Inland navigation and land use interact to impact European freshwater biodiversity

Nature Ecology and Evolution

Sexton, Aaron N.; Beisel, Jean Nicolas; Staentzel, Cybill; Wolter, Christian; Tales, Evelyne et al

https://doi.org/10.1038/s41559-024-02414-8

This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openaccess.library@wur.nl

nature ecology & evolution

Article

https://doi.org/10.1038/s41559-024-02414-8

Inland navigation and land use interact to impact European freshwater biodiversity

Received: 1 September 2023

Accepted: 10 April 2024

Aaron N. Sexton[1]✉, Jean-Nicolas Beisel[2], Cybill Staentzel[2], Christian Wolter[3], Evelyne Tales[4], Jérôme Belliard[4], Anthonie D. Buijse[5,6], Vanesa Martínez Fernández[7], Karl M. Wantzen[8,9], Sonja C. Jähnig[10,11], Carlos Garcia de Leaniz[12,13], Astrid Schmidt-Kloiber[14], Peter Haase[15,16], Marie Anne Eurie Forio[17], Gait Archambaud[18], Jean-François Fruget[19], Alain Dohet[20], Vesela Evtimova[21], Zoltán Csabai[22,23], Mathieu Floury[4], Peter Goethals[17], Gábor Várbiró[24], Miguel Cañedo-Argüelles[25], Aitor Larrañaga[26], Anthony Maire[27], Ralf B. Schäfer[16,28], James S. Sinclair[15], Rudy Vannevel[17,29], Ellen A. R. Welti[30] & Alienor Jeliazkov[4]

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

Freshwater ecosystems are among the most diverse in the world, but freshwater biodiversity is declining at a much faster pace than both terrestrial and marine biodiversity[1]. Populations of freshwater vertebrate species have declined globally by over 80% since 1970 (ref. 2). In Europe and North America, freshwater fish extinction rates are over 100 times higher than natural extinction rates[3]. Of European freshwater mussel species, 65% are listed as either Threatened or Near Threatened by the International Union for the Conservation of Nature (IUCN) Red List of species (www.iucnredlist.org). Efforts are being made to halt these declines as freshwater ecosystems harbour vital ecological, economic and cultural values[4]. This requires identifying the relevant stressors on freshwater biodiversity and how these stressors interact with each other. Habitat loss, climate change and land use intensification rank among the most common freshwater stressors, alongside poor water quality and the introduction of aquatic invasive species[1,5].

A full list of affiliations appears at the end of the paper. ✉e-mail: aaron.sexton@fondationbiodiversite.fr

Within this context, the prevalence and rise of inland navigation has received little attention in spite of its potential to affect freshwater biodiversity. Commercial shipping on rivers and lakes has been practised for centuries but is proposed to increase by 50% in Europe by 2050 as it is being touted as a carbon-friendly mode of transport[6]. Accordingly, the European Parliament has adopted the resolution in 2021 towards future-proofing inland waterway transport in Europe (2021/2015[INI]). Parliament has also given its approval for the revision of the Trans-European Network for Transport, focusing on ensuring a good navigation status for the core network, and paved the way for funding managed by the European Climate Infrastructure and Environment Executive Agency (CINEA). This potential rise in shipping would not only mean more ship traffic, but would also require the modification of navigation infrastructures (for example, heavier embankments, larger locks and ports, and additional waterways) that will impact freshwater ecosystems in ways that are difficult to predict[7,8]. Inland navigation and its infrastructures have largely been investigated as being vectors for the spread of invasive species[9–11], and not nearly as much for their direct impact on facets of native biodiversity such as richness, evenness and functional trait responses, as has been done in the case of global change stressors such as climate change and land use[5].

Additionally, with few exceptions[12,13], most research on inland navigation has been conducted at local spatial scales, examining the effects of a specific lock, river or catchment[14–17]. These studies have shown that inland navigation constitutes a notable pressure on freshwater biodiversity. Specifically, these studies have shown ship traffic to decrease fish richness, abundance and reproduction, especially that of limnophilic fish (those with preference to slow-flowing waters)[15,17,18], and modifications of river systems to accommodate for inland navigation to reduce fisheries and other riverine ecosystem services[19]. Declines in biodiversity associated with navigation are often attributed to the destruction of natural habitats, construction of artificial embankments, aquatic and acoustic pollution, and ship waves that further degrade habitats[17,18].

Given that most studies have addressed different navigation-related effects, taxa and local contexts, (for example, focused on year-over-young fish[18], or on the Rhine river[9] or Yangtze River[15], or on one canal[20]) drawing generalizations on the overall effect of inland navigation at a large scale is fraught with uncertainty. General conclusions are further challenged by potential context dependency of navigation–biodiversity relationships. For example, the landscape (for example urban versus agricultural areas) and habitat conditions (channelized rivers, disconnected from floodplains) are both known to be important determinants of freshwater communities, for example, decreased habitat connectedness or increases in intense land use leading to reductions in diversity, endangered species and shifts in community composition[21–23]. Therefore, analyses of fine-scale observations across multiple land use contexts and habitat conditions are required to assess whether the impact of inland navigation is consistent across catchments and if this impact interacts with other stressors.

In this Article, to better understand how inland navigation impacts freshwater biodiversity at a continental scale, and how the impact is moderated by landscape and habitat conditions, we compiled several local biodiversity datasets across Europe and modelled their relationships with navigation pressures. Specifically, we tested the relationship between navigation stressors (ship traffic, density of ports and locks, and degree of river channelization) and the taxonomic and functional diversity, that is taxonomic and functional richness, Simpson's Reciprocal diversity, functional dispersion, and taxonomic and functional evenness of freshwater fish and macroinvertebrate communities, as well as the prevalence of invasive taxa. We hypothesized consistently negative effects of ship traffic on taxonomic and functional richness and diversity. Additionally, in ports, especially where ships dock closely, invasive species will be most prevalent, as observed in marine and estuarine systems[24]. For example, in Canadian marine ports, invasive marine macroinvertebrates are found in ballast tanks, while Finnish ports commonly document invasive species with high eutrophic tolerance in ship ballast waters[25,26]. However, these studies and previous reviews have focused mainly on marine invasive species and maritime ports, and similar investigations in freshwater systems are lacking. In addition, we evaluated how land use and riparian degradation would interact with the effects of navigation. We hypothesized that navigation's negative impact would be lower in highly degraded landscapes, because of correlated tolerances of organisms towards landscape-related and ship traffic-related stress. Thus, although co-occurring stressors might increase the overall level of impact, this impact would be lower than if the tolerances to the stressors were either uncorrelated or negatively correlated[27].

Results

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

Navigation impact

Ship traffic was strongly associated with decreases in taxonomic richness and Simpson's reciprocal diversity, as well as functional richness of both fish and macroinvertebrates (Fig. 2; *P* values, R^2, model estimates and standard errors for all models are provided in Supplementary Table 1). Additionally, for both fish and macroinvertebrates, ship traffic was positively associated with the prevalence of invasive species and taxonomic evenness (Fig. 2 and Supplementary Table 1). For all models other than invasive species, functional diversity and evenness, ship traffic was the term in the model with the largest effect size (that is, the effect causing the greatest change in the response metric), indicating strong impacts throughout (Fig. 2).

