, 425-443 (2025).
72. Smeets, E. & Weterings, R. Environmental indicators: typology and overview. European Environment Agency. Technical Report No 25. Copenhagen, Denmark (1999).
73. Perujo, N. et al. A guideline to frame stressor effects in freshwater ecosystems. *Sci. Total Environ.* **777**, 146112 (2021).
74. Wohl, E., Lane, S.N. & Wilcox, A.C. The science and practice of river restoration. *Water Resour. Res.* **51**, 5974-5997 (2015).
75. Tickner, D. et al. Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *BioScience.* **70**, 330-342 (2020).
76. Wang, D., Xu, P.Y., An, B.W. & Guo, Q.P. Urban green infrastructure: bridging biodiversity conservation and sustainable urban development through adaptive management approach. *Front. Ecol. Evol.* **12**, 1440477 (2024).
77. Santos, L., Birk, S. & Ferreira, M.T. River conservation and restoration in croplands: can we improve the common agricultural policy as an instrument of practice? *Restor. Ecol.* **34**, e70088 (2025).
78. Grill, G. et al. Mapping the world's free-flowing rivers. *Nature.* **569**, 215-221 (2019).
79. Thieme, M. et al. Measures to safeguard and restore river connectivity. *Environ. Rev.* **32**, 366-386 (2024).
80. Kowal, J.L. et al. Over 100 years of longitudinal connectivity changes from the perspective of a migratory fish species. *Ecol. Indic.* **175**, 113436 (2025).
81. Lynch, A.J. et al. Managing for RADical ecosystem change: applying the Resist-Accept-Direct (RAD) framework. *Front. Ecol. Environ.* **19**, 461-469 (2021).

82. Cooke, S.J. et al. Is it a new day for freshwater biodiversity? Reflections on outcomes of the Kunming-Montreal Global Biodiversity Framework. *PLOS Sustainability Transform.* **2**, e0000065 (2023).
83. Hughes, A.C. & Grumbine, R.E. The Kunming-Montreal Global Biodiversity Framework: what it does and does not do, and how to improve it. *Front. Environ. Sci.* **11**, 1281536 (2023).
84. McKay, L. et al. NHDPlus version 2: User Guide (2012).
85. Vogt, J. et al. A pan-European river and catchment database. European Commission. Joint Research Centre, Technical Report EUR 22920 EN. <https://doi.org/10.2788/35907> (2007).
86. Wang, L. et al. A hierarchical spatial framework and database for the National River Fish Habitat Condition Assessment. *Fisheries.* **36**, 436-449 (2011).
87. Abell, R. et al. Freshwater Ecoregions of the World: a new map of biogeographic units for freshwater biodiversity conservation. *BioScience.* **58**, 403-414 (2008).
88. Solheim, A.L. et al. A new broad typology for rivers and lakes in Europe: development and application for large-scale environmental assessments. *Sci. Total Environ.* **697**, 134043 (2019).
89. de Carvalho, D.R. et al. A fish-based multimetric index for Brazilian savanna streams. *Ecol. Indic.* **77**, 386-396 (2017).
90. Wieferich, D.J., Williams, B., Falgout, J.T. & Foks, N.L. xstrm. U.S. Geological Survey software release. <https://doi.org/10.5066/P9P8P7Z0> (2021).
91. Dewitz, J. National Land Cover Database (NLCD) 2019 products (ver. 3.0, February 2024). US Geological Survey data release. <https://doi.org/10.5066/P9KZCM54> (2021).
92. European Environment Agency (EEA). CORINE Land Cover 2018. <https://doi.org/10.2909/960998c1-1870-4e82-8051-6485205ebbac> (2019).
93. UNEP-WCMC & IUCN. Protected Planet: The World Database on Protected Areas (WDPA). <https://www.protectedplanet.net> (2024).
94. Environmental Systems Research Institute (ESRI) ArcGIS Pro, version 3.5.1. Redlands, CA (2025).
95. Wilcoxon, F. Individual comparisons by ranking methods. *Biometrics Bulletin.* **1**, 80-83 (1945).
96. Kruskal, W.H. & Wallis, W.A. Use of ranks in one-criterion variance analysis. *J. Am. Stat. Assoc.* **47**, 583-621 (1952).
97. Côté, I.M., Darling, E.S. & Brown, C.J. Interactions among ecosystem stressors and their importance in conservation. *Proc. R. Soc. B.* **283**, 20152592 (2016).
98. Birk, S. et al. Impacts of multiple stressors on freshwater biota across spatial scales and ecosystems. *Nat. Ecol. Evol.* **4**, 1060-1068 (2020).
99. Carrier-Belleau, C., Pascal, L., Nozais, C. & Archambault, P. Tipping points and multiple drivers in changing aquatic ecosystems: a review of experimental studies. *Limnol. Oceanogr.* **67**, S312-S330 (2022).

