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## Inland navigation and land use interact to impact European freshwater biodiversity

Aaron Sexton, Jean-Nicolas Beisel, Cybill Staentzel, Christian Wolter,  
Evelyne Tales, Jérôme Belliard, Anthonie Buijse, Vanesa Martínez Fernández,  
Karl Wantzen, Sonja Jähnig, et al.

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1 **Title:**

2 Inland navigation and land use interact to impact European freshwater biodiversity

3

4 **Author list:**

5 Aaron N. Sexton<sup>1</sup>, Jean-Nicolas Beisel<sup>2</sup>, Cybill Staentzel<sup>2</sup>, Christian Wolter<sup>3</sup>, Evelyne Tales<sup>4</sup>,

6 Jérôme Belliard<sup>4</sup>, Anthonie D.Buijse<sup>5,6</sup>, Vanesa Martínez Fernández<sup>7</sup>, Karl M. Wantzen<sup>8</sup>, Sonja

7 C. Jähnig<sup>9,10</sup>, Carlos Garcia de Leaniz<sup>11</sup>, Astrid Schmidt-Kloiber<sup>12</sup>, Peter Haase<sup>13,14</sup>, Marie Anne

8 Eurie Forio<sup>15</sup>, Gait Archambaud<sup>16</sup>, Jean-François Fruget<sup>17</sup>, Alain Dohet<sup>18</sup>, Vesela Evtimova<sup>19</sup>,

9 Zoltán Csabai<sup>20, 21</sup>, Mathieu Floury<sup>4</sup>, Peter Goethals<sup>15</sup>, Várbiró Gábor<sup>22</sup>, Miguel Cañedo-

10 Argüelles<sup>23</sup>, Aitor Larrañaga<sup>24</sup>, Anthony Maire<sup>25</sup>, Ralf B. Schäfer<sup>13, 26</sup>, James S. Sinclair<sup>13</sup>, Rudy

11 Vannevel<sup>15</sup>, Ellen Welte<sup>27</sup> & Alienor Jeliakov<sup>1, 4</sup>

12

13 **Affiliations:**

14 1. Fondation pour la Recherche sur la Biodiversité (FRB), Centre de Synthèse et d'Analyse  
15 sur la Biodiversité (CESAB), Montpellier France.

16 2. Université de Strasbourg, ENGEES, CNRS, LIVE UMR 7362, F-67000 Strasbourg,  
17 France.

18 3. Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater  
19 Ecology and Inland Fisheries, Müggelseedamm 310, 12587 Berlin, Germany.

20 4. University of Paris-Saclay, INRAE, HYCAR, Antony, France.

21 5. Deltares, Department of Freshwater Ecology and Water Quality, Delft, the Netherlands.

- 22 6. Wageningen University & Research, Aquaculture and Fisheries group, Wageningen, the  
23 Netherlands.
- 24 7. Departamento de Sistemas y Recursos Naturales, E.T.S. Ingeniería de Montes, Forestal y  
25 del Medio Natural, Universidad Politécnica de Madrid.
- 26 8. UNESCO Chair “Fleuves et Patrimoine”, CNRS UMRS CITERES, Tours University,  
27 37000 Tours, and CNRS UMR LIVE, Strasbourg University, France.
- 28 9. Department of Community and Ecosystem Ecology Leibniz Institute of Freshwater  
29 Ecology and Inland Fisheries, Berlin, Germany.
- 30 10. Geography Department Humboldt-Universität zu Berlin, Berlin, Germany.
- 31 11. Centre for Sustainable Aquatic Research (CSAR), Department of Biosciences, Swansea  
32 University, Swansea, UK.
- 33 12. University of Natural Resources and Life Sciences, BOKU Vienna, Institute of  
34 Hydrobiology and Aquatic Ecosystem Management, Gregor Mendel Strasse 33, 1180  
35 Vienna, Austria.
- 36 13. Department of River Ecology and Conservation, Senckenberg Research Institute and  
37 Natural History Museum Frankfurt, Clamecystraße 12, 63571, Gelnhausen, Germany.
- 38 14. Faculty of Biology, University of Duisburg, Essen, Germany.
- 39 15. Department of Animal Sciences and Aquatic Ecology, Ghent University, Coupure Links  
40 653, 9000 Ghent, Belgium.
- 41 16. INRAE, Aix Marseille Univ, RECOVER, Aix-en-Provence, France
- 42 17. ARALEP - Ecologie des Eaux Douces, Villeurbanne 69603 France.
- 43 18. Environmental Research and Innovation (ERIN) Luxembourg Institute of Science and  
44 Technology (LIST), Belvaux, Luxembourg.

- 45 19. Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, 1  
46 Tsar Osvoboditel Blvd., Sofia 1000, Bulgaria.
- 47 20. University of Pécs, Department of Hydrobiology, 6 Ifjúság útja, H7624 Pécs, Hungary.
- 48 21. Balaton Limnological Research Institute, 3 Klebelsberg Kuno, H8237, Tihany, Hungary.
- 49 22. Department of Tisza Research, Institute of Aquatic Ecology, Centre for Ecological  
50 Research, Debrecen, Hungary.
- 51 23. FEHM Lab, Institute of Environmental Assessment and Water Research (IDAEA-CSIC),  
52 Jordi Girona, 18-26, 08034 Barcelona, Spain.
- 53 24. Department of Plant Biology and Ecology, University of the Basque Country, Leioa  
54 48940 Spain.
- 55 25. EDF R&D, LNHE (Laboratoire National d'Hydraulique et Environnement), Chatou,  
56 France.
- 57 26. Institute for Environmental Sciences, RPTU Kaiserslautern-Landau, Fortstrasse 7, 76829  
58 Landau, Germany.
- 59 27. Conservation Ecology Center, Smithsonian's National Zoo and Conservation Biology  
60 Institute, Front Royal, VA, USA.

61 **Contact Information for corresponding author:**

62 Aaron Sexton

63 Fondation sur la Recherche pour la Biodiversité

64 Montpellier, France, 34000

65 e-mail: aaron.sexton@fondationbiodiversite.fr

66 ORCID ID: 0000-0002-8926-3872

67 **Abstract**

68 Inland navigation in Europe is proposed to increase in the coming years, being promoted as a low-  
69 carbon form of transport. However, we currently lack knowledge on how this would impact  
70 biodiversity at large scales and interact with existing stressors. We addressed this knowledge gap  
71 by analyzing fish and macroinvertebrate community time series across large European rivers  
72 comprising 19,592 observations from 4,049 sampling sites spanning the last 32 years. We found  
73 ship traffic to be associated with biodiversity declines, i.e. loss of fish and macroinvertebrate  
74 taxonomic richness, diversity, and trait richness. Ship traffic was also associated with increases in  
75 taxonomic evenness, which, in concert with richness decreases, was attributed to losses in rare  
76 taxa. Ship traffic was especially harmful for benthic taxa and those preferring slow flows. These  
77 effects often depended on local land use and riparian degradation. In fish, negative impacts of  
78 shipping were highest in urban and agricultural landscapes. Regarding navigation infrastructure,  
79 the negative impact of channelization on macroinvertebrates was only evident when riparian  
80 degradation was also high. Our results demonstrate the risk of increasing inland navigation on  
81 freshwater biodiversity. Integrative waterway management accounting for riparian habitats and  
82 landscape characteristics could help to mitigate these impacts.

83 **Main Text**

84 **Introduction**

85 Freshwater ecosystems are among the most diverse in the world, but freshwater biodiversity is  
86 declining at a much faster pace than both terrestrial and marine biodiversity (Reid et al. 2019).  
87 Populations of freshwater vertebrate species have declined globally by over 80% since 1970  
88 (WWF 2018). In Europe and North America, freshwater fish extinction rates are over 100 times  
89 higher than natural extinction rates (Dias et al. 2017). Of European freshwater mussel species,  
90 65% are listed as either Threatened or Near Threatened by the International Union for the  
91 Conservation of Nature (IUCN) Red List of species ([www.iucnredlist.org](http://www.iucnredlist.org)). Efforts are being made  
92 to halt these declines as freshwater ecosystems harbor vital ecological, economic, and cultural  
93 values (Tickner et al. 2020). This requires identifying the relevant stressors on freshwater  
94 biodiversity, and how these stressors interact with each other. Habitat loss, climate change and  
95 land use intensification rank among the most common freshwater stressors, alongside poor water  
96 quality and the introduction of aquatic invasive species (Dudgeon et al. 2006; Reid et al. 2019).

97 Within this context, the prevalence and rise of inland navigation has received little attention in  
98 spite of its potential to affect freshwater biodiversity. Commercial shipping on rivers and lakes has  
99 been practiced for centuries but is proposed to increase by 50% in Europe by 2050 as it is being  
100 touted as carbon-friendly mode of transport (INE 2020). Accordingly, the European Parliament  
101 has adopted the resolution in 2021 towards future-proofing inland waterway transport in Europe  
102 (2021/2015[INI]). Parliament has also given its approval for the revision of the Trans-European  
103 Network for Transport (TEN-T), focusing on ensuring a good navigation status for the core  
104 network, and paved the way for funding managed by the European Climate Infrastructure and  
105 Environment Executive Agency (CINEA). This potential rise in shipping would not only mean

106 more ship traffic, but would also require the modification of navigation infrastructures (e.g.,  
107 heavier embankments, larger locks and ports, additional waterways) that will impact freshwater  
108 ecosystems in ways that are difficult to predict (He et al. 2021; Belletti et al. 2020). Inland  
109 navigation and its infrastructures have largely been investigated as being vectors for the spread of  
110 invasive species, (Leuven et al. 2009; Hanafiah et al. 2013; Nunes et al. 2015) and not nearly as  
111 much for their direct impact on facets of native biodiversity such as richness, evenness and  
112 functional trait responses, as has been done in the case of global change stressors such as climate  
113 change and land use (Dudgeon et al. 2006)..

114 Additionally, with few exceptions (Zajicek et al. 2018; Zajicek and Wolter 2019), most research  
115 on inland navigation has been conducted at local spatial scales, examining the effects of a specific  
116 lock, river or catchment (e.g., Bergman et al. 2022; Xiong et al. 2021; Jackson and Grey 2013;  
117 Huckstorf et al. 2011). These studies have shown that inland navigation constitutes a significant  
118 pressure on freshwater biodiversity. Specifically, these studies have shown ship traffic to decrease  
119 fish richness, abundances, and reproduction, especially that of limnophilic fish (those with  
120 preference to slow flowing waters) (Xiong et al. 2021; Huckstorf et al. 2011; Wolter 2001), and  
121 modifications of river systems to accommodate for inland navigation to reduce fisheries and other  
122 riverine ecosystem services (Zhang et al. 2018). Declines in biodiversity associated with  
123 navigation are often attributed to the destruction of natural habitats, construction of artificial  
124 embankments, aquatic and acoustic pollution, and ship waves that further degrade habitats  
125 (Huckstorf et al. 2011; Wolter 2001).

126 Given that most studies have addressed different navigation-related effects, taxa, and local  
127 contexts, (e.g. focused on YOY-fish (Wolter 2001), or on the Rhine river (Leuven et al. 2009) or  
128 Yangtze river (Xiong et al. 2021), or on one canal (Vergeynst et al. 2021)) drawing generalizations

129 on the overall effect of inland navigation at a large scale is fraught with uncertainty. General  
130 conclusions are further challenged by potential context-dependency of navigation-biodiversity  
131 relationships. For example, the landscape (e.g. urban vs. agricultural areas) and habitat conditions  
132 (channelized rivers, disconnected from floodplains) are both known to be important determinants  
133 of freshwater communities, for example decreased habitat connectedness or increases in intense  
134 land use leading to reductions in diversity, endangered species, and shifts in community  
135 composition (Brink et al. 1996; Décamps 2011; Manfrin et al. 2020). Therefore, analyses of fine-  
136 scale observations across multiple land use contexts and habitat conditions are required to assess  
137 whether the impact of inland navigation is consistent across catchments, and if this impact interacts  
138 with other stressors.