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

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

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

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

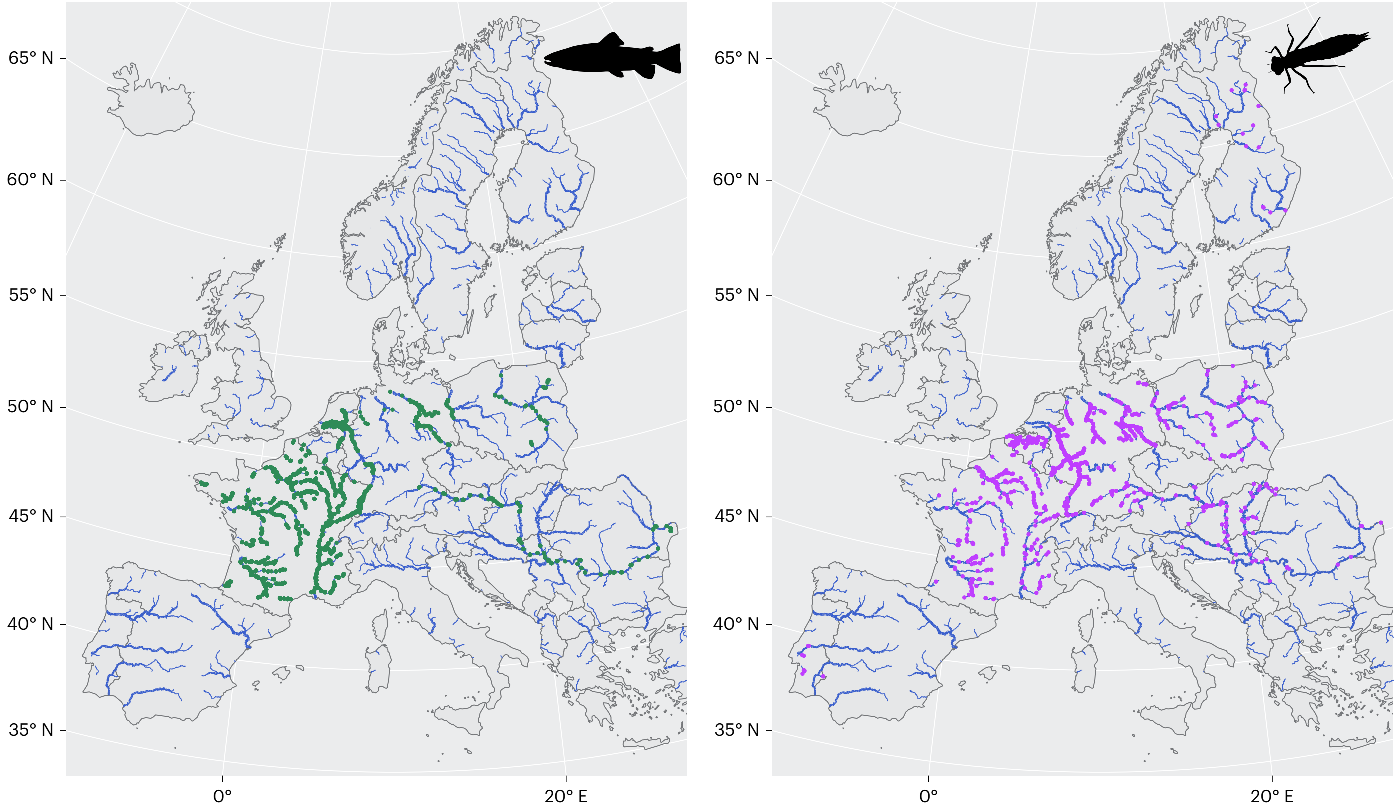


Fig. 1 | Fish and macroinvertebrate communities across Europe. The locations of all biodiversity data used in our analyses (coloured dots). **a**, Fish (*n* = 2,381). **b**, Macroinvertebrates (*n* = 1,668). Large rivers and navigated canals are shown with blue lines.

associated with slight increases in taxonomic and functional richness for both fish and macroinvertebrates (Fig. 2 and Supplementary Table 1).

Traits involved in navigation–biodiversity relationships

To better identify the guilds of species responding to navigation, we analysed the relationships between traits and navigation pressures via an RLQ–fourth-corner analysis, which quantifies the covariance between species traits (table Q) and environmental variables (table R), mediated by the species abundances at sites (table L)[28]. We found strong significant relationships between the environmental variables and species traits in both fish and macroinvertebrates.

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

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

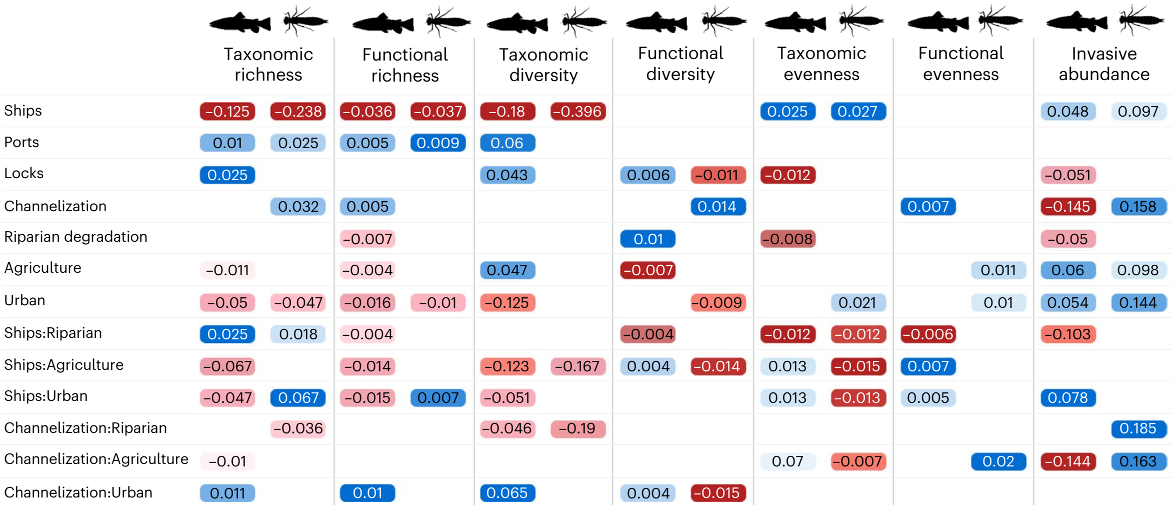
To identify how land use and riparian degradation mediated navigations effect on traits, we ran additional RLQ–fourth-corner analyses using subsets of sites with the highest degree of anthropogenic land cover and riparian degradation (top 25% of sites with each land use class). In fish, degradation did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

Discussion

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

Ship traffic

The effects on biodiversity are reflected in trait shifts in both fish and macroinvertebrate communities. Ship traffic had the strongest negative effects on benthic and limnophilic taxa and on fish species that suspend their eggs in the flow. Ship traffic was positively associated with pelagic and eurytopic taxa and those fixing their eggs in clutches to substrates. Together these trait shifts reflect selection pressures by vessel-induced waves and return currents against specialist and towards generalist life history traits[13,29]. Ship waves erode banks and resuspend sediment, degrading littoral habitats for both fish and macroinvertebrates[30]. Additionally, commonly used heavy embankments to prevent bank erosion considerably impact littoral habitats in all navigated rivers, and have been shown to reduce fish diversity[18]. Reducing ship speed



	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								0.07	–0.007		0.02	–0.144	0.163
Channelization:Urban	0.011		0.01		0.065		0.004	–0.015						

Fig. 2 | Inland navigation and other stressor effects on freshwater fish and macroinvertebrate biodiversity. Model estimates from the GLMMs. Each column represents a separate model, with the response metric and taxonomic group as the column header, with predictors of the model as rows. Red cells indicate a negative effect and blue cells represent a positive effect, with colour intensity representing the magnitude of effect. Non-significant effects are blank cells (*P* values and standard errors reported in Supplementary Table 1). 'Ships' refers to ship traffic, 'Ports' and 'Locks' represent the density of each, 'Channelization' represents the portion of the river stretch that has been channelized, 'Agriculture' and 'Urban' represent the respective portion of land use at each site, and 'Riparian degradation' represents the portion of the riparian habitat that has been lost from its potential extent. All predictors were standardized to an average value of 0 and s.d. of ± 1, allowing one to compare predictors.

and creating shallow habitats that are protected from ship waves could mitigate some of these wave-induced negative impacts. Additionally, many waterways require dredging of the river bottom to maintain navigable fairway depth[31], which has disproportionally negative impacts on benthic habitats. These known effects of ship traffic and fairway maintenance can explain the negative association with benthic species.

The community shifts described above are confirmed by the positive association between ship traffic and taxonomic evenness in both fish and macroinvertebrates. Decreasing species richness, the loss of rare taxa and small populations, resulted in ship traffic-induced increases in evenness. Correspondingly, in a follow-up analysis we found strong correlations between taxonomic evenness and the abundance and occurrence of rare taxa for both fish and macroinvertebrates (Supplementary File 2 and Extended Data Fig. 3), supporting the hypothesis that ship traffic drives losses in populations of rare species. Shipping favours the most tolerant, generalist and abundant/ubiquitous taxa and eliminates rare species, resulting in a more even community. For example, eurytopic fish tolerating a wide variety of flow rates were positively associated with ship traffic, while negatively so with flow specialists (both limnophilic and rheophilic taxa). This is a concern as it may allow invasive goby fish species, such as *Proterorhinus semilunaris*, or *Neogobius fluviatilis* that are generalists in their flow preferences, to proliferate. Additionally, this might have consequences at the ecosystem level given the role that specialist species play in ecological function and stability[32]. For example, Cao et al.[33] documented substantial losses of benthic macroinvertebrate species, especially among sensitive taxa, as a result of habitat degradation in streams leading to losses in ecosystem functionality, especially nutrient cycling.