## Figures

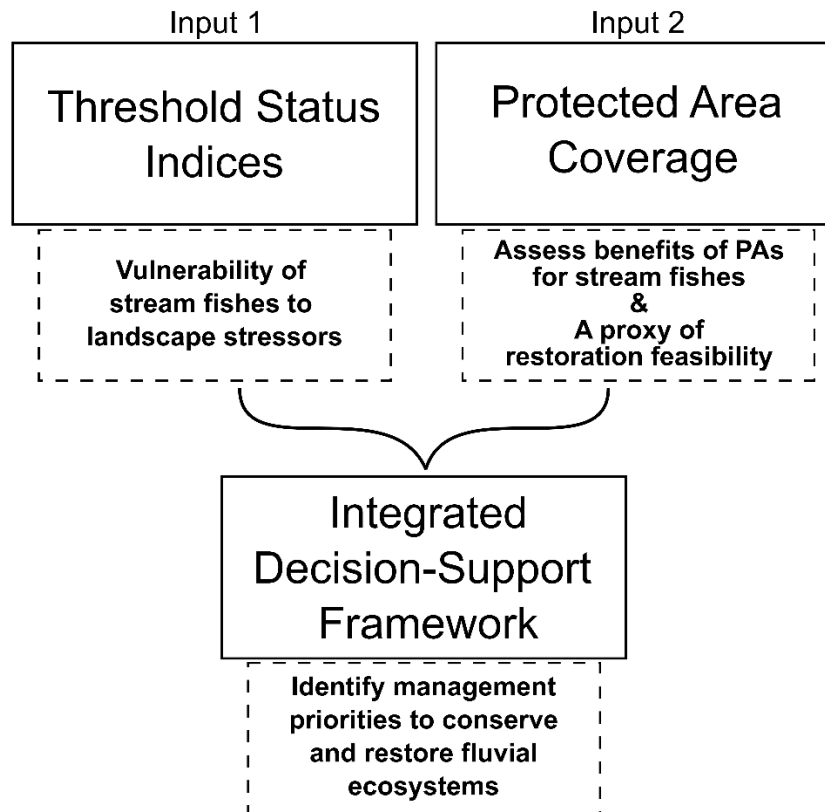


Figure 1. Workflow for integrating land use thresholds and summaries of protected area (PA) coverage (i.e., upstream protection) into a decision-support framework to identify conservation and restoration priorities for stream fishes.