139 To better understand how inland navigation impacts freshwater biodiversity at a continental scale,  
140 and how the impact is moderated by landscape and habitat conditions, we compiled several local  
141 biodiversity datasets across Europe and modelled their relationships with navigation pressures.  
142 Specifically, we tested the relationship between navigation stressors (ship traffic, density of ports  
143 and locks, and degree of river channelization) and the taxonomic and functional diversity, i.e.  
144 taxonomic and functional richness, Simpson's Reciprocal diversity, functional dispersion, and  
145 taxonomic and functional evenness of freshwater fish and macroinvertebrate communities, as well  
146 as the prevalence of invasive taxa. We hypothesized consistently negative effects of ship traffic on  
147 taxonomic and functional richness and diversity. Additionally, in ports, especially where ships  
148 dock closely, invasive species will be most prevalent, as observed in marine and estuarine systems  
149 (Keller et al. 2011). For example, in Canadian marine ports, invasive marine macroinvertebrates  
150 are found in ballast tanks, while Finnish ports commonly document invasive species with high  
151 eutrophic tolerance in ship ballast waters (Briski et al. 2011; Paavola et al. 2008). However, these



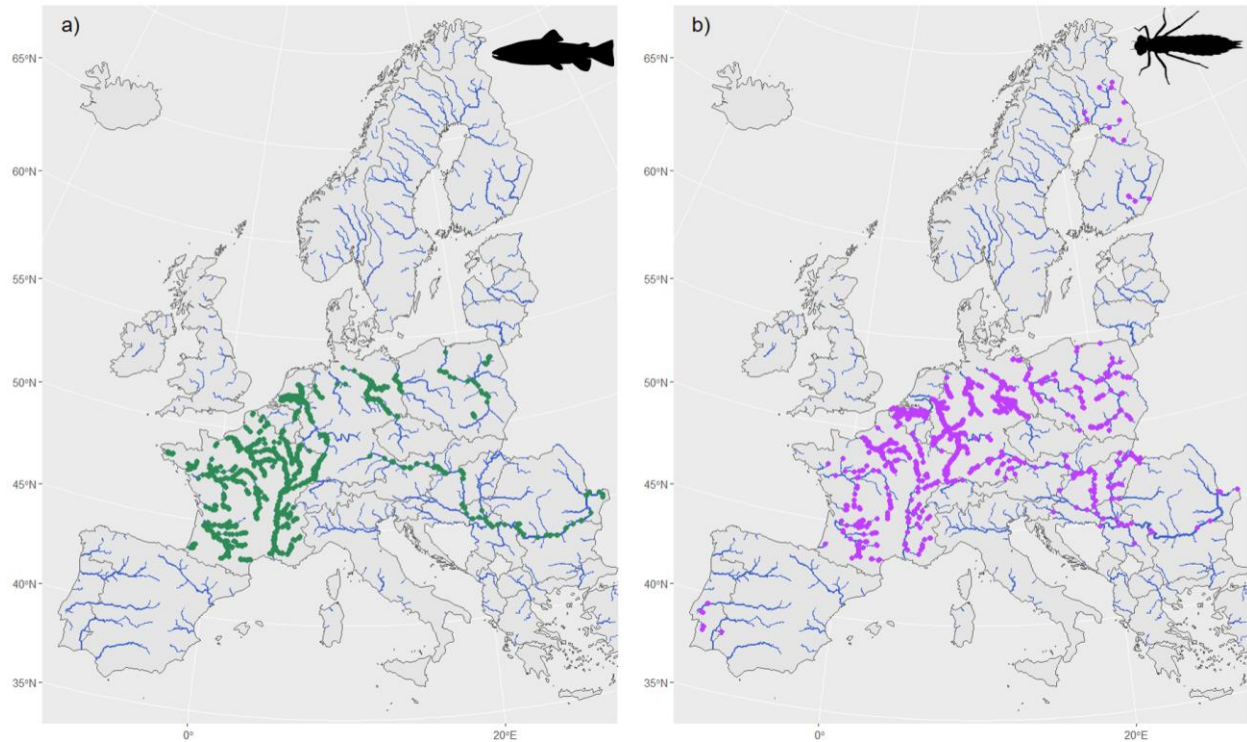
152 studies and previous reviews have focused mainly on marine invasive species and maritime ports,  
153 and similar investigations in freshwater systems are lacking. In addition, we evaluated how land  
154 use and riparian degradation would interact with the effects of navigation. We hypothesized that  
155 navigation's negative impact would be lower in highly degraded landscapes, because of correlated  
156 tolerances of organisms towards landscape-related and ship traffic-related stress. Thus, although  
157 co-occurring stressors might increase the overall level of impact, this impact would be lower than  
158 if the tolerances to the stressors were either un- or negatively correlated (Vinebrook et al. 2004).

159

## 160 **Results**

161 Our biodiversity database consisted of 19,592 samples (13,335 fish and 6,257 macroinvertebrate  
162 communities) from 4,049 sampling sites (2,381 fish [Fig.1a] and 1,668 macroinvertebrates  
163 [Fig.1b]) across Europe from 1990 to 2022. We obtained ship traffic in all large European rivers,  
164 which ranged from no recorded vessel to more than one million vessels per month, and the location  
165 of 1,215 locks and 433 ports used for inland navigation, and we calculated rates of river  
166 channelization at the landscape scale (for further details, see Methods).

167



168

169 **Fig. 1 – Fish and macroinvertebrate communities across Europe.** *Locations of all biodiversity*  
 170 *data used in our analyses (colored dots). Panel a) Fish (n = 2,381). Panel b) Macroinvertebrates (n =*  
 171 *1,668). Large rivers and navigated canals are shown in blue lines.*

172

173 *Navigation Impact*

174 Ship traffic was strongly associated with decreases in taxonomic richness and Simpson's  
 175 Reciprocal diversity, and functional richness of both fish and macroinvertebrates (Fig.2, p-values,  
 176  $R^2$ , model estimates and standard errors for all models are provided in Supplemental Table 1).  
 177 Additionally, for both fish and macroinvertebrates, ship traffic was positively associated with the  
 178 prevalence of invasive species and taxonomic evenness (Fig.2, Supplemental Table 1). For all  
 179 models other than invasive species, functional diversity and evenness, ship traffic was the term in

180 the model with the largest effect size (i.e. the effect causing the greatest change in the response  
 181 metric), indicating strong impacts throughout (Fig. 2).

182

|                            | Taxonomic Richness | Functional Richness | Taxonomic Diversity | Functional Diversity | Taxonomic Evenness | Functional Evenness | Invasive Abundance |
|----------------------------|--------------------|---------------------|---------------------|----------------------|--------------------|---------------------|--------------------|
| Ships                      | -0.125 -0.238      | -0.036 -0.037       | -0.18 -0.396        |                      | 0.025 0.027        |                     | 0.048 0.097        |
| Ports                      | 0.01 0.025         | 0.005 0.009         | 0.06                |                      |                    |                     |                    |
| Locks                      | 0.025              |                     | 0.043               | 0.006 -0.011 -0.012  |                    |                     | -0.051             |
| Channelization             | 0.032              | 0.005               |                     | 0.014                |                    | 0.007               | -0.145 0.158       |
| Riparian Degradation       |                    | -0.007              |                     | 0.01                 | -0.008             |                     | -0.05              |
| Agriculture                | -0.011             | -0.004              | 0.047               | -0.007               |                    | 0.011               | 0.06 0.098         |
| Urban                      | -0.05 -0.047       | -0.016 -0.01        | -0.125              | -0.009               | 0.021              | 0.01                | 0.054 0.144        |
| Ships:Riparian             | 0.025 0.018        | -0.004              |                     | -0.004               | -0.012 -0.012      | -0.006              | -0.103             |
| Ships:Agriculture          | -0.067             | -0.014              | -0.123 -0.167       | 0.004 -0.014         | 0.013 -0.015       | 0.007               |                    |
| Ships:Urban                | -0.047 0.067       | -0.015 0.007        | -0.051              |                      | 0.013 -0.013       | 0.005               | 0.078              |
| Channelization:Riparian    | -0.036             |                     | -0.046 -0.19        |                      |                    |                     | 0.185              |
| Channelization:Agriculture | -0.01              |                     |                     |                      | 0.007 -0.007       | 0.02                | -0.144 0.163       |
| Channelization:Urban       | 0.011              | 0.01                | 0.065               | 0.004 -0.015         |                    |                     |                    |

183

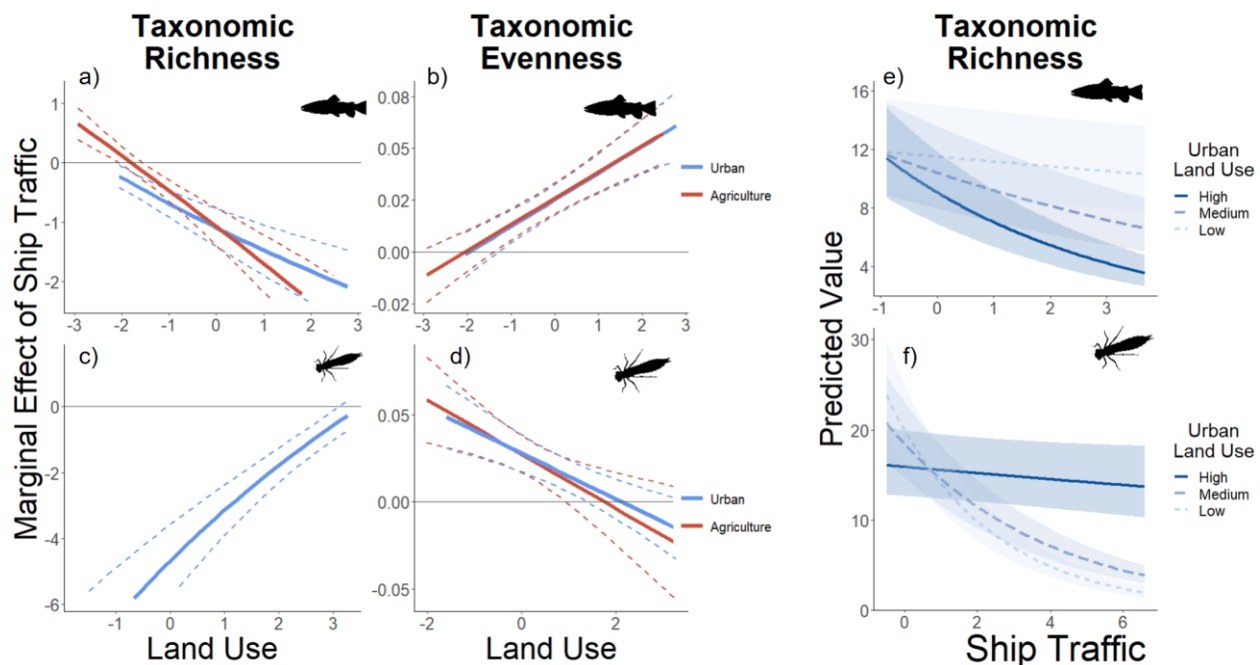
184 **Fig. 2 – Inland navigation and other stressor effects on freshwater fish and**  
 185 **macroinvertebrate biodiversity.** Model estimates from the GLMMs. Each column represents a  
 186 separate model, with the response metric and taxonomic group as the column header, with predictors of  
 187 the model as rows. Red cells indicate a negative effect and blue cells represent a positive effect, with color  
 188 intensity representing the magnitude of effect. Non-significant effects are blank cells (*p* values and standard  
 189 errors reported in Supplemental Table 1). Ships refers to ship traffic, Ports and Locks represent the density  
 190 of each, Channelization represents the portion of the river stretch that has been channelized, Agriculture  
 191 and Urban represent the respective portion of land use at each site, and Riparian Degradation represents  
 192 the portion of the riparian habitat that has been lost from its potential extent. All predictors were  
 193 standardized to an average value of 0 and SD of  $\pm 1$ , allowing one to compare predictors.

194

195 The negative effects of ship traffic on fish communities had important context dependencies  
 196 regarding urban and agricultural land use. Ship traffic's negative association with fish richness and  
 197 Simpson's Reciprocal diversity and the positive association with evenness was magnified in areas  
 198 of high agricultural and urban land use with relatively lower effects in areas of low agricultural  
 199 and urban cover (Fig.3a, b and e, Supplemental Table 1). Additionally, the positive association  
 200 between ship traffic and invasive species was magnified in highly urbanized areas (Fig.2, Extended  
 201 Data Fig. 1, Supplemental Table 1).

202

203



204

205 **Fig. 3 – Context-dependent effect of ship traffic.** *Plots a-d show the marginal effect of ship*  
 206 *traffic from the GLMMs on taxonomic richness and evenness across varying degrees of land use.*  
 207 *The x-axis represents the standardized (average of  $0 \pm 1$  SD) intensity of land use (Urban – blue*  
 208 *line or Agriculture – red line), and the corresponding y-axis value the marginal effect of ship*

209 *traffic on the biodiversity metric. The marginal effect is the additional effect for a given absolute*  
210 *effect of the other variables, here in particular land use. Negative values indicate ship traffic*  
211 *decreases the metric (e.g. decrease in macroinvertebrate taxonomic richness at low levels of*  
212 *urbanization), zero on the y-axis represents a null effect, and positive values show an increase.*  
213 *The dotted lines represent the standard error of the marginal value. Plots e and f visualize these*  
214 *changes in the marginal effect of ship traffic at specific levels of urbanization (high, medium and*  
215 *low levels of urban land use – medium representing the average level of urbanization, and high*  
216 *and low representing the max and min values) by showing the predicted values of taxonomic*  
217 *richness as ship traffic increases in across different land use scenarios. The top and bottom graphs*  
218 *show the effects on fish and macroinvertebrate communities, respectively.*

219

220 For macroinvertebrates, urban land use modulated the effect of ship traffic (Fig.3c, d and f). Ship  
221 traffic's negative effect on richness was strongly negative in areas of low urban land use, but  
222 minimal in areas of high urban land use (Fig.3c and f, Supplemental Table 1). Shipping's positive  
223 effect on taxonomic evenness was only observed in areas of low to moderate urban cover, and was  
224 also only negative in areas of high riparian degradation (Fig.3d, Supplemental Table 1).

