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1 **Title:**

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

3

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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). 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

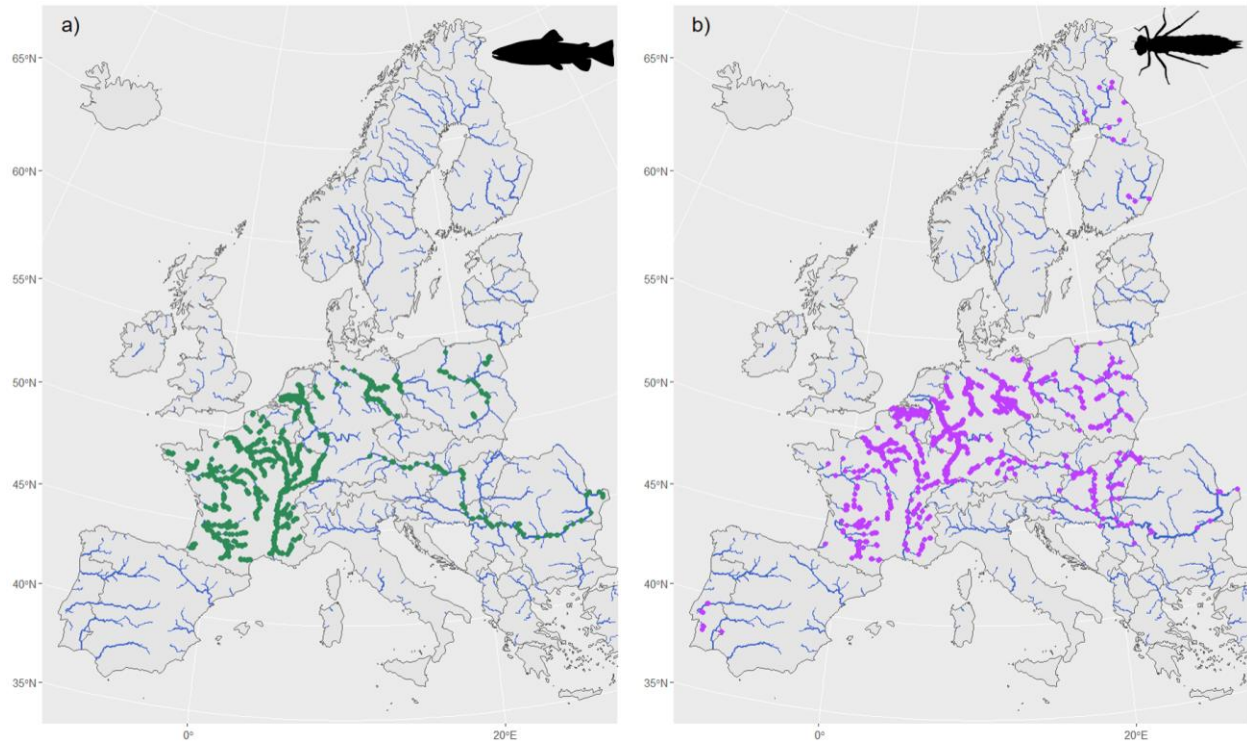
152 studies and previous reviews have focused mainly on marine invasive species and maritime ports,
153 and similar investigations in freshwater systems are lacking. In addition, we evaluated how land
154 use and riparian degradation would interact with the effects of navigation. We hypothesized that
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.*