Interaction with land use

Degraded landscapes magnified negative impacts of ship traffic on fish communities, with higher decreases in richness and diversity in urban and agricultural areas. These interactions demonstrate that land use can modify the effects of shipping and create environments where only few taxa will persist. For example, in agricultural systems, in areas with little to no riparian buffer, the dual stressors lead to fish and macroinvertebrate communities dominated by pollution-tolerant taxa[34]. Research at large scales has shown that multiple stressors such as pollution, hydromorphological modifications, land use and water use can synergistically interact to create stronger effects in combination on freshwater ecosystem services[35,36]. Several freshwater fish species living in large rivers might tolerate some level of degradation, agricultural or urban pollution and habitat modifications but still decline or disappear when another stressor such as ship traffic is added.

For macroinvertebrates, the impact of ship traffic more closely followed our original hypothesis that navigation's impact would be lessened in degraded areas, especially in urban areas. The impact of ship traffic on species richness was minimal in highly urbanized areas as depicted in Fig. 3c (that is, marginal effect of ship traffic close to zero when urban cover is high). However, the effects of ship traffic on species richness were strongly negative in areas with moderate to low levels of urbanization. This suggests that the taxa exhibited a positive co-tolerance to urbanization and ship traffic, where the same sensitive taxa are independently extirpated by each stressor. For example, a weak swimming species that is sensitive to low dissolved oxygen levels is extirpated by both stressors related to urban land use and navigation, for example, in an urban environment, either by urban run-off or vessel-induced wake wash. Several studies have documented what is described as the 'urban stream syndrome' whereby urban freshwater ecosystems have similar hydrology, ecology and pollution[37–39]. These urban streams are often characterized by increases in pH and heavy metals as well as temperature and suspended solids, which is typically accompanied by decreases in dissolved oxygen[40,41]. This combination has been shown to produce negative effects on macroinvertebrate communities[42]. Similarly, ship traffic has been reported to increase suspended sediment and release heavy metals and other toxins[43–45]. Urban waterways are particularly confined, homogeneous and simplified, which might have resulted in little negative impact of ship traffic observed, as their aquatic communities are already depauperated and composed of taxa tolerant to stressors resulting from ship traffic.

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

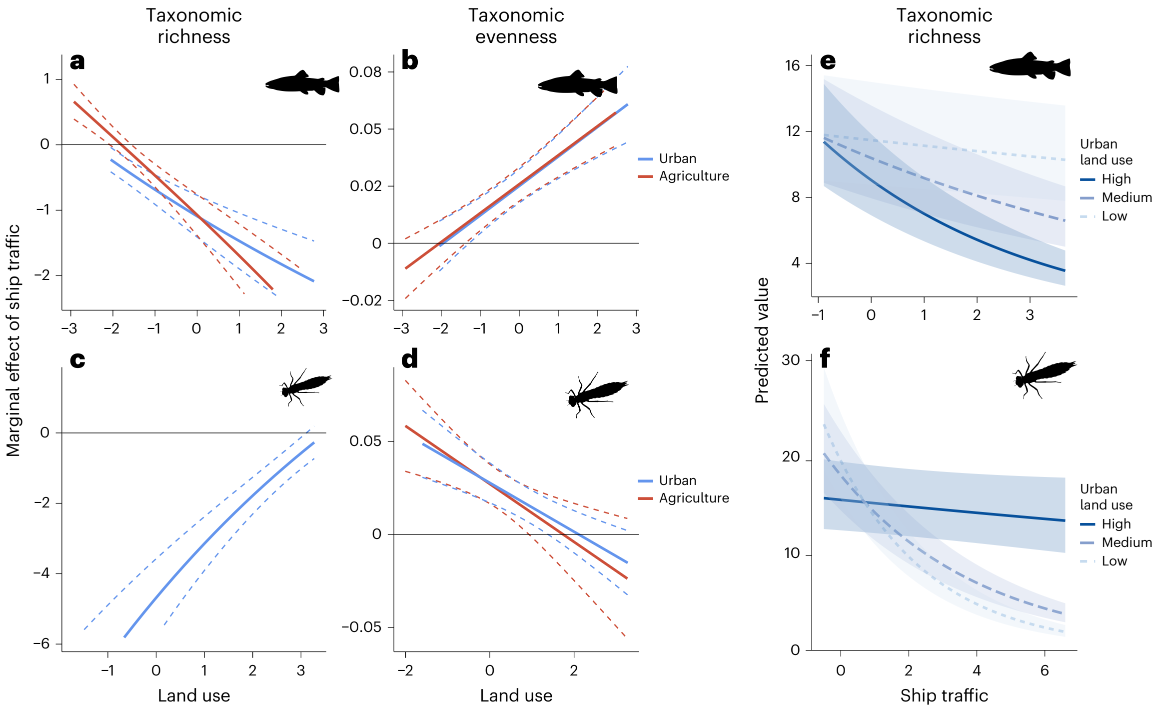


Fig. 3 | Context-dependent effect of ship traffic. a–d, Plots showing the marginal effect of ship traffic from the GLMMs on taxonomic richness and evenness for fish (**a**,**b**) and macroinvertebrate communities (**c**,**d**) across varying degrees of land use. The *x* axis represents the standardized (average of 0 ± 1 s.d.) intensity of land use ('Urban', blue line; 'Agriculture', red line), and the corresponding *y*-axis value the marginal effect of ship traffic on the biodiversity metric. The marginal effect is the additional effect for a given absolute effect of the other variables, here in particular land use. Negative values indicate ship traffic decreases the metric (for example, decrease in macroinvertebrate taxonomic richness at low levels of urbanization), zero on the *y* axis represents a null effect, and positive values show an increase. The dotted lines represent the standard error of the marginal value. **e**,**f**, Plots visualizing these changes in the marginal effect of ship traffic at specific levels of urbanization (high, medium and low levels of urban land use, with medium representing the average level of urbanization and high and low representing the maximum and minimum values) by showing the predicted values of taxonomic richness for fish (**e**) and macroinvertebrate communities (**f**) as ship traffic increases in across different land use scenarios. The error bars represent the 95% confidence interval.

magnifying the negative effect of ship traffic[46]. Moreover, fish may be more tolerant than macroinvertebrates with respect to water quality, which means that their tolerances are less correlated than for macroinvertebrates. Correspondingly, a recent study from China found that urban pollutants were a primary driver of macroinvertebrate communities, while urban fish communities were driven by dispersal limitations instead[47]. Indeed, a recent study found that landscape connectivity was more important than urbanization for fish community characteristics in Hungary[48]. Future research on how dual stressors such as urbanization and navigation can interact to influence freshwater biodiversity across taxa and functional groups is certainly warranted.

The effects of channelization on macroinvertebrate communities were also dependent on local and landscape contexts, such that in areas of high riparian degradation and agricultural cover the negative effect was aggravated. We found that channelization was associated with decreased richness and diversity and increased invasive species only when riparian degradation was also high (Extended Data Fig. 1). These interactive effects indicate potential benefits of protecting and restoring riparian habitat to mitigate the impacts of river channelization. For example, in highly channelized river stretches, the macroinvertebrate community could be partially protected by restoring the riparian habitat. Riparian vegetation provides habitat structure, shade, food resources and terrestrial habitat for aquatic insects and can control algal biomass[49,50]. In addition, riparian vegetation reduces bank erosion, thereby preserving habitat suitability for macroinvertebrates, in turn lessening navigation/channelization impacts. However, mitigation measures are also required to further improve water quality, which is often insufficient, particularly in many larger European rivers[51].

Navigation infrastructure

Fish richness tended to be higher in river segments with a higher number of locks. This is probably an impoundment effect creating more lentic habitats in the river, which then allow limnophilic species to proliferate—a finding that is corroborated by our trait analysis showing these species to be more frequent in areas of high lock densities. This, in concert with the finding of taxonomic evenness decreases in areas of high lock densities, indicates a shift in community composition near locks, and not that locks are increasing fish biodiversity. However, locks may also increase connectivity for certain species in highly fragmented rivers, because lock operation at least occasionally allows fish passage[20,52]. This is relevant for management, as oftentimes locks and dams are side by side, meaning that fish of different swimming abilities may be able to navigate through such blockages via different avenues—some via fish ladders and others via locks. Further research is needed to elucidate how locks should be best operated to reduce river fragmentation.