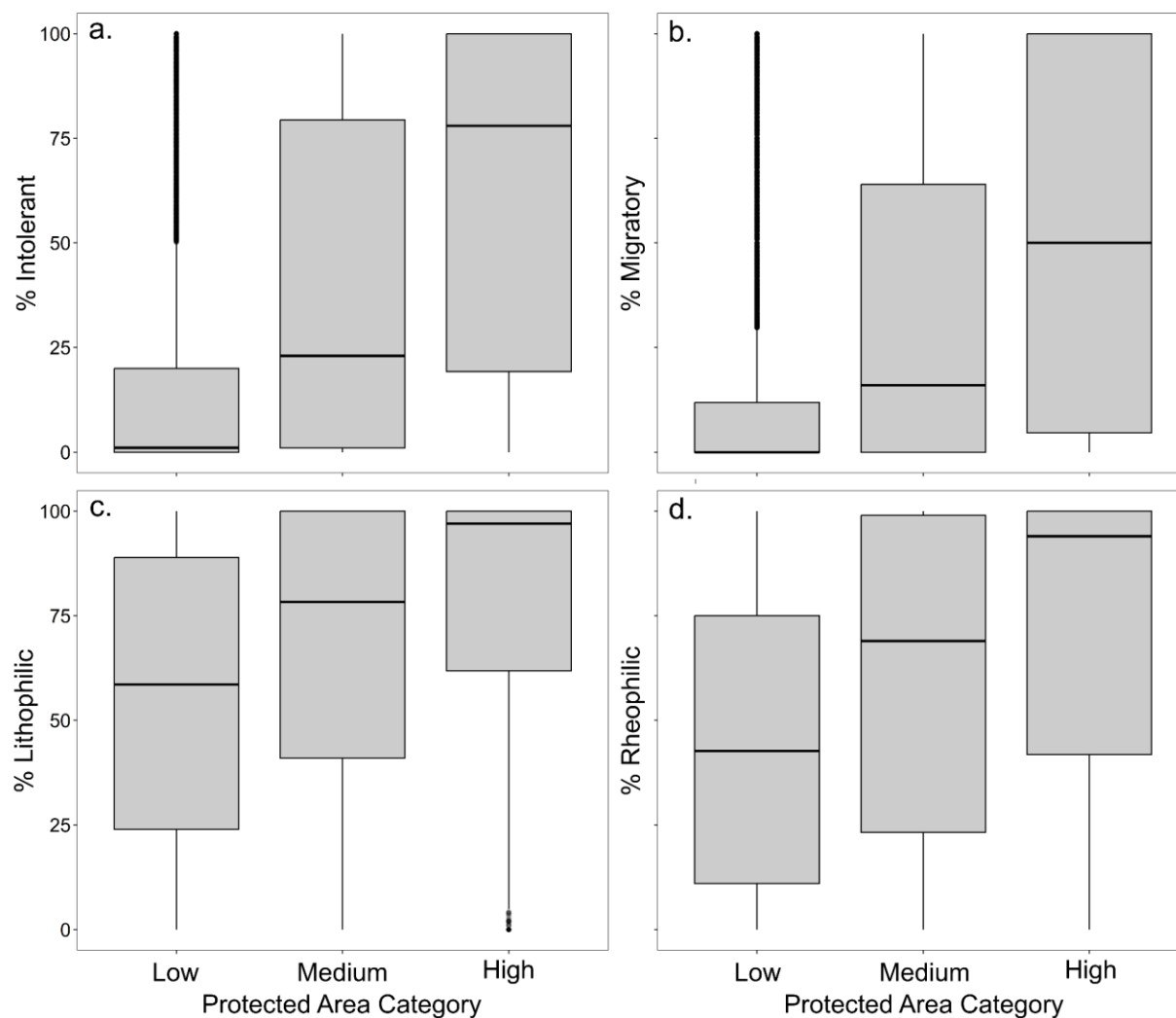


Figure 2. Relationships between protected area categories (*low*, *medium*, or *high* protection) and stream fish metrics in reaches sampled throughout the conterminous United States and Europe. Fish metrics correspond to the relative abundance of (a) intolerant, (b) migratory, (c) lithophilic, and (d) rheophilic fishes.