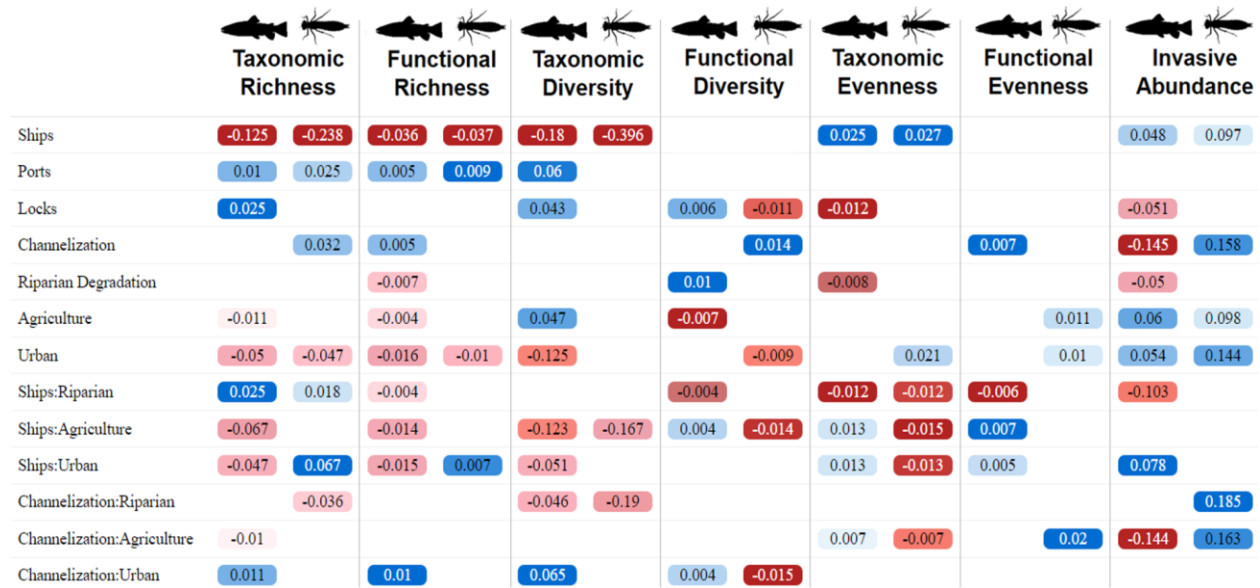
172

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



183

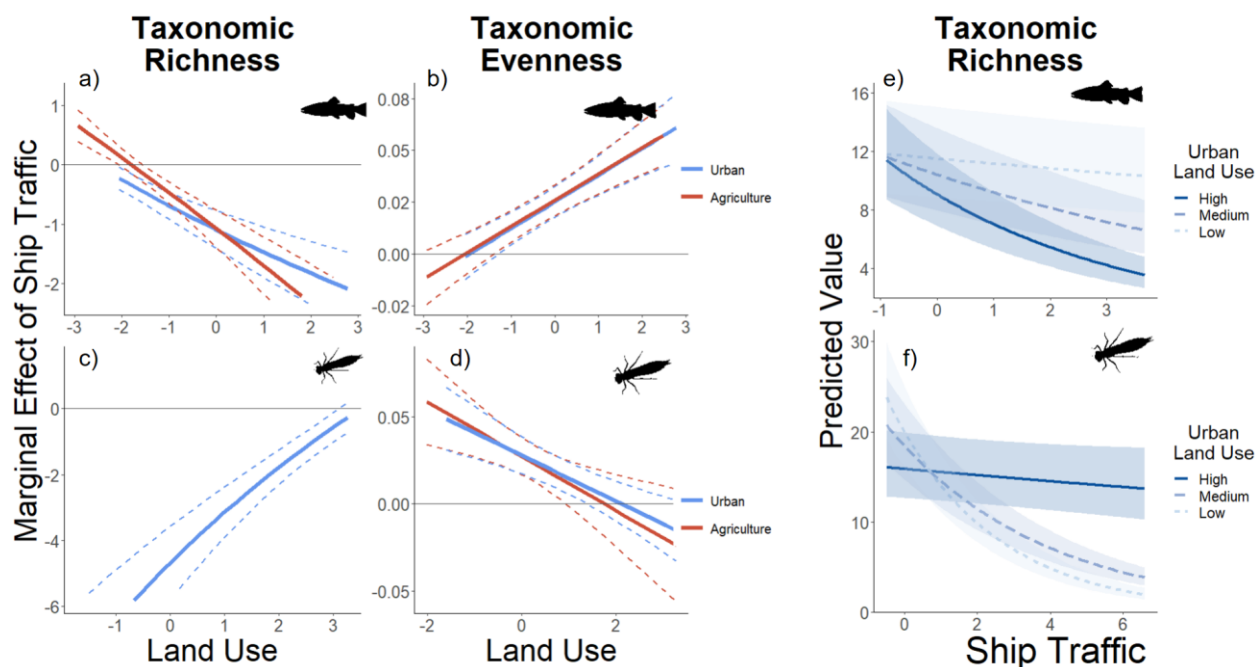
184 **Fig. 2 – Inland navigation and other stressor effects on freshwater fish and**
 185 **macroinvertebrate biodiversity.** Model estimates from the GLMMs. Each column represents a
 186 separate model, with the response metric and taxonomic group as the column header, with predictors of
 187 the model 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 ± 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 ± 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.