Richness values of both fish and macroinvertebrates were slightly higher in areas near ports. However, while statistically significant, the effect sizes were small—an order of magnitude smaller than the negative effect sizes of shipping intensity. Similar to locks, this finding probably results from shifts in community composition due to novel habitats created in ports as well as potential ballast water release therein. Ports alter the physical environment of lowland rivers by increasing depth, providing pools of standing water, and accumulating sediments[24,53]. These accumulating sediments may explain why macroinvertebrates living in sandy and gravel substrates, and fish reproducing in sandy substrates (psammophils) were positively associated with ports in our trait analysis. Ballast water mixing and release occurring in port

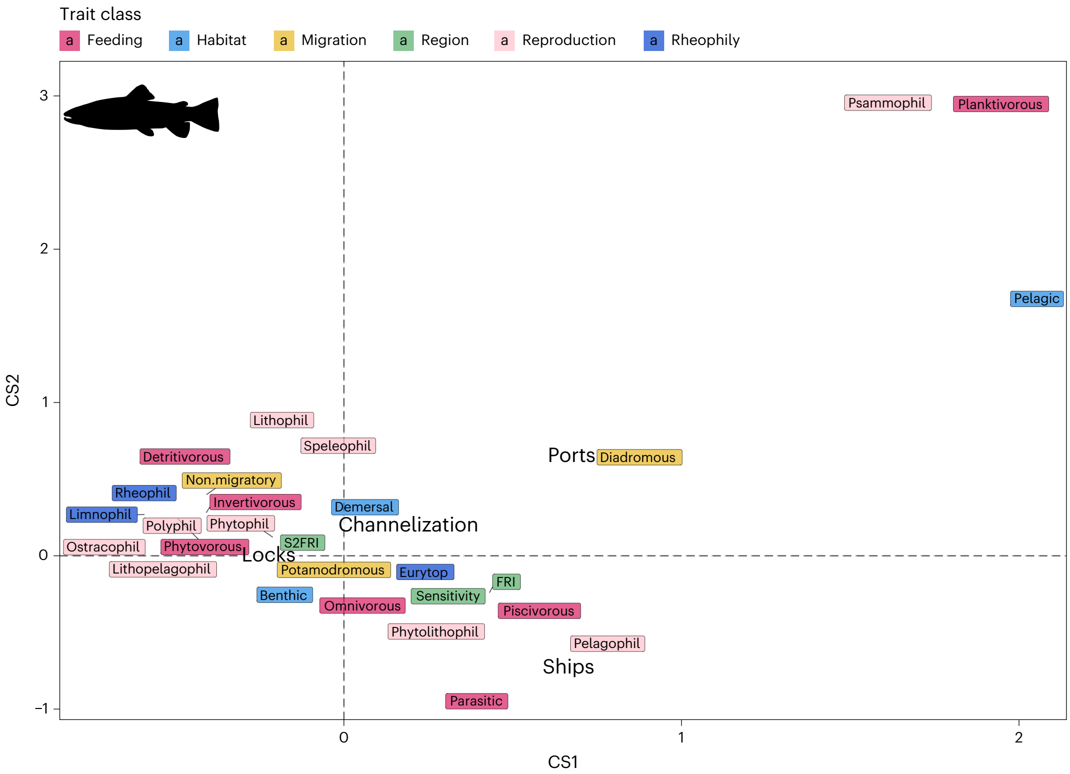


Fig. 4 | Fish trait responses to navigation. Ordinations from an RLQ–fourth-corner analysis that represents the relationships between fish traits (coloured text) and navigation pressures (bold green boxes). Both ordination axes (traits and navigation pressures) are significantly linked ($P = 0.002$). Both traits and navigation pressures with highly positive x-axis values (for example, 'Pelagic habitat' and 'Ships') are strongly associated, and the same for y-axis relationships. Axes 'CS1' and 'CS2' are species traits coefficient scores, which bound both trait and environmental variables.

areas is known to release species[54] and to spread invasive species especially by seagoing vessels[55,56]. However, here we did not find increases of invasive species in port areas. This may indicate either that the ballast water transport of non-native species by inland navigation is less relevant than in marine shipping or that the inland waterways are already widely colonized by non-native species, so that the ports did not pop up as hotspots. Further research would be warranted to scrutinize the links between ballast water and freshwater invasive and exotic species.

Conclusion

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

In addition to biodiversity declines, we observed shifts in community compositions and functional traits. These findings add to those of recent research, for example, showing shifts towards pollution-tolerant taxa in urban and agricultural streams, and climate warming shifting the average body sizes of freshwater fish communities[57,58]. We add to this by showing ship traffic to be especially negative for benthic taxa, locks to shift communities towards slow-flow taxa, and for port areas to benefit macroinvertebrates living in sandy bottom rivers. Mitigating the negative impacts on benthic taxa could be achieved via simple measures such as reducing vessel speed to reduce hydraulic forces on shoreline habitats, as well as larger efforts such as the re-establishment of shallow habitats protected from ship waves. These findings, in concert with previous work, are important for restoration plans. As a halt in freshwater biodiversity recoveries in recent years has been found[59], it is important to consider all stressors, including potentially emerging stressors such as navigation that are currently neglected, to fully restore communities. Finally, it is important to focus restoration/mitigation efforts not only on small streams but also on large rivers and balance the use of these rivers for socio-economic goods with the role they play in hosting biodiversity.

Methods

Fish and macroinvertebrate biodiversity

We combined datasets of fish ($n = 9$ datasets) and macroinvertebrate ($n = 11$) communities in large European rivers and canals from the NAVIDIV consortium (https://www.fondationbiodiversite.fr/en/the-frb-in-action/programs-and-projects/le-cesab/navidiv/), complemented by macroinvertebrate time series from Haase et al.[59] relevant for our study. We defined a 'large river' as having a Strahler order of five or greater based on the HydroSHEDS database[60]. This ensured we focused only on navigated and navigable waterways and omitted smaller rivers from the analysis because of the absence of stressors associated with navigation. However, large rivers without navigation were considered as potential reference sites. Moreover, given that larger rivers typically are more degraded than smaller rivers, the inclusion of smaller rivers may have led to an overestimation of the navigation effect because of

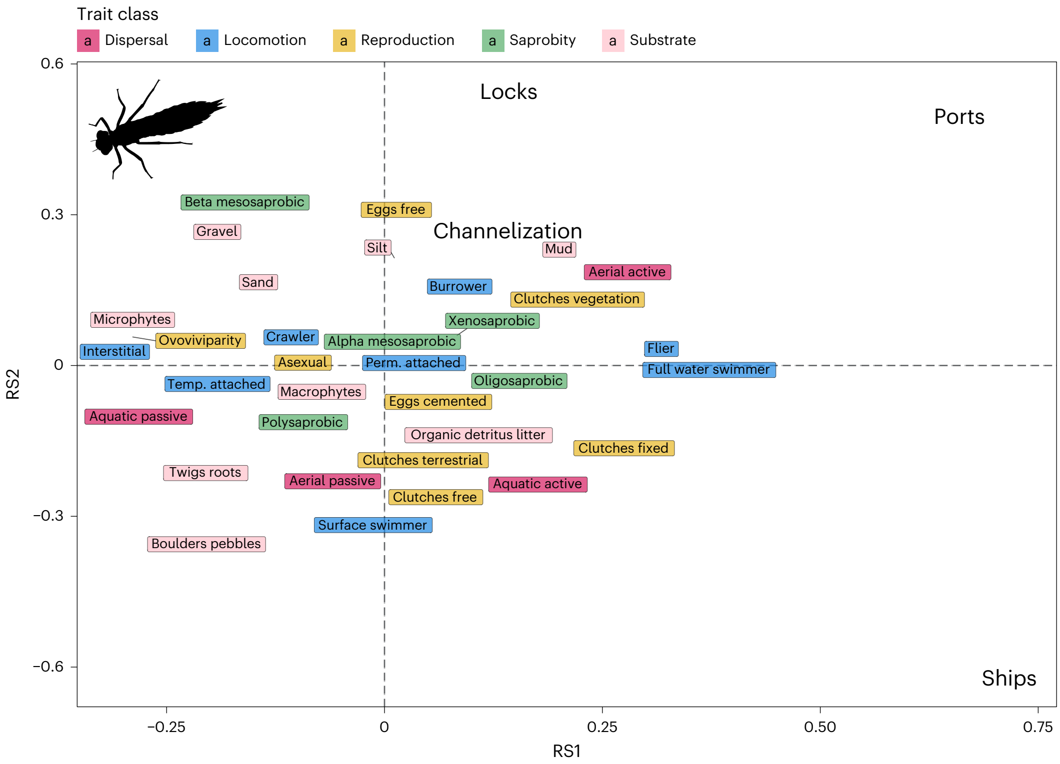


Fig. 5 | Macroinvertebrate trait responses to navigation. Ordinations from an RLQ–fourth-corner analysis that represents the relationships between macroinvertebrate traits (coloured text) and navigation pressures (bold green boxes). The axes of the two ordinations (traits and navigation pressures) are significantly linked ($P = 0.002$). Traits with highly positive y-axis values (for example, Burrower locomotion) are strongly associated with navigation pressures with highly positive y-axis values (for example, 'Locks' and 'Ports'), and the same for x-axis relationships. Axes 'RS1' and 'RS2' are environmental variable coefficient scores, which bound both trait and environmental variables.

the collinearity of river size with navigation[61]. We used data from 1992 to 2021, as the opening of the Main-Danube canal in 1992 marked the beginning of the spread of many freshwater invasive species[9]. During this time period, the total amount of goods transported by commercial navigation, a proxy for ship traffic, has remained approximately constant (see next section). One ecological community dataset consisted only of presence–absence data. These data were only used to calculate the taxonomic richness model; all other included datasets featured abundance data for multiple taxa at specific locations with spatial coordinates, years and sampling effort. While our data are pan-European, the bulk of the biodiversity data are in France and Central Europe, which aligns with the main shipping routes in Europe. To ensure that this geographic bias did not influence our results, we reran our generalized linear mixed models (GLMMs) without observations from France. This removed 4,845 fish observations, and 1,263 macroinvertebrate observations. The models resulted in the exact same interpretations (that is, no major changes in significance of model terms and interactions or R^2 values). These model outputs are provided in Supplementary Table 5.