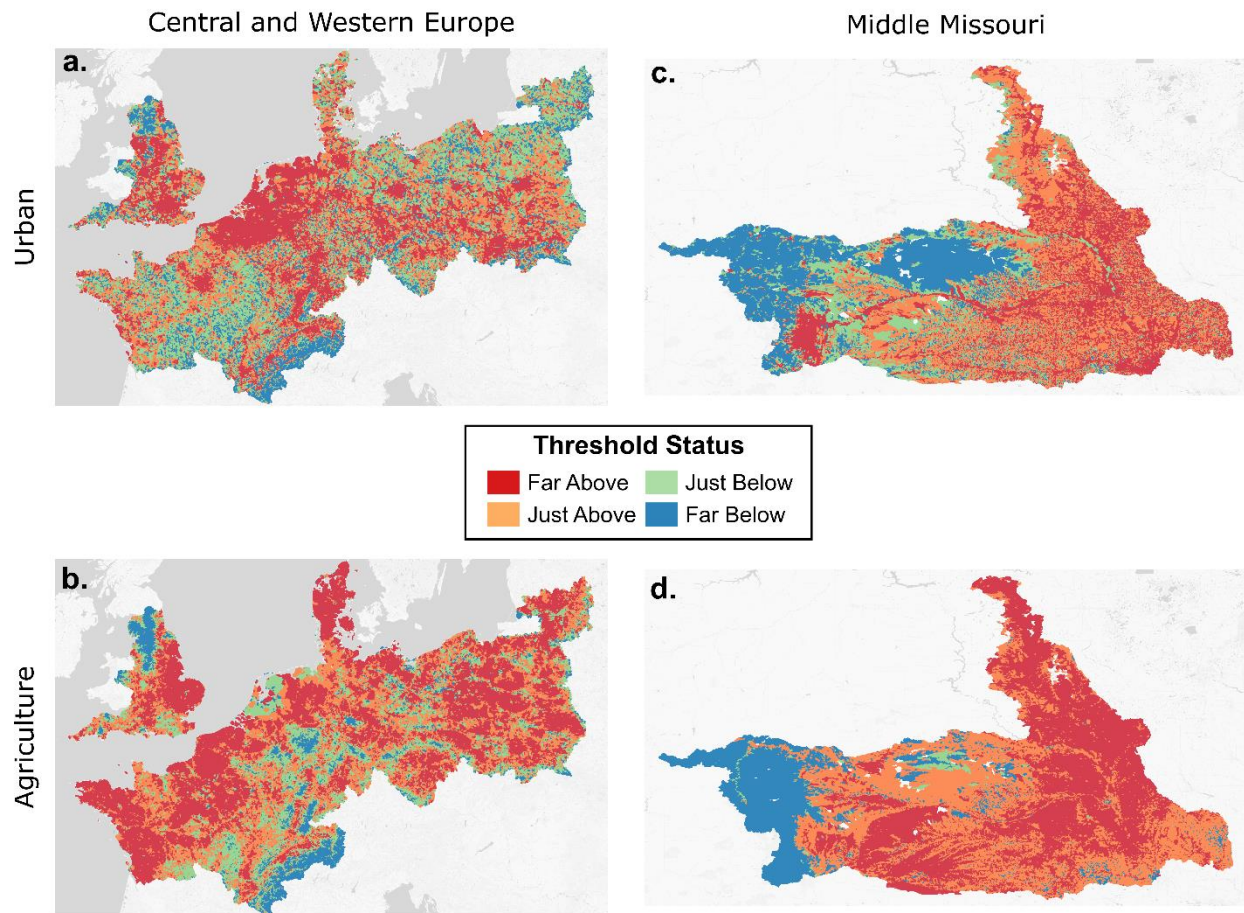


Figure 3. Threshold status classifications for catchments in the Central and Western Europe (a, b) and Middle Missouri (c, d) ecoregions. Classifications were derived by applying quantile breaks to threshold status indices reflecting the percentage of urban (a, c) and agricultural (b, d) land use within network catchments.