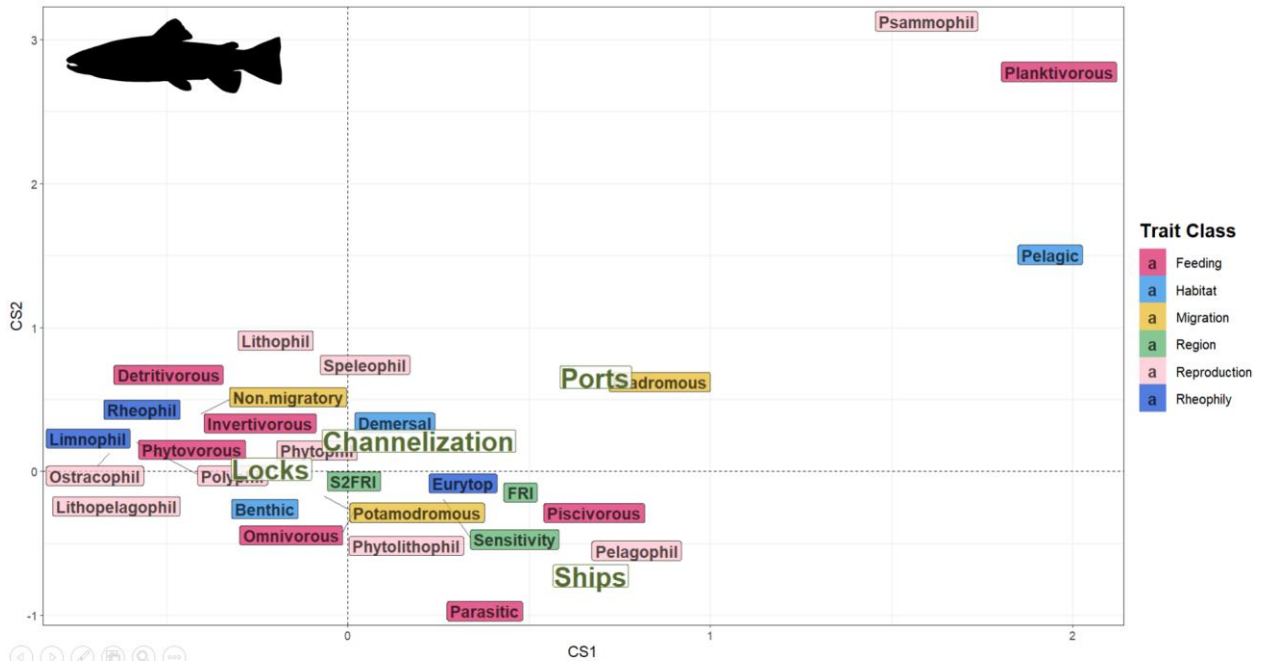
231 The density of locks was weakly associated with increases in fish taxonomic richness and
232 functional diversity, and a decrease in invasive prevalence, and with slight decreases in
233 macroinvertebrates functional diversity (Fig.2, Supplemental Table 1). Port density was associated
234 with slight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