From each dataset we calculated the taxonomic richness (as the number of taxa, most commonly at the genus level for macroinvertebrates and species level for fish), Simpson's reciprocal diversity index, using the 'diversity' function in the 'vegan' R package[62], and Simpson's evenness based on relative abundances (diversity divided by species number) of each sampling occasion. We chose to use Simpson's reciprocal diversity index, a Hill number, instead of other common metrics (for example, Shannon) because our functional metrics, calculated in the 'mFD' package, are also Hill number metrics.

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

To explore the effects of navigation on the ecological traits of these communities, we compiled ecological trait information on the traits that were expected to play a role in the response of communities. Fish traits of feeding guild, habitat, migration and reproduction were obtained from the freshwaterecology.com trait database[63]. Flow preference traits followed the FAME consortium (Development, Evaluation and Implementation of a Standardized Fish-based Assessment Method for the Ecological Status of European Rivers, EU FP5), sensitivity was obtained from van Treeck et al.[64], and fish region index (FRI) and its variation (S^2FRI) were based on Wolter et al.[65]. Macroinvertebrate traits were obtained from the Tachet database[66]. Linking these species traits to our community data, we calculated the metrics functional richness, diversity (specifically, functional dispersion of the functional space of communities[67]) and evenness, using the 'mFD' package in R[68]. The traits we use here are ecological traits, and not strictly functional traits according to ref. 69. Therefore, when we refer to functional diversity, evenness and richness, we use these terms in the broad colloquial sense to represent the diversity of organism attributes that interact with the abiotic and biotic environments (as defined in Magneville et al.[68]).

Navigation and infrastructures

Ship traffic, that is, vessel counts, was obtained from Marine Traffic (https://www.marinetraffic.com/) and compiled as the number of ships passing through 30 km stretches of river per month over the course of 2019. This grain was chosen to provide the optimal grain for our European-extent study, generating 4,174 river lengths across Europe, allowing us to compare river stretches at the continental extent. A finer grain would not have been relevant due to the linear flow of ship traffic, but a larger grain would not have allowed us to compare traffic changes between cities/ports, and our choice of grain generally aligns with the Water Framework Directives River Basin Management Plans. A comparison of the ship traffic in 2019 to independent data of ship traffic logs from locks throughout Europe including the rivers Danube, Rhine, Elbe, Spree, Oder and others provided by Zajicek et al.[12] for 1992–2015 showed that 2019 was similar to this period (Supplementary Fig. 1). Channelization was also measured at the grain of 30-km stretches. Within the same river stretches used for shipping, we calculated the total length of channelized river obtained via the Open Street Map database (https://openstreetmap.org/). Channelization represents a metric of riverine modifications that have been made for navigation, though reasons for channelization may go beyond navigation and also include manipulation of floodplain for agriculture. Almost all European navigated rivers have been channelized to some extent[70]. The location of all inland ports and locks was obtained via personal communication from the United Nations Economic Commission for Europe (UNECE) and is sourced from the UNECE Inventory of Main Standards and Parameters of the Waterway Network. We counted the number of ports and locks within a 5-km buffer (consistent with the grain of land use) around each biodiversity sampling site.

Local and landscape land use

To identify how the surrounding landscape and habitat characteristics moderate navigation's impact, we collected data on the land use and riparian degradation surrounding each biodiversity sampling site. We considered the two major land use types that are associated with the degradation of surface waters in Europe: agriculture and urbanization. We clipped land use (obtained from CORINE Land Cover 2018 (100 m positional accuracy), https://land.copernicus.eu/pan-european/corine-land-cover/clc2018) to 5-km-radius circular buffers around sampling locations. While additional research is needed to elucidate the spatial grain at which land use influences aquatic taxa, studies have shown that a grain between 1 km and 5 km is appropriate[71,72]. We found strong correlations between land use at 1 km and 5 km across our sites (Supplementary Fig. 2). Within these buffers, we obtained the surface sizes of surrounding urban and agricultural land uses for each site. To prevent collinearity issues between the two land use variables (significant Pearson's correlation test between urban and agricultural land use), we conducted a principal component analysis (PCA) on these values as the PCA creates two uncorrelated variables. We then used the site scores from each principal component (PC) that were strongly associated with each land use class. This was done for the macroinvertebrate sites, and then separately for the fish sites, such that one PCA was run on each set of sites. In macroinvertebrate sites, the first PC (PC1) had a high rotation score for urban land use, and PC2 had a high rotation score for agricultural land use. This was reversed for fish sites, such that PC1 site scores were used to represent agricultural land use, and PC2 represented urban land use. Code for this PCA and the resulting outputs (rotation scores, standard deviation, and proportional and cumulative variance) are provided in Supplementary Table 4 and in the repository for this paper linked in 'Data availability' section.

To obtain finer-grain information on habitat structure, we characterized riparian degradation at the grain of 1 km using the Green Arteries database from CORINE[73]. Within a 1-km-radius buffer around our biodiversity sampling sites, we clipped the 'potential riparian extent' (PRZ) as modelled on the basis of hydrologic and geomorphologic characteristics, and the 'actual riparian extent' (ARZ) from satellite images. Our metric of Riparian degradation around each site was then calculated as the inverse proportion of ARZ to PRZ: 1 − (ARZ/PRZ).

To control for large-scale abiotic influences and differences from one region of Europe to the next, we included data on the size of river and subcatchment for each sampling site. River size (Strahler order) and subcatchment size were both obtained from the HydroSHEDS database. We used Pfafstetter level 6 of subcatchment size (average of size of 7,972.7 m^2) because this maximized the prediction (code provided in Supplementary File 1).

Models

To assess the relationships between navigation and taxonomic and functional diversity metrics, we ran GLMMs with the function 'glmer' of the 'lme4' R package[74]. For the taxonomic richness models, a Poisson distribution was used and for all others a Gaussian distribution was used. The model structure was

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

Here, Ship Traffic was the average number of ships per month in the river stretch of the collection site and Channelization was proportion of the river that had been channelized in the river stretch of the site. Ports and Locks were the number of ports and locks within 5 km from each site, Riparian Degradation was the proportion of the riparian forest that had been lost within a 1 km buffer, and Agriculture and Urban were the site scores relating to each land use class from the PCA. Subcatchment size was the size of the Pfafstetter level six of each site, and Strahler order is the respective order of the river of a site. The random effect of (1|Study/Year) represents a nested design wherein Study represents the data source and Year represents the year that the sample was collected.

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

For macroinvertebrates, we found an effect of year on taxonomic richness—an increase in richness from 2000 to 2010, followed by a decrease from 2010 to 2020, whereas fish exhibited no trend (via a generalized additive model; see Supplementary Fig. 3 for both macroinvertebrates and fish). To control for this nonlinear pattern in diversity across years, we included a second-order polynomial term for year to the macroinvertebrate models of +(poly(yr_scaled, 2)). Plots showing the year effect on macroinvertebrates and fish are visualized in Supplementary Fig. 3. Finally, for the invasive species abundance model for both fish and macroinvertebrates, we included an 'offset' term of total community abundance (log transformed) to control for large samples.

Collinearity between our fixed effects was checked via their variable inflation factor scores and all were below 2, indicating the model was acceptable (for example, Graham[75]; Supplementary Table 1). All predictor terms were standardized to zero mean and standard deviation of ±1. Scatterplots of pairwise comparisons of predictor values are provided in Supplementary Fig. 4. We identified the marginal effects of shipping (a partial derivative from the GLMM equation) at various levels of landscape degradation (Fig. 3a–d), which was obtained using the 'margins' and 'cplot' functions in the 'margins' R package. Figure 3e,f were produced using the 'interact_plot' function in the 'interactions' R package, which allowed us to plot regressions lines at specific levels of our moderator variable (urban land use) to explore interactions[76,77]. Figures were produced using the 'ggplot' and 'ggpubr' R packages[78,79]. Silhouettes of fish and macroinvertebrates were obtained from the 'rphylopic' R package, and belong to Marie Russell (2020-12-29) licence (https://creativecommons.org/licenses/by/3.0/) and Guillaume Dera (2022-12-01) licence (https://creativecommons.org/publicdomain/zero/1.0/).