225 The effects of channelization were also context-dependent. For macroinvertebrates, taxonomic and  
226 functional diversity, and functional richness decreased in areas of high channelization, but only  
227 when riparian degradation was also high (Fig.2, Extended Data Fig.2, Supplemental Table 1).  
228 Additionally, when riparian degradation was high, channelization was associated with significant  
229 increases in invasive species prevalence (Fig.2, Extended Data Fig.2, Supplemental Table 1). In  
230 areas of low to moderate riparian degradation, channelization had no effect on the studied metrics.

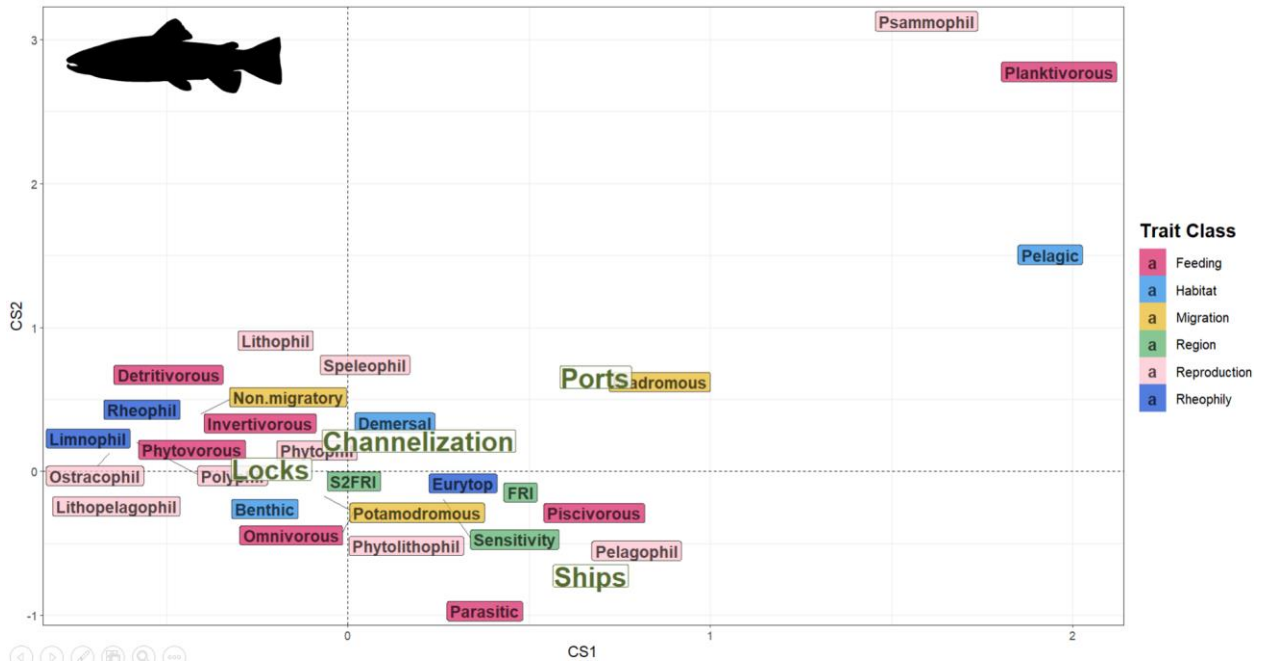
231 The density of locks was weakly associated with increases in fish taxonomic richness and  
232 functional diversity, and a decrease in invasive prevalence, and with slight decreases in  
233 macroinvertebrates functional diversity (Fig.2, Supplemental Table 1). Port density was associated  
234 with slight increases in taxonomic and functional richness for both fish and macroinvertebrates  
235 (Fig.2, Supplemental Table 1).

#### 236 *Traits involved in navigation-biodiversity relationships*

237 To better identify the guilds of species responding to navigation, we analyzed the relationships  
238 between traits and navigation pressures via an RLQ-Fourth Corner analysis, which quantifies the  
239 covariance between species traits and environmental variables, mediated by the species  
240 abundances at sites (Dray et al. 2014). We found strong significant relations between the  
241 environmental variables and species traits in both fish and macroinvertebrates.

242 In fish, we found increased ship traffic positively associated with traits such as pelagic  
243 environment, planktivorous feeding, and diadromous migration, generalist flow preferences  
244 (eurytopic) and negatively with stagnant water preference (limnophilic) (Fig.4, Supplemental  
245 Table 2). Limnophilic species were more likely to occur in areas around locks. Additionally, we  
246 found the presence of ports positively associated with planktivorous and detritivorous feeding  
247 traits, and with psammophilic and lithophilic reproduction (gravel spawning) (Fig.4, Supplemental  
248 Table 2).

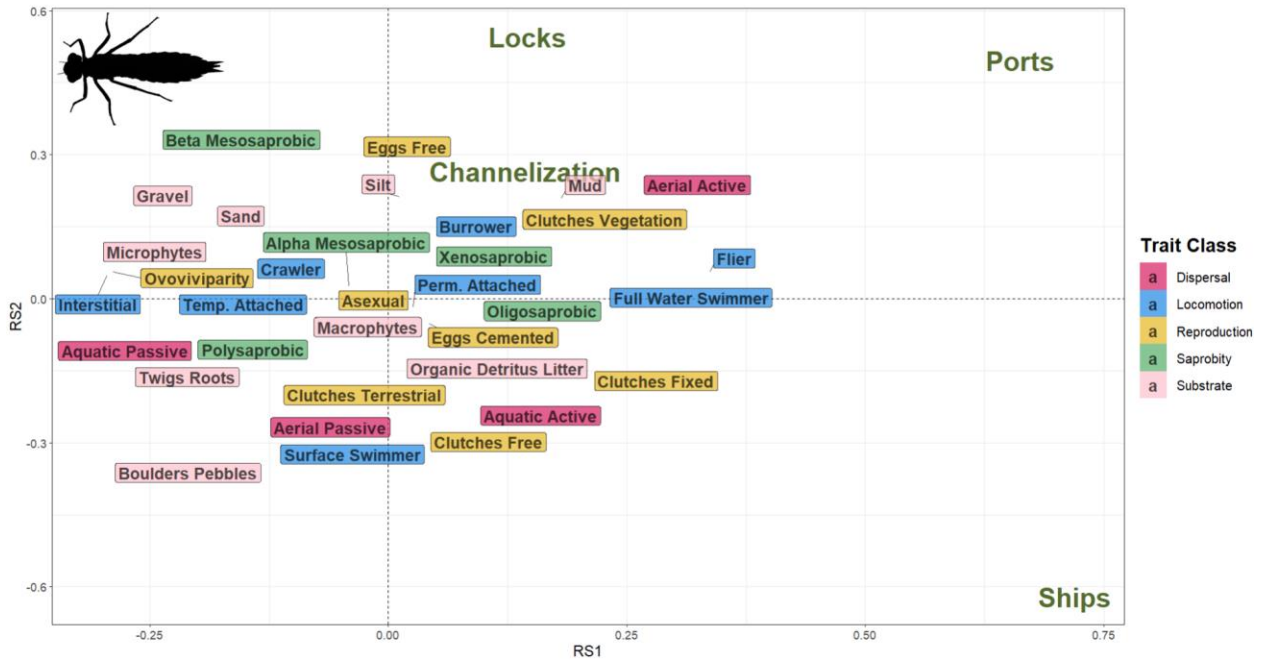
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251

252 **Fig. 4 – Fish trait responses to navigation.** Ordinations from an RLQ-Fourth corner analysis  
 253 that represents the relationships between fish traits (colored text) and navigation pressures (bold  
 254 green boxes). Both ordination axes (traits and navigation pressures) are significantly linked ( $p =$   
 255  $0.002$ ). Both traits and navigation pressures with highly positive x-axis values (e.g. Pelagic habitat  
 256 and Ships) are strongly associated, and the same for y-axis relationships.

257



259

260 **Fig. 5 – Macroinvertebrate trait responses to navigation.** Ordinations from an RLQ-Fourth  
 261 corner analysis which represents the relationships between macroinvertebrate traits (colored text)  
 262 and navigation pressures (bold green boxes). The axes of the two ordinations (traits and  
 263 navigation pressures) are significantly linked ( $p = 0.002$ ). Traits with highly positive y-axis values  
 264 (e.g. Burrower locomotion) are strongly associated with navigation pressures with highly positive  
 265 y-axis values (e.g. Locks & Ports), and the same for x-axis relationships.

266

267 For macroinvertebrates, we found increased ship traffic negatively associated with  
 268 interstitial/crawling species and passive aquatic dispersers, and positively with fliers, aquatic  
 269 active dispersers and locomotive swimmers. Increases in navigation infrastructures such as ports  
 270 and locks were associated with increases in active aerial dispersal, free eggs, and those inhabiting  
 271 gravel, sandy, and silty substrates. (Fig.5, Supplemental Table 2).



272

273 To identify how land use and riparian degradation mediated navigations effect on traits, we ran  
274 additional RLQ-Fourth Corner analyses using subsets of sites with the highest degree of  
275 anthropogenic land cover and riparian degradation (top 25% of sites with each land use class). In  
276 fish, degradation did not change the effect of navigation on traits (Extended Data Fig.2,  
277 Supplemental Table 3). In macroinvertebrates, trait responses also did not change at agricultural  
278 sites, but in highly urbanized sites the association of ship traffic with burrowing species and those  
279 laying clutches in terrestrial sites turned from positive (full dataset) to strongly negative (Extended  
280 Data Fig.2, Supplemental Table 3).

281

## 282 **Discussion**

283 Our results suggest that inland navigation has strongly negative impacts on freshwater biodiversity  
284 at the European scale. In particular, we found negative responses (decreases in richness and  
285 diversity) of both fish and macroinvertebrates to ship traffic, at both taxonomical and  
286 trait/functional levels, and increases in the prevalence of invasive species. This confirms previous  
287 studies at local scales reporting negative impacts of navigation on freshwater fish and  
288 macroinvertebrate communities. This study goes beyond existing work in showing that inland  
289 navigation affects the whole 35,000 km European inland waterway network and threatens  
290 biodiversity of multiple taxa, building on previous work that focused on only sections of a  
291 particular river at a time.

292 *Ship traffic*

293 The effects on biodiversity are reflected in trait shifts in both fish and macroinvertebrate  
294 communities. Ship traffic had the strongest negative effects on benthic and limnophilic taxa and  
295 on fish species that suspend their eggs in the flow. Ship traffic was positively associated with  
296 pelagic and eurytopic taxa and those fixing their eggs in clutches to substrates. Together these trait  
297 shifts reflect selection pressures by vessel-induced waves and return currents against specialist and  
298 towards generalist life history traits (Zajicek and Wolter 2019; Gabel et al. 2017). Ship waves  
299 erode banks and re-suspend sediment both degrading littoral habitats for fish and  
300 macroinvertebrates (Gabel et al. 2011). Additionally, commonly used heavy embankments to  
301 prevent bank erosion considerably impact littoral habitats in all navigated rivers, and have been  
302 shown to reduce fish diversity (Wolter, 2001). Reducing ship speed and creating shallow habitats  
303 that are protected from ship waves could mitigate some of these wave-induced negative impacts.  
304 Additionally, many waterways require dredging of the river bottom to maintain navigable fairway  
305 depth (Grygoruk et al. 2015), which has disproportionately negative impacts on benthic habitats.  
306 These known effects of ship traffic and fairway maintenance can explain negative association with  
307 benthic species.

308 The community shifts described above are confirmed by the positive association between ship  
309 traffic and taxonomic evenness in both fish and macroinvertebrates. Decreasing species richness,  
310 the loss of rare taxa and small populations, resulted in ship traffic induced increases in evenness.  
311 Correspondingly, in a follow-up analysis we found strong correlations between taxonomic  
312 evenness and the abundance and occurrence of rare taxa for both fish and macroinvertebrates,  
313 (Supplemental File 2, Extended Data Fig.3) supporting the hypothesis that ship traffic drives losses  
314 in populations of rare species. Shipping favors the most tolerant, generalist and  
315 abundant/ubiquitous taxa and eliminates rare species, resulting in a more even community. For

316 example, eurytopic fish tolerating a wide variety of flow rates were positively associated with ship  
317 traffic, while negatively so with flow specialists (both limnophilic and rheophilic taxa). This is a  
318 concern as it may allow invasive goby fish species, such as *Proterorhinus semilunaris*, or  
319 *Neogobius fluviatilis* that are generalists in their flow preferences, to proliferate. Additionally, this  
320 might have consequences at the ecosystem level given the role that specialist species play in  
321 ecological function and stability (Hooper et al. 2005). For example, Cao et al. (2018) documented  
322 significant losses of benthic macroinvertebrate species, especially among sensitive taxa, as a result  
323 of habitat degradation in streams leading to losses in ecosystem functionality, especially nutrient  
324 cycling.

#### 325 *Interaction with land use*

326 Degraded landscapes magnified negative impacts of ship traffic on fish communities, with higher  
327 decreases in richness and diversity in urban and agricultural areas. These interactions demonstrate  
328 that land use can modify the effects of shipping and create environments where only few taxa will  
329 persist. For example, in agricultural systems, in areas with little to no riparian buffer, the dual  
330 stressors lead to fish and macroinvertebrate communities dominated by pollution tolerant taxa  
331 (Effert-Fanta et al. 2019). Research at large scales has shown that multiple stressors like pollution,  
332 hydromorphological modifications, land use, and water use can synergistically interact to create  
333 stronger effects in combination on freshwater ecosystem services (Elmhagen et al 2015; Wen et  
334 al. 2017). Several freshwater fish species living in large rivers might tolerate some level of  
335 degradation, agricultural or urban pollution and habitat modifications, but still decline or disappear  
336 when another stressor such as ship traffic is added.