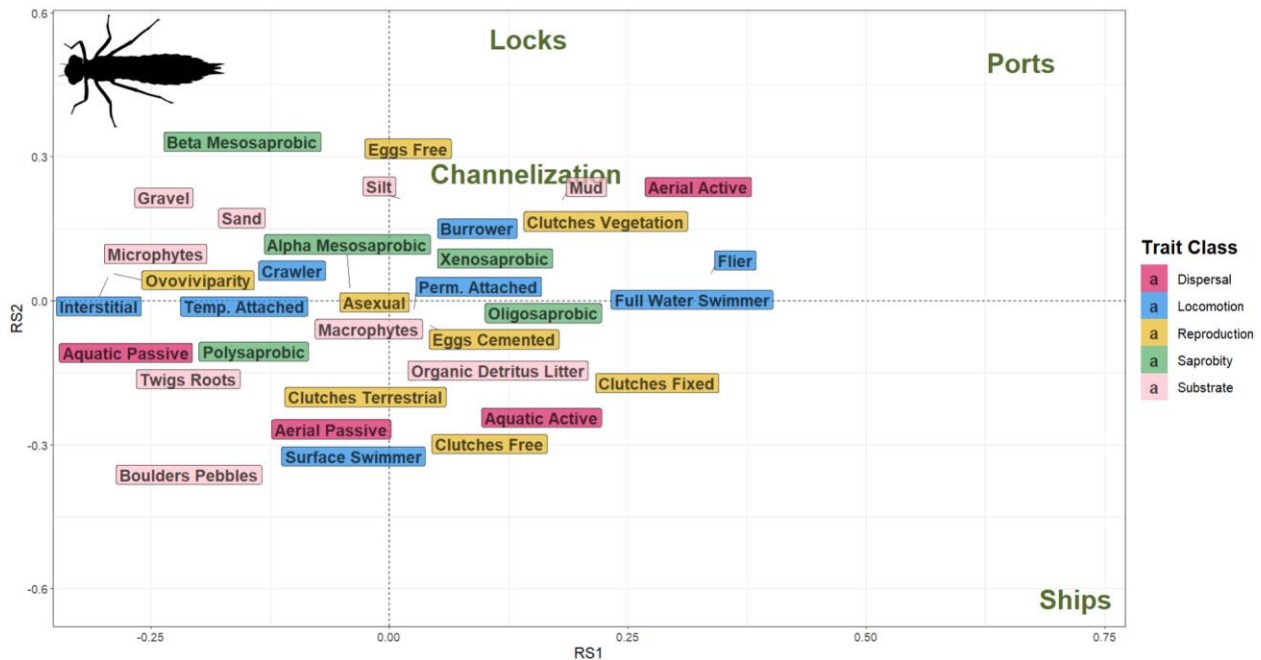
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251

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 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 (S²FRI) 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 m²) 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/Sextonetal_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**

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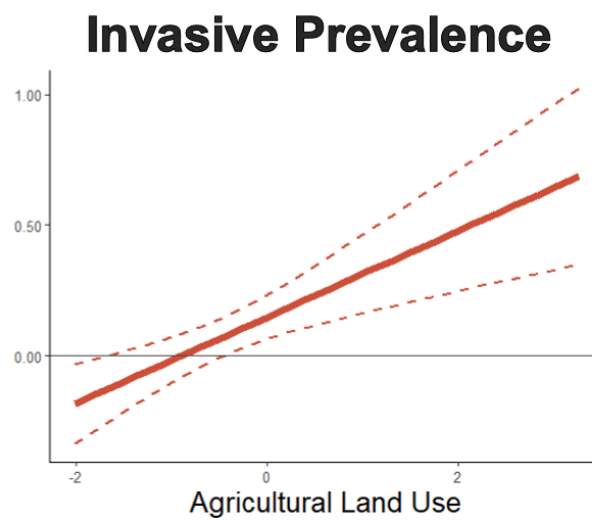
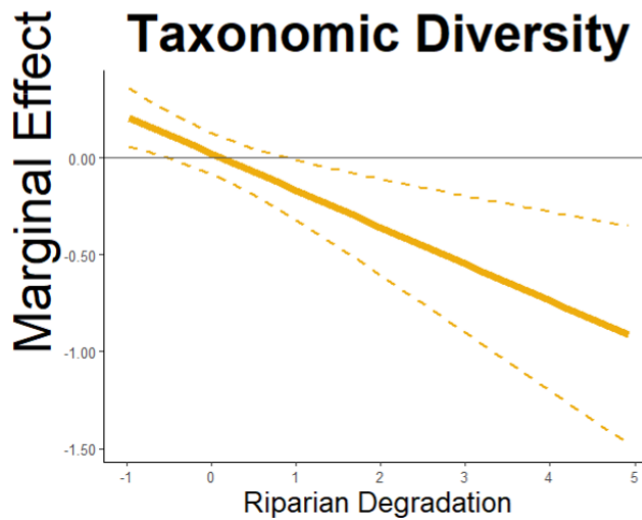
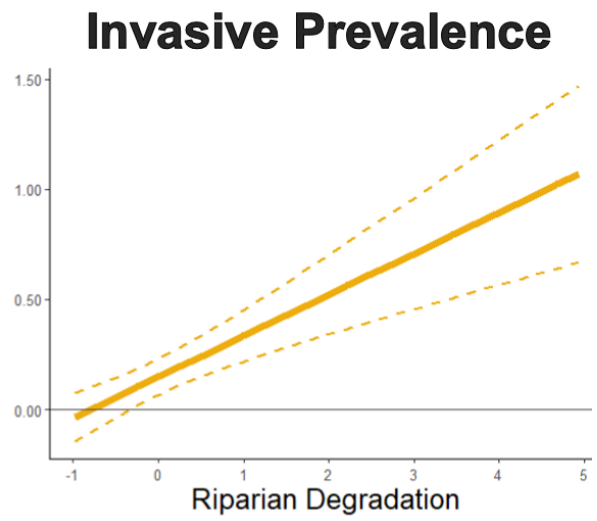
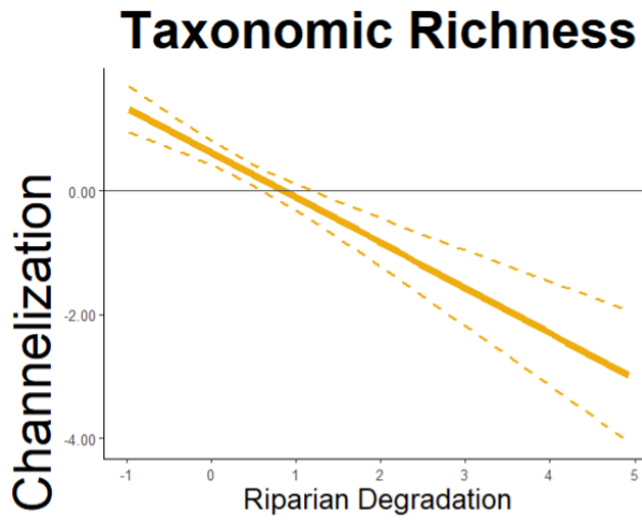
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923 **Extended Data Figures**