Trait analysis

To understand the guilds of species responding to navigation, we analysed the relationships between functional traits and navigation pressures via an RLQ–fourth-corner analysis, which quantifies the covariance between traits and environmental variables, mediated by the species abundances[28]. This multivariate method analyses the links between species traits and environmental variables via an ordination approach. Specifically, we combined the environmental variables (ship traffic, count of ports and locks, and rate of channelization) at sites (creating a matrix R), the species abundances at these sites (matrix L) and the species traits (matrix Q) to create a 'fourth corner' (matrix M) that is an environmental–trait relationship matrix. Each of these matrices is turned into ordinations to allow for direct comparability and computational analysis (via a correspondence analysis to the species table and a PCA to the environmental and trait tables), and then the analysis finds linear combinations of environmental variables and linear combinations of traits that maximize their squared cross-covariance. A permutation test ($n = 999$ permutations) is then conducted to test global significance of the traits–environment relationships (Supplementary Table 2). As this is an ordination approach, this generates suites of traits that commonly co-occur and identifies how they relate to environmental ordination axes. This analysis was conducted using the 'ade4' R package[80], applying the function 'rlq' to join the three matrices, and the 'fourthcorner.rlq' function was used to run the permutation analysis following Dray et al.[28] (Supplementary Table 2). The same suite of traits used to calculate functional richness, diversity and evenness were used in this RLQ–fourth-corner analysis for both fish and macroinvertebrates.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data and R code used in this study are available in an open-source repository (https://github.com/aaronsexton/Sextonetal_Navigation_Biodiversity_Supplementals).

Code availability

R code used in this study are also available in the same open-source repository as the data (https://github.com/aaronsexton/Sextonetal_Navigation_Biodiversity_Supplementals).

References

1. Reid, A. J. et al. Emerging threats and persistent conservation challenges for freshwater biodiversity. *Biol. Rev.* **94**, 849–873 (2019).
2. *Living Planet Report—2018: Aiming Higher* (World Wildlife Foundation, 2018).
3. Dias, M. S. et al. Anthropogenic stressors and riverine fish extinctions. *Ecol. Indic.* **79**, 37–46 (2017).
4. Tickner, D. et al. Bending the curve of global freshwater biodiversity loss: an emergency recovery plan. *Bioscience* **70**, 330–342 (2020).
5. Dudgeon, D. et al. Freshwater biodiversity: importance, threats, status and conservation challenges. *Biol. Rev.* **81**, 163–182 (2006).
6. Naiades programme for post-Covid growth. *Inland Navigation Europe* https://www.inlandnavigation.eu/naiades-programme-for-post-covid-growth/ (2020).
7. He, F. Z. et al. Impacts of loss of free-flowing rivers on global freshwater megafauna. *Biol. Conserv.* **263**, 109335 (2021).
8. Belletti, B. et al. More than one million barriers fragment Europe's rivers. *Nature* **588**, 436 (2020).
9. Leuven, R. et al. The river Rhine: a global highway for dispersal of aquatic invasive species. *Biol. Invasions* **11**, 1989–2008 (2009).
10. Hanafiah, M. M., Leuven, R., Sommerwerk, N., Tockner, K. & Huijbregts, M. A. J. Including the introduction of exotic species in life cycle impact assessment: the case of inland shipping. *Environ. Sci. Technol.* **47**, 13934–13940 (2013).
11. Nunes, A. L., Tricarico, E., Panov, V. E., Cardoso, A. C. & Katsanevakis, S. Pathways and gateways of freshwater invasions in Europe. *Aquat. Invasions* **10**, 359–370 (2015).
12. Zajicek, P., Radinger, J. & Wolter, C. Disentangling multiple pressures on fish assemblages in large rivers. *Sci. Total Environ.* **627**, 1093–1105 (2018).
13. Zajicek, P. & Wolter, C. The effects of recreational and commercial navigation on fish assemblages in large rivers. *Sci. Total Environ.* **646**, 1304–1314 (2019).
14. Bergman, J. N. et al. Historical, contemporary, and future perspectives on a coupled social-ecological system in a changing world: Canada's historic Rideau Canal. *Environ. Rev.* **30**, 72–87 (2022).
15. Xiong, F. Y. et al. Riparian land use and in-channel stressors drive fish community structure in the Yangtze River. *Landsc. Ecol.* **36**, 3079–3095 (2021).
16. Jackson, M. C. & Grey, J. Accelerating rates of freshwater invasions in the catchment of the River Thames. *Biol. Invasions* **15**, 945–951 (2013).
17. Huckstorf, V., Lewin, W. C., Mehner, T. & Wolter, C. Impoverishment of YOY-fish assemblages by intense commercial navigation in a large lowland river. *River Res. Appl.* **27**, 1253–1263 (2011).
18. Wolter, C. Conservation of fish species diversity in navigable waterways. *Landsc. Urban Plan.* **53**, 135–144 (2001).
19. Zhang, H. et al. Rapid change in Yangtze fisheries and its implications for global freshwater ecosystem management. *Fish Fish.* **21**, 601–620 (2020).
20. Vergeynst, J. et al. Shipping canals on the downstream migration route of European eel (*Anguilla anguilla*): opportunity or bottleneck? *Ecol. Freshw. Fish.* **30**, 73–87 (2021).
21. Brink, F. W. B., Velde, G., Buijse, A. D. & Klink, A. G. Biodiversity in the Lower Rhine and Meuse river-floodplains: its significance for ecological river management. *Neth. J. Aquat. Ecol.* **30**, 129–149 (1996).
22. Décamps, H. River networks as biodiversity hotlines. *C. R. Biol.* **334**, 420–434 (2011).
23. Manfrin, A. et al. The effect of lateral connectedness on the taxonomic and functional structure of fish communities in a lowland river floodplain. *Sci. Total Environ.* **719**, 137169 (2020).
24. Keller, R. P., Drake, J. M., Drew, M. B. & Lodge, D. M. Linking environmental conditions and ship movements to estimate invasive species transport across the global shipping network. *Divers. Distrib.* **17**, 93–102 (2011).
25. Briski, E., Ghabooli, S., Bailey, S. A. & MacIsaac, H. J. Invasion risk posed by macroinvertebrates transported in ships' ballast tanks. *Biol. Invasions* **14**, 1843–1850 (2012).
26. Paavola, M., Laine, A. O., Helavuori, M. & Kraufvelin, P. Profiling four brackish-water harbours: zoobenthic composition and invasion status. *Boreal Environ. Res.* **13**, 159–175 (2008).
27. Vinebrooke, R. D. et al. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. *Oikos* **104**, 451–457 (2004).
28. Dray, S. et al. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology* **95**, 14–21 (2014).
29. Gabel, F., Lorenz, S. & Stoll, S. Effects of ship-induced waves on aquatic ecosystems. *Sci. Total Environ.* **601**, 926–939 (2017).
30. Gabel, F., Stoll, S., Fischer, P., Pusch, M. T. & Garcia, X. F. Waves affect predator–prey interactions between fish and benthic invertebrates. *Oecologia* **165**, 101–109 (2011).