337 For macroinvertebrates, the impact of ship traffic more closely followed our original hypothesis  
338 that navigation's impact would be lessened in degraded areas – especially in urban areas. The

339 impact of ship traffic on species richness was minimal in highly urbanized areas as depicted in  
340 Figure 3c (i.e. marginal effect of ship traffic close to zero when urban cover is high). However,  
341 the effects of ship traffic on species richness were strongly negative in areas with moderate to low  
342 levels of urbanization. This suggests that the taxa exhibited a positive co-tolerance to urbanization  
343 and ship traffic, where the same sensitive taxa are independently extirpated by each stressor. For  
344 example, a weak swimming species that is sensitive to low dissolved oxygen levels is extirpated  
345 by both stressors related to urban land use and navigation, e.g. in an urban environment, either by  
346 urban runoff or vessel-induced wake wash. Several studies have documented what is described as  
347 the “urban stream syndrome” whereby urban freshwater ecosystems have similar hydrology,  
348 ecology and pollution (Booth et al. 2004; Halstead et al. 2014, Wantzen et al. 2019). These urban  
349 streams are often characterized by increases in pH and heavy metals as well as temperature and  
350 suspended solids, which is typically accompanied by decreases in dissolved oxygen (Winter and  
351 Duthie 2013; Martins et al. 2017). This combination has been shown to produce negative effects  
352 on macroinvertebrate communities (Gal et al. 2019). Similarly, ship traffic has been reported to  
353 increase suspended sediment, release heavy metals and other toxins (Fetters et al. 2016; Prygiel et  
354 al. 2016; Floehr et al. 2013). Urban waterways are particularly confined, homogeneous and  
355 simplified, which might have resulted in little negative impact of ship traffic observed, as their  
356 aquatic communities are already depauperated and composed of taxa tolerant to stressors resulting  
357 from ship traffic.

358 The contrasting result that urban land use magnified the impact of ship traffic on fish, but lowered  
359 it on macroinvertebrates as discussed above might be explained by the particular simplified habitat  
360 structure of urban waterways. Steep bank slopes, hard embankments and the lack of shelter  
361 structures particularly expose fish to vessel-induced physical forces, like return currents and wake

362 wash, thereby magnifying the negative effect of ship traffic (Wolter 2008). Moreover, fish may be  
363 more tolerant than macroinvertebrates with respect to water quality, which means that their  
364 tolerances are less correlated than for macroinvertebrates. Correspondingly, a recent study from  
365 China found that urban pollutants were a primary driver of macroinvertebrate communities, while  
366 urban fish communities were driven by dispersal limitations instead (Xu et al. 2023). Indeed, a  
367 recent study found that landscape connectivity was more important than urbanization for fish  
368 community characteristics in Hungary (Czeglédi et al. (2020). Future research on how dual  
369 stressors such as urbanization and navigation can interact to influence freshwater biodiversity  
370 across taxa and functional groups is certainly warranted.

371 The effects of channelization on macroinvertebrate communities were also dependent on local and  
372 landscape contexts, such that in areas of high riparian degradation and agricultural cover the  
373 negative effect was aggravated. We found that channelization was associated with decreased  
374 richness and diversity and increased invasive species only when riparian degradation was also high  
375 (Extended Data Fig.1). These interactive effects indicate potential benefits of protecting and  
376 restoring riparian habitat to mitigate the impacts of river channelization. For example, in highly  
377 channelized river stretches, the macroinvertebrate community could be partially protected by  
378 restoring the riparian habitat. Riparian vegetation provides habitat structure, shade, food resources,  
379 terrestrial habitat for aquatic insects and can control algal biomass, (Li et al. 1994; Corline et al.  
380 2023). In addition, riparian vegetation reduces bank erosion, thereby preserving habitat suitability  
381 for macroinvertebrates, in turn lessening navigation/channelization impacts. However, mitigation  
382 measures are also required to further improve water quality, which is often insufficient, particularly  
383 in many larger European rivers (Lemm et al. 2021).

384 *Navigation infrastructure*

385 Fish richness tended to be higher in river segments with a higher number of locks. This is likely  
386 an impoundment effect creating more lentic habitats in the river, which then allow limnophilic  
387 species to proliferate – a finding that is corroborated by our trait analysis showing these species to  
388 be more frequent in areas of high lock densities. This, in concert with the finding of taxonomic  
389 evenness decreases in areas of high lock densities indicates a shift in community composition near  
390 locks, and not that locks are increasing fish biodiversity. However, locks may also increase  
391 connectivity for certain species in highly fragmented rivers, because lock operation at least  
392 occasionally allows fish passage (Lin et al. 2013; Vergeynst et al. 2021). This is relevant for  
393 management, as oftentimes locks and dams are side-by-side, meaning that fish of different  
394 swimming abilities may be able to navigate through such blockages via different avenues – some  
395 via fish ladders and others via locks. Further research is needed to elucidate how locks should be  
396 best operated to reduce river fragmentation.

397 Richness values of both fish and macroinvertebrates were slightly higher in areas near ports.  
398 However, while statistically significant, the effect sizes were small – an order of magnitude smaller  
399 than the negative effect sizes of shipping intensity. Similar to locks, this finding probably results  
400 from shifts in community composition due to novel habitats created in ports as well as potential  
401 ballast water release therein. Ports alter the physical environment of lowland rivers by increasing  
402 depth, providing pools of standing water, and accumulating sediments (Samsami et al. 2022; Keller  
403 et al. 2011). These accumulating sediments may explain why macroinvertebrates living in sandy  
404 and gravel substrates, and fish reproducing in sandy substrates (psammophils) were positively  
405 associated with ports in our trait analysis. Ballast water mixing and release occurring in port areas  
406 is known to release species (Costello et al. 2022) and to spread invasive species especially by  
407 seagoing vessels (Wan et al. 2021; Molnar et al. 2008). However, here we did not find increases

408 of invasive species in port areas. This may indicate that either the ballast water transport of non-  
409 native species by inland navigation is less relevant than in marine shipping, or that the inland  
410 waterways are already widely colonized by non-native species, so that the ports did not pop up as  
411 hotspots. Further research would be warranted to scrutinize the links between ballast water and  
412 freshwater invasive and exotic species.

### 413 *Conclusion*

414 Europe's large rivers host a wealth of Europe's freshwater biodiversity, and are vital socio-  
415 economic systems. Here we show that inland navigation can have negative impacts on this  
416 biodiversity – mainly via frequent ship traffic. This impact on biodiversity is highlighted by ship  
417 traffic being associated with declines in taxonomic and functional richness and diversity, declines  
418 in rare taxa, and increases in invasive species prevalence. These findings are important in regard  
419 to both recent biodiversity declines and composition shifts in freshwater communities and global  
420 and European initiatives and strategies to hold biodiversity loss. Importantly though, we show that  
421 this impact is context-dependent – shifting in relation to land use and riparian degradation.  
422 Riparian habitats can serve as a potential mitigation tool, especially reducing the negative impacts  
423 of river channelization. This may become important if inland navigation, and the river management  
424 required to support it, would increase in the coming years. Overall, our results inform global and  
425 European initiatives and strategies to halt and reverse biodiversity loss.

426 In addition to biodiversity declines, we observed shifts in community compositions and functional  
427 traits. These findings add to those of recent research, for example showing shifts towards pollution-  
428 tolerant taxa in urban and agricultural streams, and climate warming shifting the average body  
429 sizes of freshwater fish communities (Rumschlag et al. 2023; Arranz et al. 2023). We add to this  
430 by showing ship traffic to be especially negative for benthic taxa, locks to shift communities

431 towards slow-flow taxa, and for port areas to benefit macroinvertebrates living in sandy bottom  
432 rivers. Mitigating the negative impacts on benthic taxa could be achieved via simple measures  
433 such as reducing vessel speed to reduce hydraulic forces on shoreline habitats, as well as larger  
434 efforts such as the re-establishment of shallow habitats protected from ship waves. These findings,  
435 in concert with previous work, are important for restoration plans. As a halt in freshwater  
436 biodiversity recoveries in recent years has been found (Haase et al. 2023), it is important to  
437 consider all stressors, including potentially emerging stressors such as navigation that are currently  
438 neglected, to fully restore communities. Finally, it is important to focus restoration/mitigation  
439 efforts not only on small streams, but also large rivers and balance the use of these rivers for socio-  
440 economic goods with the role they play in hosting biodiversity.

441

## 442 **Methods**

### 443 *Fish & Macroinvertebrate Biodiversity*

444 We combined data sets of fish (n = 9 datasets) and macroinvertebrate (n = 11) communities in  
445 large European rivers and canals from the NAVIDIV consortium (Inland navigation infrastructures  
446 and biodiversity: impacts and opportunities for waterwayscape management -  
447 [https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-](https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-cesab/navidiv/)  
448 [cesab/navidiv/](https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-cesab/navidiv/)), complemented by macroinvertebrate time series from Haase et al. (2023) relevant  
449 for our study. We defined a “large river” as having a Strahler order of five or greater based on the  
450 HydroSHEDS database (Lehner et al. 2008). This ensured we focused only on navigated and  
451 navigable waterways and omitted smaller rivers from the analysis because of the absence of  
452 stressors associated with navigation. However, large rivers without navigation were considered as



453 potential reference sites. Moreover, given that larger rivers typically are more degraded than  
454 smaller rivers, the inclusion of smaller rivers may have led to an overestimation of the navigation  
455 effect because of the collinearity of river size with navigation (Nilsson et al. 2005). We used data  
456 from 1992 to 2021, as the opening of the Main-Danube canal in 1992 marked the beginning of the  
457 spread of many freshwater invasive species (Leuven et al. 2009). During this time period the total  
458 amount of goods transported by commercial navigation, a proxy for ship traffic has remained  
459 approximately constant (see next section). One ecological community dataset consisted only of  
460 presences-absence data. These data were only used to calculate the taxonomic richness model; all  
461 other included datasets featured abundance data for multiple taxa at specific locations with spatial  
462 coordinates, years and sampling effort. While our data are pan-European, the bulk of the  
463 biodiversity data are in France and Central Europe, which aligns with the main shipping routes in  
464 Europe. To ensure that this geographic bias did not influence our results, we re-ran our GLMMs  
465 without observations from France. This removed 4,845 fish observations, and 1,263  
466 macroinvertebrate observations. The models resulted in the exact same interpretations (i.e. no  
467 major changes in significance of model terms and interactions or  $R^2$  values). These model outputs  
468 are provided in Supplemental Table 5.

469 From each dataset we calculated the taxonomic richness (as the number of taxa, most commonly  
470 at the genus level for macroinvertebrates and species level for fish), Simpson's Reciprocal  
471 Diversity Index, using the 'diversity' function in the "vegan" R package (Oksanen et al. 2022),  
472 and Simpson's evenness based on relative abundances (diversity divided by species number) of  
473 each sampling occasion. We chose to use Simpson's Reciprocal Diversity Index, a Hill number,  
474 instead of other common metrics (e.g. Shannon) because our functional metrics, calculated in the  
475 "mFD" package, are also Hill number metrics.

476 Additionally, we calculated the relative abundance of invasive taxa. Taxa were identified as  
477 invasive on a dataset-by-dataset basis, and relied on expert opinion from either the data  
478 collector/provider, or an expert in the region on fish or macroinvertebrates. Biodiversity metrics  
479 (richness, diversity, evenness, invasive prevalence) were calculated for each sampling effort of  
480 each database, then combined into one file for running models, such that each row was an  
481 individual sample with diversity metrics, the database identifier, sampling effort identifier, and the  
482 navigation and landscape predictors used for analyses.

483 To explore the effects of navigation on the ecological traits of these communities, we compiled  
484 ecological trait information on the traits that were expected to play a role in the response of  
485 communities. Fish traits of feeding guild, habitat, migration, and reproduction were obtained from  
486 the [freshwaterecology.com](http://freshwaterecology.com) trait database (Schmidt-Kloiber, & Hering 2015). Flow preference  
487 traits followed the FAME consortium (Development, Evaluation and Implementation of a  
488 Standardized Fish-based Assessment Method for the Ecological Status of European Rivers, EU  
489 FP5), sensitivity was obtained from van Treeck et al. (2020), Fish Region Index (FRI) and its  
490 variation ( $S^2$ FRI) were based on Wolter et al. (2021). Macroinvertebrate traits were obtained from  
491 the Tachet database (Tachet et al. 2010). Linking these species traits to our community data, we  
492 calculated the metrics functional richness, diversity (specifically Functional Dispersion of the  
493 functional space of communities [Villéger et al. 2008]), and evenness, using the “mFD” package  
494 in R (Magneville et al. 2021). The traits we use here are *ecological* traits, and not strictly *functional*  
495 traits according to (Violle et al. 2007). Therefore when we refer to functional diversity, evenness  
496 and richness, we use these terms in the broad colloquial sense to represent the diversity of organism  
497 attributes that interact with the abiotic and biotic environments (as defined in Magneville et al.  
498 2021).