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 ± 1 .

931



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

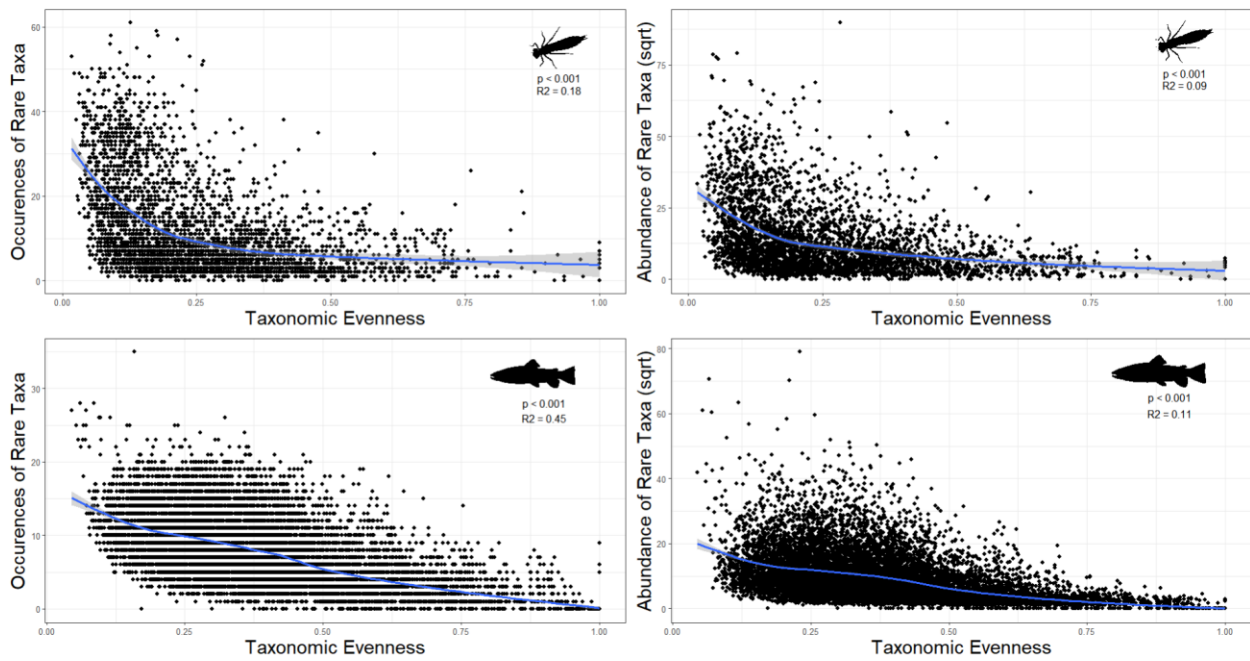
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943 **Figure 3.** Relationships between taxonomic evenness and the abundance and occurrences of rare
944 species in fish and macroinvertebrates. We defined a rare species as a species whose abundance
945 accounting for less than 25% of the total community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



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