31. Grygoruk, M., Frak, M. & Chmielewski, A. Agricultural rivers at risk: dredging results in a loss of macroinvertebrates. preliminary observations from the Narew Catchment. *Pol. Water* **7**, 4511–4522 (2015).
32. Hooper, D. U. et al. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* **75**, 3–35 (2005).
33. Cao, X. et al. Loss of biodiversity alters ecosystem function in freshwater streams: potential evidence from benthic macroinvertebrates. *Ecosphere* **9**, e02445 (2018).
34. Effert-Fanta, E. L., Fischer, R. U. & Wahl, D. H. Effects of riparian forest buffers and agricultural land use on macroinvertebrate and fish community structure. *Hydrobiologia* **841**, 45–64 (2019).
35. Elmhagen, B. et al. Interacting effects of change in climate, human population, land use, and water use on biodiversity and ecosystem services. *Ecol. Soc.* **20**, 10 (2015).
36. Wen, Y. R., Schoups, G. & van de Giesen, N. Organic pollution of rivers: combined threats of urbanization, livestock farming and global climate change. *Sci. Rep.* **7**, 43289 (2017).
37. Booth, D. B. et al. Reviving urban streams: land use, hydrology, biology, and human behavior. *J. Am. Water Resour. Assoc.* **40**, 1351–1364 (2004).
38. Halstead, J. A., Kliman, S., Berheide, C. W., Chaucer, A. & Cock-Esteb, A. Urban stream syndrome in a small, lightly developed watershed: a statistical analysis of water chemistry parameters, land use patterns, and natural sources. *Environ. Monit. Assess.* **186**, 3391–3414 (2014).
39. Wantzen, K. M. et al. Urban stream and wetland restoration in the Global South—a DPSIR analysis. *Sustainability* **11**, 4975 (2019).
40. Winter, J. G. & Duthie, H. C. Effects of urbanization on water quality, periphyton and invertebrate communities in a southern ontario stream. *Can. Water Resour. J.* **23**, 245–257 (1998).
41. Martins, R. T., Couceiro, S. R. M., Melo, A. S., Moreira, M. P. & Hamada, N. Effects of urbanization on stream benthic invertebrate communities in Central Amazon. *Ecol. Indic.* **73**, 480–491 (2017).
42. Gal, B., Szivak, I., Heino, J. & Schmera, D. The effect of urbanization on freshwater macroinvertebrates—knowledge gaps and future research directions. *Ecol. Indic.* **104**, 357–364 (2019).
43. Fetters, K. J., Costello, D. M., Hammerschmidt, C. R. & Burton, G. A. Toxicological effects of short-term resuspension of metal-contaminated freshwater and marine sediments. *Environ. Toxicol. Chem.* **35**, 676–686 (2016).
44. Prygiel, E. et al. Active biomonitoring for assessing effects of metal polluted sediment resuspension on gammarid amphipods during fluvial traffic. *Environ. Pollut.* **218**, 129–139 (2016).
45. Floehr, T. et al. Solution by dilution?—A review on the pollution status of the Yangtze River. *Environ. Sci. Pollut. Res.* **20**, 6934–6971 (2013).
46. Wolter, C. in *Urban Ecology. An International Perspective on the Interaction between Humans and Nature* (eds Marzluff, J. et al.) 425–436 (Springer, 2008).
47. Xu, X. M. et al. Environmental DNA metabarcoding reveals the impacts of anthropogenic pollution on multitrophic aquatic communities across an urban river of western China. *Environ. Res.* **216**, 114512 (2023).
48. Czegledi, I., Kern, B., Toth, R., Seress, G. & Eros, T. Impacts of urbanization on stream fish assemblages: the role of the species pool and the local environment. *Front. Ecol. Evol.* https://doi.org/10.3389/fevo.2020.00137 (2020).
49. Li, H. W. et al. Cumulative effects of riparian disturbances along high desert trout streams of the John Day Basin, Oregon. *Trans. Am. Fish. Soc.* **123**, 627–640 (1994).
50. Corline, N. J. et al. When humans work like beavers: riparian restoration enhances invertebrate gamma diversity and habitat heterogeneity. *Restor. Ecol.* **31**, e13690 (2023).
51. Lemm, J. U. et al. Multiple stressors determine river ecological status at the European scale: towards an integrated understanding of river status deterioration. *Glob. Change Biol.* **27**, 1962–1975 (2021).
52. Lin, P. C., Brosse, S., Gao, X., Liu, C. C. & Liu, H. Z. Species composition and temporal pattern of fish passing through the navigation locks in the middle reach of Yangtze River: implications for fish conservation. *J. Appl. Ichthyol.* **29**, 1441–1444 (2013).
53. Samsami, F., Haghshenas, S. A. & Soltanpour, M. Physical and rheological characteristics of sediment for nautical depth assessment in bushehr port and its access channel. *Water* **14**, 4116 (2022).
54. Costello, K. E., Lynch, S. A., McAllen, R., O'Riordan, R. M. & Culloty, S. C. Assessing the potential for invasive species introductions and secondary spread using vessel movements in maritime ports. *Mar. Pollut. Bull.* **177**, 113496 (2022).
55. Wan, Z., Shi, Z. F., Nie, A. W., Chen, J. H. & Wang, Z. J. Risk assessment of marine invasive species in Chinese ports introduced by the global shipping network. *Mar. Pollut. Bull.* **173**, 112950 (2021).
56. Molnar, J. L., Gamboa, R. L., Revenga, C. & Spalding, M. D. Assessing the global threat of invasive species to marine biodiversity. *Front. Ecol. Environ.* **6**, 485–492 (2008).
57. Rumschlag, S. L. et al. Density declines, richness increases, and composition shifts in stream macroinvertebrates. *Sci. Adv.* **9**, eadf4896 (2023).
58. Arranz, I., Grenouillet, G. & Cucherousset, J. Human pressures modulate climate-warming-induced changes in size spectra of stream fish communities. *Nat. Ecol. Evol.* **7**, 1072–1078 (2023).
59. Haase, P. et al. The recovery of European freshwater biodiversity has come to a halt. *Nature* **620**, 582–588 (2023).
60. Lehner, B., Verdin, K. & Jarvis, A. New global hydrography derived from spaceborne elevation data. *Eos Trans. AGU* **89**, 93–94 (2008).
61. Nilsson, C., Reidy, C. A., Dynesius, M. & Revenga, C. Fragmentation and flow regulation of the world's large river systems. *Science* **308**, 405–408 (2005).
62. Oksanen, J. et al. (2022) vegan: Community Ecology Package. R package version 2.6-2. https://cran.r-project.org/package=vegan (2022).
63. Schmidt-Kloiber, A. & Hering, D. www.freshwaterecology.info—an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecol. Indic.* **53**, 271–282 (2015).
64. van Treeck, R., Van Wichelen, J. & Wolter, C. Fish species sensitivity classification for environmental impact assessment, conservation and restoration planning. *Sci. Total Environ.* **708**, 135173 (2020).
65. Wolter, C. et al. Characterization of European lampreys and fishes by their longitudinal and lateral distribution traits. *Ecol. Indic.* **123**, 107350 (2021).
66. Tachet, H., Richoux, P., Bournaud, M. & Usseglio-Polatera, P. *Invertébrés d'eau douce: systématique, biologie, écologie* 3rd edn (CNRS Éditions, 2010).
67. Villéger, S., Mason, N. W. H. & Mouillot, D. New multidimensional functional diversity indices for a multifaceted framework in functional ecology\. *Ecology* **89**, 2290–2301 (2008).
68. Magneville, C. et al. mFD: a computation of functional spaces and functional indices. R package version 1.0.0. https://github.com/CmlMagneville/mFD (2021).
69. Violle, C. et al. Let the concept of trait be functional! *Oikos* **116**, 882–892 (2007).
70. Petts, G. E., Möller, H. & Roux, A. L. *Historical Change of Large Alluvial Rivers: Western Europe* (John Wiley & Sons, 1989).

71. Wang, L. Z., Lyons, J. & Kanehl, P. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environ. Manag.* **28**, 255–266 (2001).
72. Bergerot, B., Hugueny, B. & Belliard, J. When local extinction and colonization of river fishes can be predicted by regional occupancy: the role of spatial scales. *PLoS ONE* **8**, e84138 (2013).
73. Weissteiner, C. J. et al. Europe's green arteries—a continental dataset of riparian zones. *Remote Sens.* **8**, (2016).
74. Bates, D., Maechler, M., Bolker, B. & Walker, S. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* https://doi.org/10.18637/jss.v067.i01 (2015).
75. Graham, M. H. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**, 2809–2815 (2003).
76. Leeper, T. J. margins: marginal effects for model objects. R package version 0.3.26. https://cran.r-project.org/package=margins (2021).
77. Long, J. A. interactions: comprehensive, user-friendly toolkit for probing interactions. R package version 1.1.0. https://cran.r-project.org/package=interactions (2019).
78. Wickham, H. *ggplot2: Elegant Graphics for Data Analysis* (Springer, 2016).
79. Kassambara, A. ggpubr: 'ggplot2' based publication ready plots. R package version 0.4.0. https://cran.r-project.org/package=ggpubr (2020).
80. Dray, S., Dufour, A. & Chessel, D. The ade4 package—II: two-table and K-table methods. *R News* **7**, 47–52 (2007).

Acknowledgements

We thank N. Casajus for providing continued assistance and recommendations on analyses and data representation. Additionally, we thank the UNECE for providing locations of inland ports locks and canals. This research is a product of the NAVIDIV group funded by the synthesis centre CESAB of the French Foundation for Research on Biodiversity (FRB; www.fondationbiodiversite.fr) and by the French National Research Program on Transport Infrastructure, Territories, Ecosystems and Landscapes (ITTECOP; https://www.ittecop.fr/en/) of the French Ministry of Ecological Transition (MTE). S.C.J acknowledges funding through the Leibniz Competition project 'Freshwater Megafauna Futures'. P.H. received funding from the EU Horizon 2020 project eLTER PLUS (grant agreement no. 871128). A.L. received funding from the Spanish Ministry of Science and Innovation (project PID2020-115830GB-100). A.D.B. received funding from EU Horizon 2020 MERLIN project (grant agreement no. 101036337).