499 *Navigation & Infrastructures*

500 Ship traffic, i.e. vessel counts were obtained from Marine Traffic (<https://www.marinetraffic.com/>)  
501 and compiled as the number of ships passing through 30 km stretches of river per-month over the  
502 course of 2019. This grain was chosen to provide the optimal grain for our European-extent study  
503 – generating 4,174 river lengths across Europe, allowing us to compare river stretches at the  
504 continental extent. A finer grain would not have been relevant due to the linear flow of ship traffic,  
505 but a larger grain would not have allowed us to compare traffic changes between cities/ports, and  
506 our choice of grain generally aligns with the Water Framework Directives River Basin  
507 Management Plans. A comparison of the ship traffic in 2019 to independent data of ship traffic  
508 logs from locks throughout Europe including the rivers Danube, Rhine, Elbe, Spree, Oder, and  
509 others provided by Zajicek et al. (2018) for 1992 to 2015 showed that 2019 was similar to this  
510 period (Supplemental Figure 1). Channelization was also measured at the grain of 30 km stretches.  
511 Within the same river stretches used for shipping we calculated the total length of channelized  
512 river obtained via the Open Street Map database (<https://openstreetmap.org/>). Channelization  
513 represents a metric of riverine modifications that have been made for navigation, though reasons  
514 for channelization may go beyond navigation and also include manipulation of floodplain for  
515 agriculture. Almost all European navigated rivers have been channelized to some extent (Petts et  
516 al. 1989). The location of all inland ports and locks was obtained via personal communication from  
517 the United Nations Economic Commission for Europe (UNECE), and is sourced from the UNECE  
518 Inventory of Main Standards and Parameters of the Waterway Network. We counted the number  
519 of ports and locks within a 5 km buffer (consistent with the grain of land use) around each  
520 biodiversity sampling site.

521 *Local and landscape land use*

522 To identify how the surrounding landscape and habitat characteristics moderate navigation's  
523 impact, we collected data on the land use and riparian degradation surrounding each biodiversity  
524 sampling site. We considered the two major land use types that are associated with the degradation  
525 of surface waters in Europe: agriculture and urbanization. We clipped land use (obtained from  
526 CORINE Land Cover 2018, [100 m positional accuracy] [https://land.copernicus.eu/pan-](https://land.copernicus.eu/pan-european/corine-land-cover/clc2018)  
527 [european/corine-land-cover/clc2018](https://land.copernicus.eu/pan-european/corine-land-cover/clc2018)) to 5 km-radius circular buffers around sampling locations.  
528 While additional research is needed to elucidate the spatial grain at which land use influences  
529 aquatic taxa, studies have shown that a grain between 1-5 km is appropriate (Wang et al. 2001;  
530 Bergerot et al. 2013). We found strong correlations between land use at 1 km and 5 km across our  
531 sites (Supplemental Figure 2). Within these buffers, we obtained the surface sizes of surrounding  
532 urban and agricultural land uses for each site. To prevent collinearity issues between the two land  
533 use variables (significant Pearson's correlation test between urban and agricultural land use), we  
534 conducted a Principal Component Analysis (PCA) on these values as the PCA creates two  
535 uncorrelated variables. We then used the site scores from each Principle Component (PC) that  
536 were strongly associated with each land use class. This was done for the macroinvertebrate sites,  
537 and then separately for the fish sites, such that one PCA was run on each set of sites. In  
538 macroinvertebrate sites, the first PC (PC1) had a high rotation score for urban land use, and PC2  
539 had a high rotation score for agricultural land use. It was reversed for fish sites, such that PC1 site  
540 scores were used to represent agricultural land use, and PC2 represented urban land use. Code for  
541 this PCA and the resulting outputs (rotation scores, standard deviation, and proportional and  
542 cumulative variance) are provided in Supplemental Table 4 and in the repository for this paper  
543 linked in the data availability section.

544 To obtain finer-grain information on habitat structure, we characterized riparian degradation at the  
545 grain of 1 km using the Green Arteries database from CORINE (Weissteiner et al. 2016). Within  
546 a 1 km radius buffer around our biodiversity sampling sites, we clipped the “Potential Riparian  
547 Extent” (PRZ) as modeled based on hydrologic and geomorphologic characteristics, and the  
548 “Actual Riparian Extent” (ARZ) from satellite images. Our metric of Riparian degradation around  
549 each site was then calculated as the inverse proportion of ARZ to PRZ:  $[ 1 - (ARZ/PRZ) ]$ .

550 To control for large-scale abiotic influences and differences from one region of Europe to the next,  
551 we included data on the size of river and subcatchment for each sampling site. River size (Strahler  
552 order) and subcatchment size were both obtained from the HydroSHEDS database. We used  
553 Pfafstetter level six of subcatchment size (average of size of 7,972.7 m<sup>2</sup>) because this maximized  
554 the prediction (code provided in Supplemental File 1).

### 555 *Models*

556 To assess the relationships between navigation and taxonomic and functional diversity metrics, we  
557 ran Generalized Linear Mixed Models (GLMMs) with the function ‘glmer’ of the “lme4” R  
558 package (Bates et al. 2015). For the taxonomic richness models, a Poisson distribution was used  
559 and for all others a Gaussian distribution was used. The model structure was:

560 Biodiversity Response ~ Ship Traffic + Ports + Locks + Channelization + Riparian Degradation +  
561 Agriculture + Urban + Ship:Riparian + Ship:Agriculture + Ship:Urban + Channelization:Riparian  
562 + Channelization:Agriculture + Channelization:Urban + Subcatchment Size + Strahler order +  
563 (1|Study/Year).

564 Here, Ship Traffic was the average number of ships per month in the river stretch of the collection  
565 site and Channelization was proportion of the river that had been channelized in the river stretch

566 of the site. Ports and Locks were the number of ports and locks within 5 km from each site, Riparian  
567 Degradation was the proportion of the riparian forest that had been lost within a 1 km buffer, and  
568 Agriculture and Urban were the site scores relating to each land use class from the PCA.  
569 Subcatchment size was the size of the Pfafstetter level six of each site, and Strahler order is the  
570 respective order of the river of a site. The random effect of (1|Study/Year) represents a nested  
571 design wherein Study represents the data source, and Year represents the year that the sample was  
572 collected.

573 We used this model to test the effect of navigation and associated infrastructures, and their  
574 interactions with local and landscape stressors while controlling for hydrotopographic factors that  
575 differ between river basins and size (Strahler order, subcatchment size). Additionally, the inclusion  
576 of the random effect (Study/Year) allowed us to remove potential influences of different data  
577 sources and of temporal trends, which may, for example, be due to climatic changes.

578 For macroinvertebrates, we found an effect of year on taxonomic richness – an increase in richness  
579 from 2000-2010, followed by a decrease from 2010-2020, whereas fish exhibited no trend (via a  
580 Generalized Additive Model [GAM] see Supplemental Figure 3 for both macroinvertebrates and  
581 fish). To control for this non-linear pattern in diversity across years, we included a second order  
582 polynomial term for year to the macroinvertebrate models of: + (poly(yr\_scaled, 2). Plot's showing  
583 the year effect on macroinvertebrates and fish are visualized in Supplemental Fig. 3. Finally, for  
584 the invasive species abundance model for both fish and macroinvertebrates, we included an  
585 “offset” term of total community abundance (log transformed) to control for large samples.

586 Collinearity between our fixed effects was checked via their Variable Inflation Factors (VIF)  
587 scores and all were below two, indicating the model was acceptable (e.g. Graham 2003;  
588 Supplemental Table 1). All predictor terms were standardized to zero mean and standard deviation

589 of +/- 1. Scatterplots of pairwise comparisons of predictor values are provided in Supplemental  
590 Fig.4. We identified the marginal effects of shipping (a partial derivative from the GLMM  
591 equation) at various levels of landscape degradation (Fig. 3a-d), which was obtained using the  
592 ‘margins’ and ‘cplot’ functions in the “margins” R package. Fig. 3e-f were produced using the  
593 ‘interact\_plot’ function in the “interactions” R package, which allowed us to plot regressions lines  
594 at specific levels of our moderator variable (urban land use) to explore interactions. (Leeper 2021;  
595 Long 2019). Figures were produced using the “ggplot” and “ggpubr” R packages (Wickham 2016;  
596 Kassambara 2020). Silhouettes of fish and macroinvertebrates were obtained from the “rphylopic”  
597 R package, and belong to Marie Russell (2020-12-29) License:  
598 <https://creativecommons.org/licenses/by/3.0/> and Guillaume Dera (2022-12-01) License:  
599 <https://creativecommons.org/publicdomain/zero/1.0/>.

#### 600 *Trait Analysis*

601 To understand the guilds of species responding to navigation, we analyzed the relationships  
602 between functional traits and navigation pressures via an RLQ-Fourth Corner analysis, which  
603 quantifies the covariance between traits and environmental variables, mediated by the species  
604 abundances (Dray et al. 2014). This multivariate method analyzes the links between species traits  
605 and environmental variables via an ordination approach. Specifically, we combined the  
606 environmental variables (ship traffic, count of ports and locks, and rate of channelization) at sites  
607 (creating a matrix R), the species abundances at these sites (matrix L) and the species traits (matrix  
608 Q) to create a “fourth corner” (matrix M) that is an environmental-trait relationship matrix. Each  
609 of these matrices is turned into ordinations to allow for direct comparability and computational  
610 analysis (via a correspondence analysis to the species table and a principal component analysis to  
611 the environmental and trait tables), and then the analysis finds linear combinations of

612 environmental variables and linear combinations of traits that maximize their squared cross-  
613 covariance. A permutation test (n = 999 permutations) is then conducted to test global significance  
614 of the traits-environment relationships (Supplemental Table 2). As this is an ordination approach,  
615 this generates suites of traits that commonly co-occur and identifies how they relate to  
616 environmental ordination axes. This analysis was conducted using the “ade4” R package (Dray et  
617 al. 2007), applying the function ‘rlq’ to join the three matrices and the ‘fourthcorner.rlq’, function  
618 was used to run the permutation analysis following Dray et al. (2014) (Supplemental Table 2).  
619 The same suite of traits used to calculate functional richness, diversity and evenness were used in  
620 this RLQ-Fourth Corner analysis for both fish and macroinvertebrates.

621

## 622 **Data availability**

623 All data and R code used in this study are available in an open-source repository  
624 ([https://github.com/aaronsexton/Sextonetel\\_Navigation\\_Biodiversity\\_Supplementals](https://github.com/aaronsexton/Sextonetel_Navigation_Biodiversity_Supplementals)).

625

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639

#### 640 **Author Contributions Statement**

641 A.N.S, A.J. and J.N.B. conceived of the study. C.S., C.W., E.T., J.B., A.D.B, V.M.F., K.M.W.,  
642 S.C.J., C.G.L., A.S.K. contributed to initial ideas. A.N.S. and A.J. designed and conducted  
643 analyses. P.H., M.A.E.F, G.A., J.F.F., A.D., V.E., Z.C., M.F., P.G., V.G., M.CA., A.L. A.M.,  
644 R.B.S., J.S.S., R.V., E.W., C.W., E.T., and J.B. provided biodiversity data, and all authors provided  
645 significant input on manuscript writing.

646

#### 647 **Competing Interest Statement**

648 The authors report no competing interests.

649

#### 650 **Figure Captions**

651

652

#### 653 **References**

654 Arranz, I., Grenouillet, G. & Cucherousset, J. (2023) Human pressures modulate climate-  
655 warming-induced changes in size spectra of stream fish communities. *Nat Ecol Evol* 7,  
656 1072–1078.

657 Belletti, B., de Leaniz, C. G., Jones, J., Bizzi, S., Borger, L., Segura, G., Castelletti, A., van de  
658 Bund, W., Aarestrup, K., Barry, J., Belka, K., Berkhuisen, A., Birnie-Gauvin, K.,  
659 Bussettini, M., Carolli, M., Consuegra, S., Dopico, E., Feierfeil, T., Fernandez, S., Garrido,  
660 P. F., Garcia-Vazquez, E., Garrido, S., Giannico, G., Gough, P., Jepsen, N., Jones, P. E.,  
661 Kemp, P., Kerr, J., King, J., Lapinska, M., Lazaro, G., Lucas, M. C., Marcello, L., Martin,  
662 P., McGinnity, P., O'Hanley, J., del Amo, R. O., Parasiewicz, P., Pusch, M., Rincon, G.,  
663 Rodriguez, C., Royte, J., Schneider, C. T., Tummers, J. S., Vallesi, S., Vowles, A.,  
664 Verspoor, E., Wanningen, H., Wantzen, K. M., Wildman, L. and Zalewski, M. (2020)  
665 'More than one million barriers fragment Europe's rivers', *Nature*, 588(7838), pp. 436-+.

666 Bergman, J. N., Beaudoin, C., Mistry, I., Turcotte, A., Vis, C., Minelga, V., Neigel, K., Lin, H.  
667 Y., Bennett, J. R., Young, N., Rennie, C., Trottier, L. L., Abrams, A. E. I., Beaupre, P.,  
668 Glassman, D., Blouin-Demers, G., Garant, D., Donaldson, L., Vermaire, J. C., Smol, J. P.  
669 and Cooke, S. J. (2022) Historical, contemporary, and future perspectives on a coupled  
670 social-ecological system in a changing world: Canada's historic Rideau Canal.  
671 *Environmental Reviews*, 30(1), pp. 72-87.