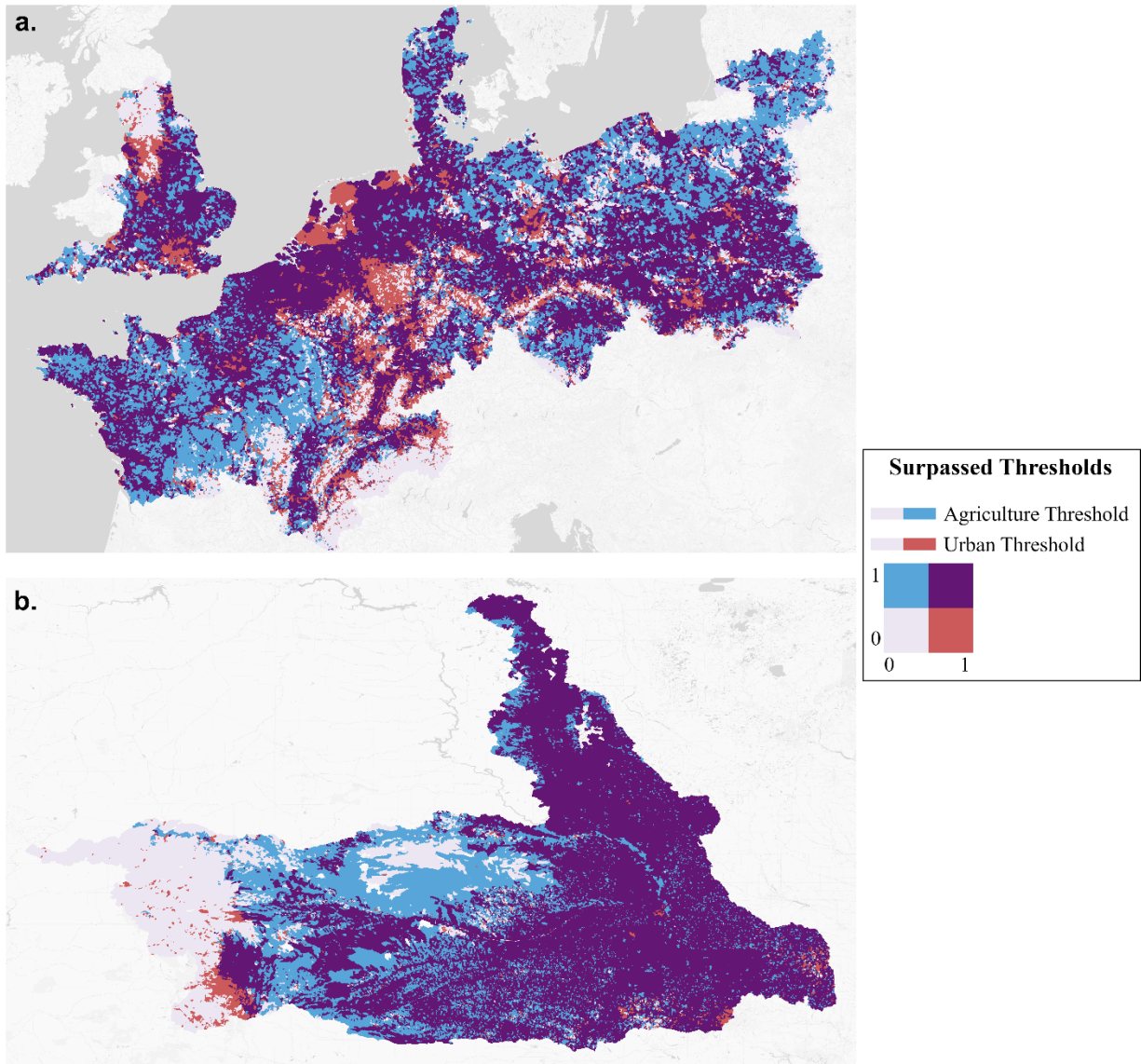


Figure 4. Multiple stressor configurations for catchments in the (a) Central and Western Europe and (b) Middle Missouri ecoregions. Catchments that have not passed an agricultural or urban land use threshold (0) are shown in grey, whereas those that have exceeded (1) both thresholds are shown in purple.

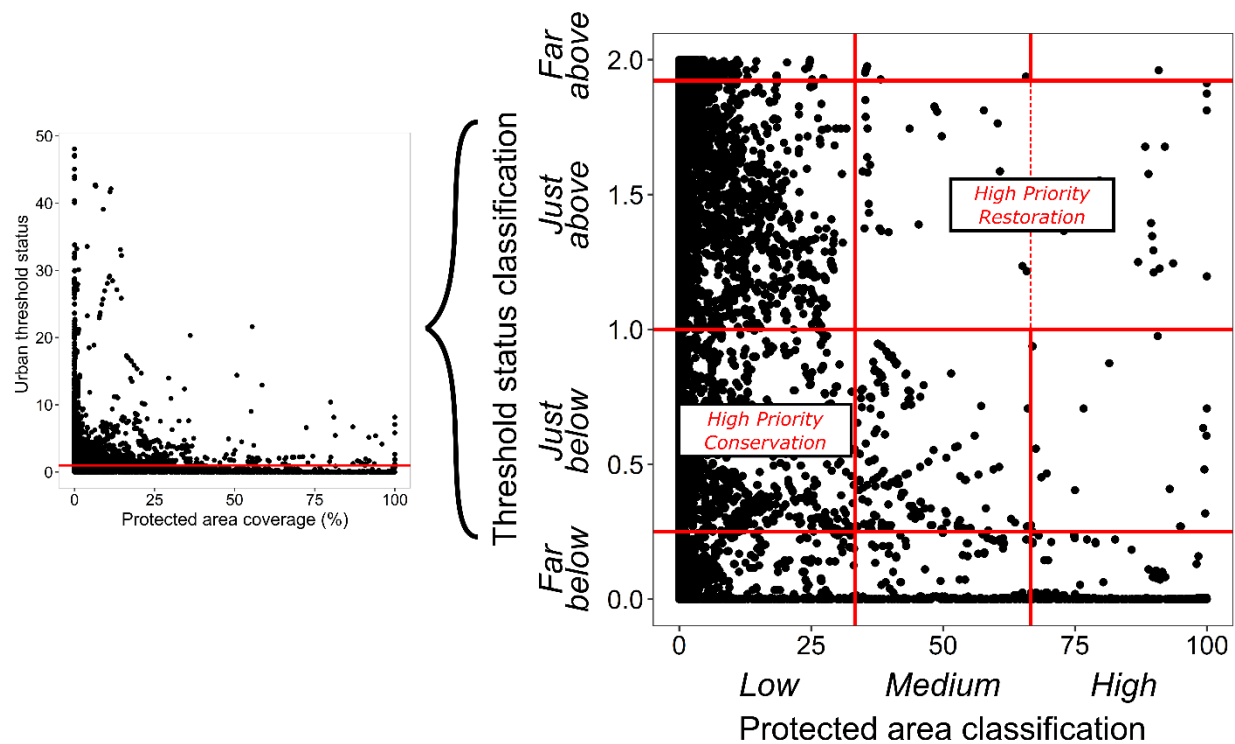


Figure 5. Relationship between protected area coverage and threshold status indices for rivers in the Middle Missouri ecoregion. In the left panel, the red horizontal line that intersects the y-axis at a value of 1 corresponds to the urban land use threshold. Black points located above this line represent catchments that have exceeded the threshold. In the right panel, red horizontal lines differentiate among the four threshold status classifications depicted in Figure 3; red vertical lines separate catchments into the *low*, *medium*, and *high* protection categories depicted in Figure 2. Catchments that are *just below* the threshold and in the *low* protection category are considered high priority for urban conservation because they are relatively close to crossing the threshold and have relatively little protection. Similarly, catchments that are *just above* the threshold and in the *medium* or *high* protection categories are considered high priority for urban restoration, as existing protected areas provide opportunities for implementing restoration actions, reducing landscape pressures, and potentially improving the ecological status of fishes. In this framework, catchments that are far from a threshold in either direction, highly protected and relatively undisturbed, or poorly protected and relatively disturbed are not considered priorities.