672 Bergerot, B., Hugueny, B. and Belliard, J. (2013) 'When Local Extinction and Colonization of  
673 River Fishes Can Be Predicted by Regional Occupancy: the Role of Spatial Scales', *Plos*  
674 *One*, 8(12).

675 Booth, D. B., Karr, J. R., Schauman, S., Konrad, C. P., Morley, S. A., Larson, M. G. and Burges,  
676 S. J. (2004) 'Reviving urban streams: Land use, hydrology, biology, and human behavior',  
677 Journal of the American Water Resources Association, 40(5), pp. 1351-1364.

678 Brink F.W.B., Velde G., Buijse A.D., Klink A.G. (1996) Biodiversity in the Lower Rhine and  
679 Meuse river-floodplains: Its significance for ecological river management. Netherlands  
680 Journal of Aquatic Ecology, 30: 129–149.

681 Cao, X., L. Chai, D. Jiang, J. Wang, Y. Liu, and Y. Huang. (2018). Loss of biodiversity alters  
682 ecosystem function in freshwater streams: potential evidence from benthic  
683 macroinvertebrates. Ecosphere 9(10).

684 Corline, N. J., Vasquez-Housley, P., Yokel, E., Gilmore, C., Stapleton, B. and Lusardi, R. A.  
685 (2023) 'When humans work like beavers: riparian restoration enhances invertebrate gamma  
686 diversity and habitat heterogeneity', Restoration Ecology, 31(1).

687 Costello, K. E., Lynch, S. A., McAllen, R., O'Riordan, R. M. and Culloty, S. C. (2022) Assessing  
688 the potential for invasive species introductions and secondary spread using vessel  
689 movements in maritime ports, Marine Pollution Bulletin, 177.

690 Czeglédi, I., Kern, B., Toth, R., Seress, G. and Eros, T. (2020) Impacts of Urbanization on  
691 Stream Fish Assemblages: The Role of the Species Pool and the Local Environment,  
692 Frontiers in Ecology and Evolution, 8.

693 Décamps H. (2011) River networks as biodiversity hotlines. Comptes Rendus Biologies. 334: pp.  
694 420–434.

695 Dias, M. S., Tedesco, P. A., Huguény, B., Jezequel, C., Beauchard, O., Brosse, S. and Oberdorff,  
696 T. (2017) Anthropogenic stressors and riverine fish extinctions, Ecological Indicators, 79,  
697 pp. 37-46.

698 Dray S, Dufour A, Chessel D (2007). "The ade4 Package - II: Two-Table and K-Table  
699 Methods." *\_R News\_*, \*7\*(2), 47-52. URL: <https://cran.r-project.org/doc/Rnews/>  
700 Dray, S., Legendre, P. (2008) Testing the Species Traits–Environment Relationships: The  
701 Fourth-Corner Problem Revisited. *Ecology* 89, 3400–3412.

702 Dray, S., Choler, P., Doledec, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S. and ter Braak, C. J.  
703 F. (2014) 'Combining the fourth-corner and the RLQ methods for assessing trait responses  
704 to environmental variation', *Ecology*, 95(1), pp. 14-21.

705 Dudgeon, D., Arthington, A. H., Gessner, M. O., Kawabata, Z. I., Knowler, D. J., Leveque, C.,  
706 Naiman, R. J., Prieur-Richard, A. H., Soto, D., Stiassny, M. L. J. and Sullivan, C. A.  
707 (2006) 'Freshwater biodiversity: importance, threats, status and conservation challenges',  
708 *Biological Reviews*, 81(2), pp. 163-182.

709 Effert-Fanta, E.L., Fischer, R.U. & Wahl, D.H. (2019) Effects of riparian forest buffers and  
710 agricultural land use on macroinvertebrate and fish community structure. *Hydrobiologia*  
711 841, pp.45–64.

712 Elmhagen, B., Destouni, G., Angerbjorn, A., Borgstrom, S., Boyd, E., Cousins, S. A. O., Dalen,  
713 L., Ehrlen, J., Ermold, M., Hamback, P. A., Hedlund, J., Hylander, K., Jaramillo, F.,  
714 Lagerholm, V. K., Lyon, S. W., Moor, H., Nykvist, B., Pasanen-Mortensen, M., Plue, J.,  
715 Prieto, C., van der Velde, Y. and Lindborg, R. (2015) 'Interacting effects of change in  
716 climate, human population, land use, and water use on biodiversity and ecosystem  
717 services', *Ecology and Society*, 20(1).

718 Fetters, K. J., Costello, D. M., Hammerschmidt, C. R. and Burton, G. A. (2016) 'Toxicological  
719 Effects Of Short-Term Resuspension Of Metal-Contaminated Freshwater And Marine  
720 Sediments', *Environmental Toxicology and Chemistry*, 35(3), pp. 676-686.

721 Floehr, T., Xiao, H. X., Scholz-Starke, B., Wu, L. L., Hou, J. L., Yin, D. Q., Zhang, X. W., Ji,  
722 R., Yuan, X. Z., Ottermanns, R., Ross-Nickoll, M., Schaffer, A. and Hollert, H. (2013)  
723 'Solution by dilution?-A review on the pollution status of the Yangtze River',  
724 Environmental Science and Pollution Research, 20(10), pp. 6934-6971.

725 Friberg, N., Buijse, T., Carter, C., Hering, D., Spears, B.M., Verdonschot, P., Moe, T.F. (2017)  
726 Effective restoration of aquatic ecosystems: scaling the barriers. WIREs Water, 4, e1190.

727 Gabel, F., Lorenz, S. and Stoll, S. (2017) 'Effects of ship-induced waves on aquatic ecosystems',  
728 Science of the Total Environment, 601, pp. 926-939.

729 Gabel, F., Stoll, S., Fischer, P., Pusch, M. T. and Garcia, X. F. (2011) 'Waves affect predator-  
730 prey interactions between fish and benthic invertebrates', Oecologia, 165(1), pp. 101-109.

731 Gal, B., Szivak, I., Heino, J. and Schmera, D. (2019) 'The effect of urbanization on freshwater  
732 macroinvertebrates - Knowledge gaps and future research directions', Ecological  
733 Indicators, 104, pp. 357-364.

734 Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. Ecology  
735 84, pp.2809–2815.

736 Grygoruk, M., Frak, M. and Chmielewski, A. (2015) Agricultural Rivers at Risk: Dredging  
737 Results in a Loss of Macroinvertebrates. Preliminary Observations from the Narew  
738 Catchment, Poland. Water, 7(8), pp. 4511-4522.

739 Haase, P., D.E. Bowler, N.J. Baker, N. Bonada, S. Domisch, J. Garcia Marquez, J. Heino, D.  
740 Hering, S. Jähnig, A. Schmidt-Kloiber, R. Stubbington, F. Altermatt, M. Álvarez-Cabria,  
741 G. Amatulli, D. Angeler, G. Archambaud-Suard, I. Arrate Jorrín, T. Aspin, I. Azpiroz, I.  
742 Bañares, J. Barquín Ortiz, C. Bodin, L. Bonacina, R. Bottarin, M. Cañedo-Argüelles, Z.  
743 Csabai, T. Datry, E. de Eyto, A. Dohet, G. Dörflinger, E. Drohan, K.A. Eikland, J.

744 England, T. Eriksen, V. Evtimova, M.J. Feio, M. Ferreol, M. Floury, M. Forcellini, M.A.  
745 Forio, R. Fornaroli, N. Friberg, J.-F. Fruget, G. Georgieva, P. Goethals, M. Graça, W.  
746 Graf, A. House, K.-L. Huttunen, T. Jensen, R. Johnson, J. Jones, J. Kiesel, L. Kuglerová,  
747 A. Larrañaga, P. Leitner, L. L'Hoste, M. H. Lizée, A. Lorenz, A. Maire, J.A. Manzanos  
748 Arnaiz, B. McKie, A. Millán, D. Monteith, T. Muotka, J. Murphy, D. Ozolins, R. Paavola,  
749 P. Paril, F. Peñas, F. Pilotto, M. Polášek, J.J. Rasmussen, M. Rubio, D. Sánchez-  
750 Fernández, L. Sandin, R. Schaefer, A. Scotti, L. Shen, A. Skuja, S. Stoll, M. Straka, H.  
751 Timm, V. Tyufekchieva, I. Tziortzis, Y. Uzunov, G. van der Lee, R. Vannevel, E.  
752 Varadinova, G. Várбірó, G. Velle, P. Verdonschot, R. Verdonschot, Y. Vidi-nova, P.  
753 Wiberg-Larsen, E.A.R. Welti (2023) The recovery of European freshwater biodiversi-ty  
754 has come to a halt. *Nature* 620(7974). DOI: 10.1038/s41586-023-06400-1

755 Halstead, J. A., Kliman, S., Berheide, C. W., Chaucer, A. and Cock-Esteb, A. (2014) 'Urban  
756 stream syndrome in a small, lightly developed watershed: a statistical analysis of water  
757 chemistry parameters, land use patterns, and natural sources', *Environmental Monitoring  
758 and Assessment*, 186(6), pp. 3391-3414.

759 Hanafiah, M. M., Leuven, R., Sommerwerk, N., Tockner, K. and Huijbregts, M. A. J. (2013)  
760 Including the Introduction of Exotic Species in Life Cycle Impact Assessment: The Case of  
761 Inland Shipping. *Environmental Science & Technology*, 47(24), pp. 13934-13940.

762 He, F. Z., Thieme, M., Zarfl, C., Grill, G., Lehner, B., Hogan, Z., Tockner, K. and Jahnig, S. C.  
763 (2021) 'Impacts of loss of free-flowing rivers on global freshwater megafauna', *Biological  
764 Conservation*, 263.

765 Hooper, D. U., Chapin, F. S., Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H.,  
766 Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A. J., Vandermeer,

767 J. and Wardle, D. A. (2005) 'Effects of biodiversity on ecosystem functioning: A consensus  
768 of current knowledge', *Ecological Monographs*, 75(1), pp. 3-35.

769 Huckstorf, V., Lewin, W. C., Mehner, T. and Wolter, C. (2011) Impoverishment of YOY-fish  
770 assemblages by intense commercial navigation in a large Lowland river. *River Research  
771 and Applications*, 27(10), pp. 1253-1263.

772 INE, 2020. Naiades, Inland Navigation Europe [WWW Document]. Inland Navigation Europe.  
773 URL [http://www.inlandnavigation.eu/news/policy/naiades-programme-for-post-covid-  
774 growth](http://www.inlandnavigation.eu/news/policy/naiades-programme-for-post-covid-growth).

775 Jackson, M. C. and Grey, J. (2013) Accelerating rates of freshwater invasions in the catchment of  
776 the River Thames. *Biological Invasions*, 15(5), pp. 945-951.

777 Kassambara A. (2020). ggpubr: 'ggplot2' Based Publication Ready Plots. R package version  
778 0.4.0. <https://CRAN.R-project.org/package=ggpubr>

779 Keller, R. P., Drake, J. M., Drew, M. B. and Lodge, D. M. (2011) 'Linking environmental  
780 conditions and ship movements to estimate invasive species transport across the global  
781 shipping network', *Diversity and Distributions*, 17(1), pp. 93-102.

782 Leeper T.J. (2021). margins: Marginal Effects for Model Objects. R package version 0.3.26.

783 Lehner, B., K. Verdin, and A. Jarvis (2008), New Global Hydrography Derived From  
784 Spaceborne Elevation Data, *Eos Trans. AGU*, 89(10), 93–94.

785 Lemm J.U., Venohr M., Globevnik L., Stefanidis K., Panagopoulos Y., Gils J., et al. (2021).  
786 Multiple stressors determine river ecological status at the European scale: Towards an  
787 integrated understanding of river status deterioration. *Global Change Biology* 27, 1962–  
788 1975.

789 Leuven, R., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. J. R. and  
790 de Vaate, A. B. (2009). 'The river Rhine: a global highway for dispersal of aquatic invasive  
791 species', *Biological Invasions*, 11(9), pp. 1989-2008.

792 Li, H. W., Lamberti, G. A., Pearsons, T. N., Tait, C. K., Li, J. L. and Buckhouse, J. C. (1994)  
793 'Cumulative Effects Of Riparian Disturbances Along High Desert Trout Streams Of The  
794 John Day Basin, Oregon', *Transactions of the American Fisheries Society*, 123(4), pp. 627-  
795 640.

796 Lin, P. C., Brosse, S., Gao, X., Liu, C. C. and Liu, H. Z. (2013) 'Species composition and  
797 temporal pattern of fish passing through the navigation locks in the middle reach of  
798 Yangtze River: implications for fish conservation', *Journal of Applied Ichthyology*, 29(6),  
799 pp. 1441-1444.

800 Long J.A. (2019). `_interactions`: Comprehensive, User-Friendly Toolkit for Probing  
801 Interactions\_. R package version 1.1.0, <URL: [https://cran.r-](https://cran.r-project.org/package=interactions)  
802 [project.org/package=interactions](https://cran.r-project.org/package=interactions)>.