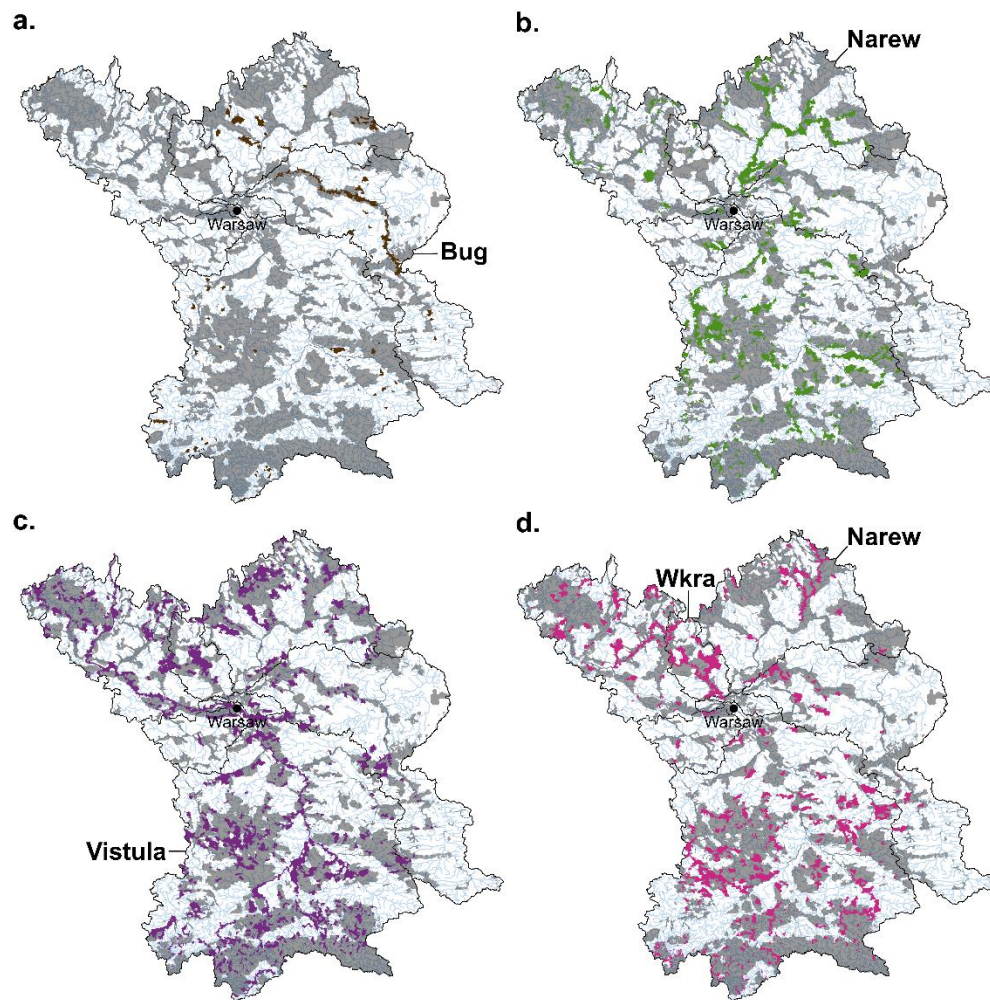


Figure 6. Recommendations for catchments (colored) within subbasins of the Vistula River watershed, Poland (outlined in black), depicted as subsets of Figure S2a. The figure shows locations of priority catchments in relation to protected areas (grey polygons) and stream networks (blue lines). In general, the Bug River has yet to exceed thresholds for agricultural and urban land use but is characterized by relatively low levels of protection. According to the framework presented in Figure 5, this combination of factors makes the Bug River a high priority for proactive agricultural and urban conservation efforts (a; brown). Similarly, contiguous sections of the Narew River (b) are moderately to highly protected but have marginally exceeded both agricultural and urban land use thresholds, making the Narew River a high priority both for agricultural and urban (b; green), and urban (d; pink), restoration efforts. Throughout its course, the Vistula River was identified as a high priority for agricultural restoration (c; purple), whereas the Wkra River was identified as a high priority for urban restoration (d; pink). Together, these examples illustrate how the framework can be applied across scales, from identifying opportunities within individual catchments to drawing broader inferences about subbasins and watersheds.

## Tables

Table 1. A summary of thresholds for creeks (C) and rivers (R) in ecoregion across Europe and the United States (US). Thresholds were sourced from Üblacker et al.<sup>17</sup> and correspond to percentages of agriculture, pasture, and urban land use within network catchments. Ecoregion IDs align with those reported in Figure S1.

ID	Ecoregion	% Agriculture	% Pasture	% Urban
<i>Europe</i>				
1	Cantabric Coast – Languedoc	1.23 (R)		1.05 (R)
2	Central and Western Europe	24.58 (C*)		3.50 (C); 2.25 (R)
3	Dniester – Lower Danube		7.26 (R)	4.68 (C); 5.15 (R)
4	Upper Danube			3.90 (R)
5	Western Iberia	40.06 (C)		1.75 (C); 0.08 (R)
<i>US</i>				
6	Appalachian Piedmont	2.49 (C); 0.58 (R)		9.31 (R)
7	Central Prairie	2.07 (C)		
8	Chesapeake Bay			7.01 (R)
9	Colorado	0.19 (R)	5.05 (C); 15.43 (R)	0.96 (C); 0.61 (R)
10	Columbia Unglaciaded	0.20 (C); 5.97 (R)		10.04 (C)
11	Cumberland	2.83 (R)		
12	Laurentian Great Lakes	0.19 (R)		12.30 (C)
13	Middle Missouri	0.25 (C); 0.10 (R)	5.46 (C)	2.54 (C); 2.08 (R)
14	Northeast US Atlantic Drainages		7.25 (C)	11.51 (C)
15	Ozark Highlands	1.05 (C); 6.67 (R)		
16	Sacramento – San Joaquin	6.19 (R)		
17	Teays – Old Ohio			9.58 (R)
18	Upper Mississippi		1.52 (C)	3.79 (C); 6.22 (R)
19	Upper Missouri			0.88 (R)

\*For illustrative purposes, the threshold value for rivers was assumed to be the same as that for creeks.