803 Magneville C, Loiseau N, Albouy C, Casajus N, Claverie T, Escalas A, Leprieur F, Maire E,  
804 Mouillot D, Villeger S (2021). `_mFD`: A Computation of Functional Spaces and Functional  
805 Indices\_. R package version 1.0.0, <URL: <https://github.com/CmlMagneville/mFD>>.

806 Manfrin A, Bunzel-Drueke M, Lorenz AW, Maire A, Scharf M, Zimball O, Stoll S. (2020) The  
807 effect of lateral connectedness on the taxonomic and functional structure of fish  
808 communities in a lowland river floodplain. *Sci Total Environment*, 719: 137169.

809 Martins, R. T., Couceiro, S. R. M., Melo, A. S., Moreira, M. P. and Hamada, N. (2017) 'Effects  
810 of urbanization on stream benthic invertebrate communities in Central Amazon',  
811 *Ecological Indicators*, 73, pp. 480-491.



812 Molnar, J.L., Gamboa, R.L., Revenga, C. and Spalding, M.D. (2008), Assessing the global threat  
813 of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, 6:  
814 pp. 485-492.

815 Morris, O. F., Loewen, C. J. G., Woodward, G., Schafer, R. B., Piggott, J. J., Vinebrooke, R. D.  
816 and Jackson, M. C. (2022) 'Local stressors mask the effects of warming in freshwater  
817 ecosystems', *Ecology Letters*, 25(11), pp. 2540-2551.

818 Navarro-Ortega, A., Acuna, V., Bellin, A., Burek, P., Cassiani, G., Choukr-Allah, R., Doledec,  
819 S., Elozegi, A., Ferrari, F., Ginebreda, A., Grathwohl, P., Jones, C., Rault, P. K., Kok, K.,  
820 Koundouri, P., Ludwig, R. P., Merz, R., Milacic, R., Munoz, I., Nikulin, G., Paniconi, C.,  
821 Paunovic, M., Petrovic, M., Sabater, L., Sabater, S., Skoulikidis, N. T., Slob, A., Teutsch,  
822 G., Voulvoulis, N. and Barcelo, D. (2015) 'Managing the effects of multiple stressors on  
823 aquatic ecosystems under water scarcity. The GLOBAQUA project', *Science of the Total  
824 Environment*, 503, pp. 3-9.

825 Nilsson, C.; Reidy, C. A.; Dynesius, M.; Revenga, C. Fragmentation and flow regulation of the  
826 world's large river systems. *Science* 2005, 308 (5720), 405-408.

827 Nunes, A. L., Tricarico, E., Panov, V. E., Cardoso, A. C. and Katsanevakis, S. (2015) Pathways  
828 and gateways of freshwater invasions in Europe. *Aquatic Invasions*, 10(4), pp. 359-370.

829 Oksanen J, Gavin L. Simpson, F. Guillaume Blanchet, Roeland Kindt, Pierre Legendre, Peter R.  
830 Minchin, R.B. O'Hara, Peter Solymos, M. Henry H. Stevens, Eduard Szoecs, Helene  
831 Wagner, Matt Barbour, Michael Bedward, Ben Bolker, Daniel Borcard, Gustavo Carvalho,  
832 Michael Chirico, Miquel De Caceres, Sebastien Durand, Heloisa Beatriz Antoniazi  
833 Evangelista, Rich FitzJohn, Michael Friendly, BrendanFurneaux, Geoffrey Hannigan,  
834 Mark O. Hill, Leo Lahti, Dan McGlenn, Marie-Helene Ouellette, Eduardo Ribeiro Cunha,

835 Tyler Smith, Adrian Stier, Cajo J.F. Ter Braak and James Weedon. (2022) vegan:  
836 Community Ecology Package. R package version 2.6-2. [https://CRAN.R-](https://CRAN.R-project.org/package=vegan)  
837 [project.org/package=vegan](https://CRAN.R-project.org/package=vegan).

838 Petts, G.E., Möller, H., Roux, A.L., 1989. Historical Change of Large Alluvial Rivers: Western  
839 Europe. John Wiley & Sons, Chichester.

840 Prygiel, E., Billon, G., Francois, A., Dumoulin, D., Chaumot, A., Geffard, O., Criquet, J. and  
841 Prygiel, J. (2016) 'Active biomonitoring for assessing effects of metal polluted sediment  
842 resuspension on gammarid amphipods during fluvial traffic', *Environmental Pollution*, 218,  
843 pp. 129-139.

844 Reid, A. J., Carlson, A. K., Creed, I. F., Eliason, E. J., Gell, P. A., Johnson, P. T. J., Kidd, K. A.,  
845 MacCormack, T. J., Olden, J. D., Ormerod, S. J., Smol, J. P., Taylor, W. W., Tockner, K.,  
846 Vermaire, J. C., Dudgeon, D. and Cooke, S. J. (2019) 'Emerging threats and persistent  
847 conservation challenges for freshwater biodiversity', *Biological Reviews*, 94(3), pp. 849-  
848 873.

849 Rumschlag, S. L., Mahon, M. B., Jones, D. K., Battaglin, W., Behrens, J., Bernhardt, E. S.,  
850 Bradley, P., Brown, E., De Laender, F., Hill, R., Kunz, S., Lee, S. Y., Rosi, E., Schaefer,  
851 R., Schmidt, T. S., Simonin, M., Smalling, K., Voss, K., Rohr, J. R. (2023). Density  
852 declines, richness increases, and composition shifts in stream macroinvertebrates. *Science*  
853 *Advances*, 9(18), Article eadf4896.

854 Samsami, F.; Haghshenas, S.A.; Soltanpour, M. (2022) Physical and Rheological Characteristics  
855 of Sediment for Nautical Depth Assessment in Bushehr Port and Its Access Channel.  
856 *Water*, 14, 4116.

857 Schmidt-Kloiber, A. & Hering D. (2015): [www.freshwaterecology.info](http://www.freshwaterecology.info) - an online tool that  
858 unifies, standardises and codifies more than 20,000 European freshwater organisms and  
859 their ecological preferences. *Ecological Indicators* 53: 271-282.

860 Tachet H., Richoux P., Bournaud M., Usseglio-Polatera P. (2010) *Invertébrés d'eau douce:*  
861 *systématique, biologie, écologie*, 3rd edn. CNRS Éditions, Paris.

862 Thioulouse J, Dray S, Dufour A, Siberchicot A, Jombart T, Pavoine S (2018). *Multivariate*  
863 *Analysis of Ecological Data with ade4\_*. Springer.

864 Tickner, D.; Opperman, J. J.; Abell, R.; Acreman, M.; Arthington, A. H.; Bunn, S. E.; Cooke, S.  
865 J.; Dalton, J.; Darwall, W.; Edwards, G.; et al. Bending the Curve of Global Freshwater  
866 Biodiversity Loss: An Emergency Recovery Plan. *Bioscience* 2020, 70 (4), 330-342.

867 Van Treeck, R., Van Wichelen, J. & Wolter, C. (2020) Fish species sensitivity classification for  
868 environmental impact assessment, conservation and restoration planning. *Science of the*  
869 *Total Environment* 708: 135173.

870 Vergeynst, J., Pauwels, I., Baeyens, R., Mouton, A., De Mulder, T. and Nopens, I. (2021)  
871 'Shipping canals on the downstream migration route of European eel (*Anguilla anguilla*):  
872 Opportunity or bottleneck?', *Ecology of Freshwater Fish*, 30(1), pp. 73-87.

873 Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. and Garnier, E. (2007)  
874 'Let the concept of trait be functional!', *Oikos*, 116(5), pp. 882-892.

875 Wan, Z., Shi, Z. F., Nie. A. W., Chen, J. H., Wang, Z.J. (2021) Risk assessment of marine  
876 invasive species in Chinese ports introduced by the global shipping network. *Marine*  
877 *Pollution Bulletin*. 173(A).

878 Wang, L. Z., Lyons, J. and Kanehl, P. (2001) 'Impacts of urbanization on stream habitat and fish  
879 across multiple spatial scales', *Environmental Management*, 28(2), pp. 255-266.

880 Wantzen, K.M., Alves, C.B., Badiane, S.D., Bala, R. M., Blettler M. C. M., Callisto, M., Cao,  
881 Y., Kolb, M., Leite, M.F., Macedo, D.R., Mahdi, O., Neves, M., Peralta, E. M., Rotgé, V.,  
882 Rueda-Delgado, G., Scharager, A., Serra-Llobet, A., Yengué, J. L., Zingraff-Hamed, A.,  
883 Kondolf, G. M. (2019): Urban stream and wetland restoration in the Global South – a  
884 DPSIR analysis. *Sustainability* 2019, 11, 4975

885 Weissteiner, C. J., Ickerott, M., Ott, H., Probeck, M., Ramminger, G., Clerici, N., Dufourmont,  
886 H. and de Sousa, A. M. R. (2016) 'Europe's Green Arteries-A Continental Dataset of  
887 Riparian Zones', *Remote Sensing*, 8(11).

888 Wen, Y. R., Schoups, G. and van de Giesen, N. (2017) 'Organic pollution of rivers: Combined  
889 threats of urbanization, livestock farming and global climate change', *Scientific Reports*, 7.

890 Wickham H. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag New York, 2016.

891 Wolter, C. (2001) Conservation of fish species diversity in navigable waterways, *Landscape and  
892 Urban Planning*, 53(1-4), pp. 135-144.

893 Wolter, C. (2008) Towards a mechanistic understanding of urbanization's impacts on fish. In:  
894 Marzluff, J., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon,  
895 U. & ZumBrunnen, C. (eds) *Urban Ecology. An International Perspective on the  
896 Interaction Between Humans and Nature*. New York: Springer: 425-436.

897 Wolter, C., Borcharding, J., Ferreira, T., Freyhof, J., Gessner, J., Górski, K., Nastase, A.,  
898 Schomaker, C. & Erős, T. (2021) Characterization of European lampreys and fishes by  
899 their longitudinal and lateral distribution traits. *Ecological Indicators* 123: 107350.

900 World Wildlife Foundation (WWF), "Living Planet Report—2018: Aiming Higher" (WWF,  
901 2018).

902 Xiong, F. Y., Olden, J. D., Lu, Y., Liu, H., Qu, X., Xia, W. T., Guo, C. A. B., Wu, X. H., Infante,  
903 D. M., Wang, L. Z. and Chen, Y. S. (2021) 'Riparian land use and in-channel stressors  
904 drive fish community structure in the Yangtze River', *Landscape Ecology*, 36(10), pp.  
905 3079-3095.

906 Xu, X. M., Yuan, Y. B., Wang, Z. L., Zheng, T., Cai, H. T., Yi, M. L., Li, T. H., Zhao, Z. J.,  
907 Chen, Q. and Sun, W. L. (2023) 'Environmental DNA metabarcoding reveals the impacts  
908 of anthropogenic pollution on multitrophic aquatic communities across an urban river of  
909 western China', *Environmental Research*, 216.

910 Villéger, S., Mason, N.W.H. and Mouillot, D. (2008), New Multidimensional Functional  
911 Diversity Indices For A Multifaceted Framework In Functional Ecology. *Ecology*, 89:  
912 2290-2301.

913 Vinebrooke R.D., Cottingham K.L., Norberg J., Scheffer M., Dodson S.I., Maberly S.C., *et al.*  
914 (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of  
915 species co-tolerance. *Oikos* **104**, 451–457

916 Zajicek, P., Radinger, J. and Wolter, C. (2018) Disentangling multiple pressures on fish  
917 assemblages in large rivers. *Science of the Total Environment*, 627, pp. 1093-1105.

918 Zajicek, P. and Wolter, C. (2019) 'The effects of recreational and commercial navigation on fish  
919 assemblages in large rivers', *Science of the Total Environment*, 646, pp. 1304-1314.

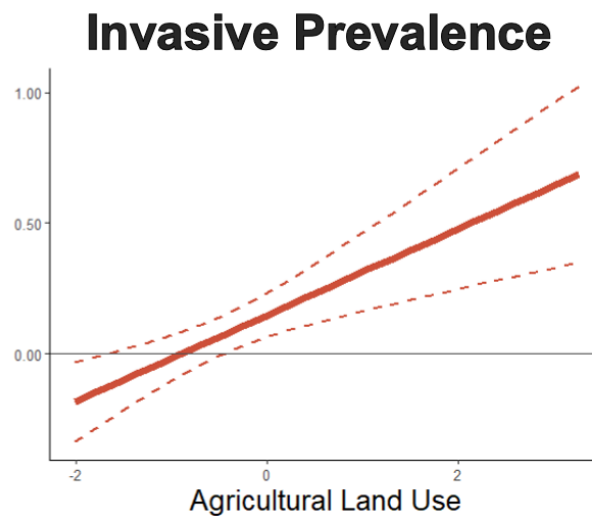
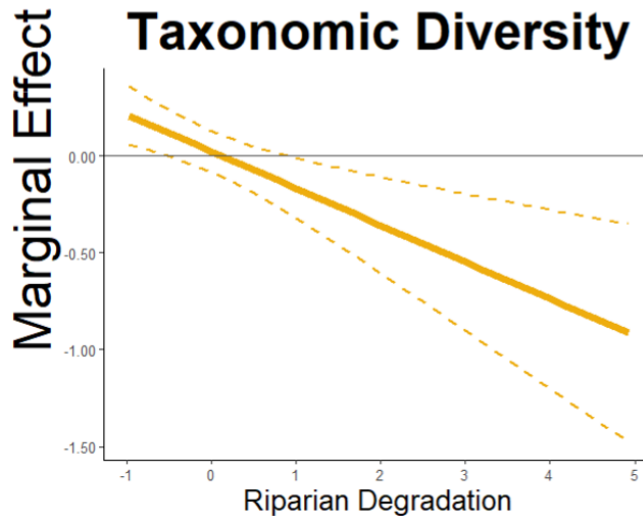
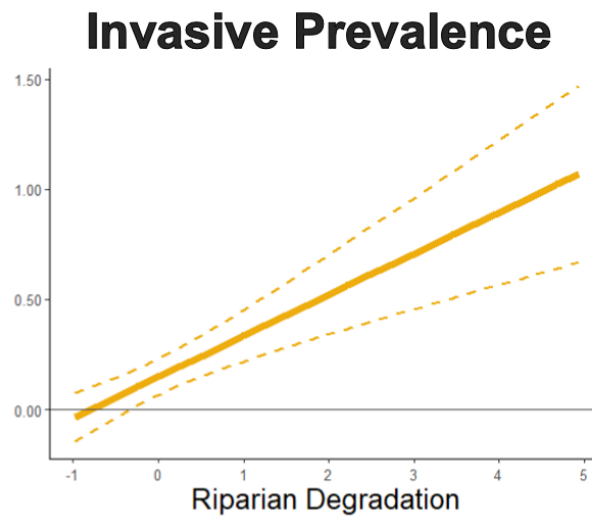
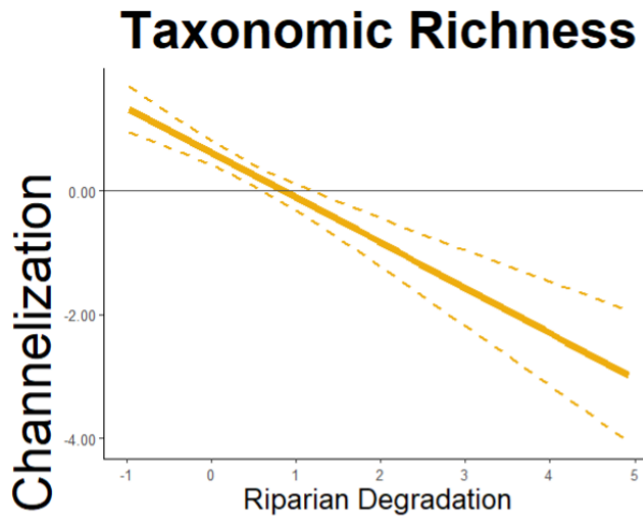
920 Zhang H, Kang M, Shen L, et al. (2020) Rapid change in Yangtze fisheries and its implications  
921 for global freshwater ecosystem management. *Fish Fish.* 21: pp.601–620.

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923 **Extended Data Figures**

924 **Figure 1.** Macroinvertebrate's response to channelization is dependent on riparian degradation  
925 and agricultural cover. The panels show the marginal effect of channelization from the GLMMs  
926 on macroinvertebrate communities along a gradient of riparian degradation and agricultural land  
927 use. A negative value on the y-axis indicates a negative impact of channelization on said metric  
928 (e.g. a decrease in taxonomic richness), and a value at 0 (grey horizontal line) indicates a null  
929 effect. Left panel shows the relationships of taxonomic richness and right panel shows the  
930 prevalence of invasive taxa. Predictors were standardized to zero mean and a SD of  $\pm 1$ .

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933 **Figure 2.** Fish and macroinvertebrate trait relationships with ship traffic across different land use  
 934 scenarios. Trait scores associated with the environmental axis of heightened ship traffic in the  
 935 RLQ analysis are shown in the ‘Full Dataset’ column, and are the values shown in the ordination  
 936 of Figures 4 and 5. Columns two and three of each table show the trait associations with  
 937 heightened ship traffic when the RLQ is re-run in highly agricultural sites (those with the top  
 938 25% of agricultural cover across the datasets) and in highly urbanized sites.

**Macroinvertebrate Trait Associations with Ship Traffic Across Land Use Scenarios**

| Trait Class  | Trait                | Full Dataset | Highly Agricultural Sites | Highly Urbanized Sites |
|--------------|----------------------|--------------|---------------------------|------------------------|
| Locomotion   | Flier                | 0.337        | 0.363                     | 0.311                  |
| Dispersal    | Aerial Active        | 0.298        | 0.411                     | -0.034                 |
| Locomotion   | Full Water Swimmer   | 0.292        | 0.261                     | 0.332                  |
| Reproduction | Clutches Fixed       | 0.255        | 0.158                     | 0.340                  |
| Substrate    | Mud                  | 0.181        | 0.263                     | -0.033                 |
| Reproduction | Clutches Vegetation  | 0.141        | 0.057                     | 0.191                  |
| Dispersal    | Aquatic Active       | 0.134        | 0.085                     | 0.234                  |
| Saprobity    | Oligosaprobic        | 0.095        | 0.140                     | 0.001                  |
| Substrate    | Organic Detritus     | 0.088        | 0.105                     | 0.067                  |
| Saprobity    | Xenosaprobic         | 0.082        | 0.154                     | 0.016                  |
| Locomotion   | Burrower             | 0.067        | 0.072                     | -0.221                 |
| Reproduction | Clutches Terrestrial | 0.064        | 0.114                     | -0.232                 |
| Reproduction | Eggs Cemented        | 0.042        | -0.023                    | 0.224                  |
| Reproduction | Clutches Free        | 0.039        | 0.057                     | -0.150                 |
| Locomotion   | Perm. Attached       | 0.026        | 0.085                     | 0.011                  |
| Substrate    | Silt                 | 0.012        | 0.095                     | -0.106                 |
| Locomotion   | Surface Swimmer      | 0.007        | -0.040                    | -0.111                 |
| Dispersal    | Aerial Passive       | 0.000        | 0.012                     | -0.162                 |
| Reproduction | Eggs Free            | -0.006       | -0.069                    | -0.200                 |
| Saprobity    | Alpha.Mesosaprobic   | -0.041       | -0.077                    | 0.087                  |
| Reproduction | Asexual              | -0.056       | -0.026                    | -0.022                 |
| Substrate    | Macrophytes          | -0.064       | -0.081                    | 0.148                  |
| Locomotion   | Crawler              | -0.078       | 0.059                     | -0.005                 |
| Saprobity    | Polysaprobic         | -0.113       | 0.025                     | -0.299                 |
| Substrate    | Sand                 | -0.125       | 0.007                     | -0.246                 |
| Locomotion   | Temp. Attached       | -0.127       | -0.121                    | -0.044                 |
| Saprobity    | Beta.Mesosaprobic    | -0.180       | -0.137                    | -0.096                 |
| Substrate    | Boulders Pebbles     | -0.185       | -0.180                    | -0.139                 |
| Substrate    | Twigs Roots          | -0.186       | -0.125                    | -0.152                 |
| Substrate    | Gravel               | -0.211       | -0.126                    | -0.167                 |
| Substrate    | Microphytes          | -0.270       | -0.230                    | -0.100                 |
| Reproduction | Ovoviviparity        | -0.290       | -0.244                    | -0.135                 |
| Locomotion   | Interstitial         | -0.295       | -0.244                    | -0.123                 |
| Dispersal    | Aquatic Passive      | -0.302       | -0.376                    | -0.100                 |

**Fish Trait Associations with Ship Traffic Across Land Use Scenarios**

| Trait Class  | Trait           | Full Dataset | Highly Agricultural Sites | Highly Urbanized Sites |
|--------------|-----------------|--------------|---------------------------|------------------------|
| Habit        | Pelagic         | 2.005        | -0.445                    | -0.571                 |
| Feeding      | Planktivorous   | 1.895        | -0.500                    | -0.732                 |
| Reproduction | Psammophil      | 1.664        | 0.500                     | 0.524                  |
| Migration    | Diadromous      | 0.928        | -0.235                    | -0.421                 |
| Reproduction | Pelagophil      | 0.730        | -0.302                    | 0.353                  |
| Feeding      | Piscivorous     | 0.528        | 0.619                     | 0.359                  |
| Feeding      | Parasitic       | 0.445        | -0.107                    | 1.121                  |
| Region       | Fri             | 0.430        | 0.318                     | 0.274                  |
| Rheophily    | Eurytop         | 0.292        | 0.291                     | 0.158                  |
| Region       | Sensitivity     | 0.263        | 0.117                     | 0.386                  |
| Reproduction | Phytolithophil  | 0.222        | 0.561                     | 0.362                  |
| Feeding      | Omnivorous      | 0.023        | 0.263                     | 0.194                  |
| Habit        | Demersal        | 0.011        | -0.031                    | 0.287                  |
| Migration    | Potamodromous   | -0.067       | 0.136                     | 0.191                  |
| Reproduction | Speleophil      | -0.069       | 0.728                     | 0.744                  |
| Region       | S2Fri           | -0.070       | 0.287                     | 0.043                  |
| Habit        | Benthic         | -0.123       | 0.087                     | 0.065                  |
| Reproduction | Lithophil       | -0.131       | -0.627                    | -0.722                 |
| Reproduction | Phytophil       | -0.209       | -0.430                    | 0.284                  |
| Feeding      | Invertivorous   | -0.409       | -0.580                    | -0.179                 |
| Migration    | Nonmigratory    | -0.409       | -0.598                    | -0.490                 |
| Feeding      | Detritivorous   | -0.419       | -0.896                    | -0.227                 |
| Feeding      | Phytovorous     | -0.493       | -1.006                    | -0.287                 |
| Rheophily    | Rheophil        | -0.501       | -0.644                    | -0.537                 |
| Reproduction | Polyphil        | -0.586       | -0.622                    | -1.036                 |
| Rheophily    | Limnophil       | -0.588       | -0.774                    | -1.509                 |
| Reproduction | Ostracophil     | -0.657       | -0.796                    | -1.695                 |
| Reproduction | Lithopelagophil | -0.706       | -0.886                    | -1.910                 |

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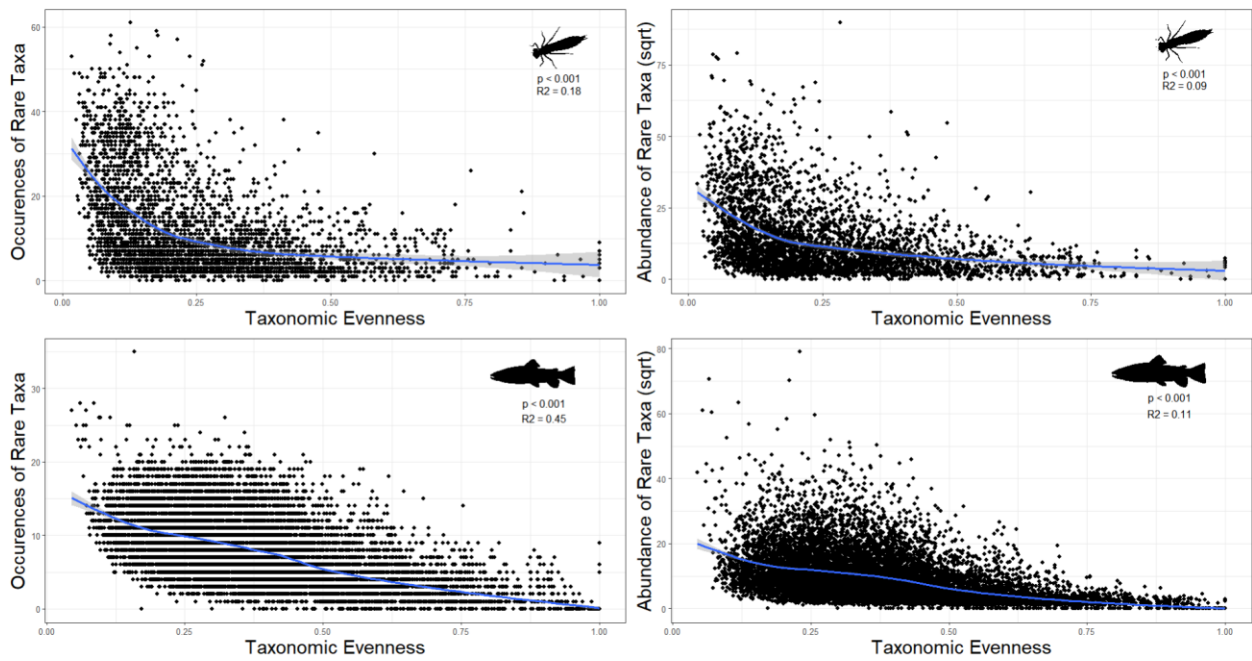
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943 **Figure 3.** Relationships between taxonomic evenness and the abundance and occurrences of rare  
944 species in fish and macroinvertebrates. We defined a rare species as a species whose abundance  
945 accounting for less than 25% of the total community abundance (see Supplemental file 2 for  
946 details).



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