Author contributions

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., S.C.J., C.G.L. and A.S.-K. contributed to initial ideas. A.N.S. and A.J. designed and conducted analyses. P.H., M.A.E.F, G.A., J.-F.F., A.D., V.E., Z.C., M.F., P.G., G.V., M.C.-A., A.L. A.M., R.B.S., J.S.S., R.V., E.W., C.W., E.T. and J.B. provided biodiversity data, A.N.S. wrote the first draft of the manuscript and all authors provided important input on manuscript writing.

Competing interests

The authors declare no competing interests.

Additional information

Extended data is available for this paper at https://doi.org/10.1038/s41559-024-02414-8.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41559-024-02414-8.

Correspondence and requests for materials should be addressed to Aaron N. Sexton.

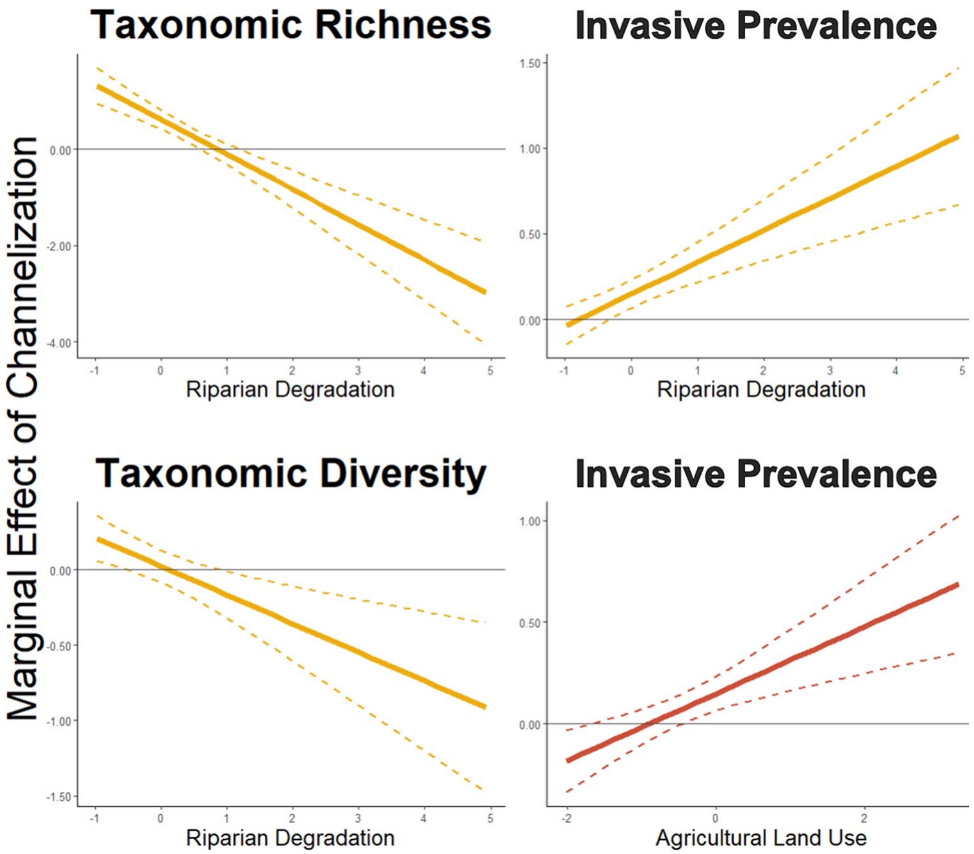
Peer review information *Nature Ecology & Evolution* thanks Ignasi Arranz, Thiago Couto and the other, anonymous, reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

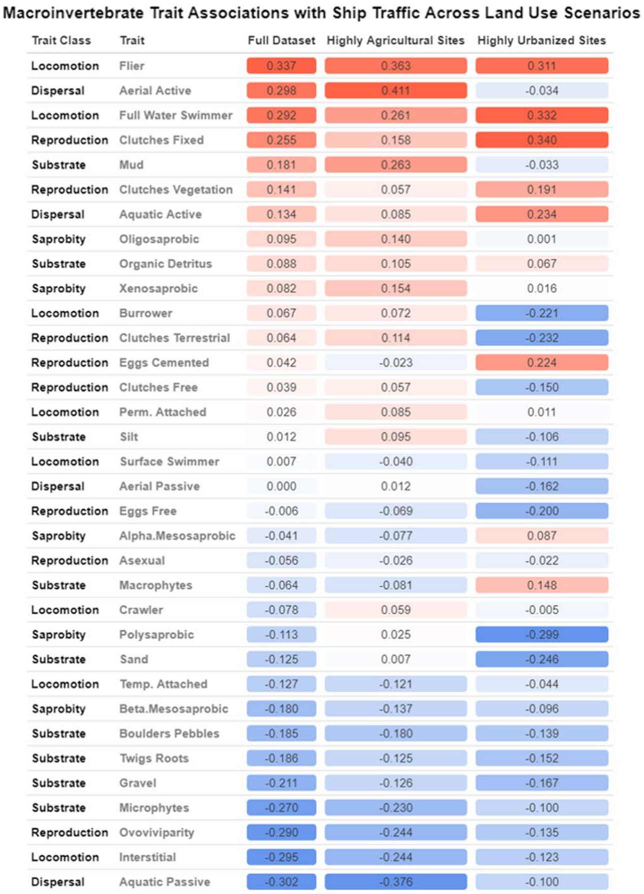
---

[1]Fondation pour la Recherche sur la Biodiversité, Centre de Synthèse et d'Analyse sur la Biodiversité, Montpellier, France. [2]Université de Strasbourg, ENGEES, CNRS, LIVE UMR 7362, Strasbourg, France. [3]Department of Fish Biology, Fisheries and Aquaculture, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany. [4]University of Paris-Saclay, INRAE, HYCAR, Antony, France. [5]Department of Freshwater Ecology and Water Quality, Deltares, Delft, the Netherlands. [6]Aquaculture and Fisheries Group, Wageningen University & Research, Wageningen, the Netherlands. [7]Departamento de Sistemas y Recursos Naturales, E.T.S. Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Madrid, Spain. [8]UNESCO Chair 'Fleuves et Patrimoine', CNRS UMRS CITERES, Tours University, Tours, France. [9]CNRS UMR LIVE, Strasbourg University, Strasbourg, France. [10]Department of Community and Ecosystem Ecology, Leibniz Institute of Freshwater Ecology and Inland Fisheries, Berlin, Germany. [11]Geography Department, Humboldt-Universität zu Berlin, Berlin, Germany. [12]Centre for Sustainable Aquatic Research, Department of Biosciences, Swansea University, Swansea, UK. [13]CIM Marine Reseach Center, University of Vigo, Vigo, Spain. [14]Institute of Hydrobiology and Aquatic Ecosystem Management, University of Natural Resources and Life Sciences, BOKU Vienna, Vienna, Austria. [15]Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany. [16]Faculty of Biology, University of Duisburg, Essen, Germany. [17]Department of Animal Sciences and Aquatic Ecology, Ghent University, Ghent, Belgium. [18]INRAE, Aix Marseille University, RECOVER, Aix-en-Provence, France. [19]ARALEP—Ecologie des Eaux Douces, Villeurbanne, France. [20]Environmental Research and Innovation Department, Luxembourg Institute of Science and Technology, Belvaux, Luxembourg. [21]Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Sofia, Bulgaria. [22]Department of Hydrobiology, University of Pécs, Pécs, Hungary. [23]HUN-REN Balaton Limnological Research Institute, Tihany, Hungary. [24]Department of Tisza Research, Institute of Aquatic Ecology, Centre for Ecological Research, Debrecen, Hungary. [25]FEHM Lab, Institute of Environmental Assessment and Water Research IDAEA, CSIC, Barcelona, Spain. [26]Department of Plant Biology and Ecology, University of the Basque Country, Leioa, Spain. [27]Laboratoire National d'Hydraulique et Environnement, EDF R&D, Chatou, France. [28]University Alliance Ruhr, Research Center One Health Ruhr, Essen, Germany. [29]Environment Agency, VMM Flanders, Aalst, Belgium. [30]Conservation Ecology Center, Smithsonian's National Zoo and Conservation Biology Institute, Front Royal, VA, USA. ✉e-mail: aaron.sexton@fondationbiodiversite.fr



Extended Data Fig. 1 | Macroinvertebrate's response to channelization is dependent on riparian degradation and agricultural cover. The panels show the marginal effect of channelization from the GLMMs on macroinvertebrate communities along a gradient of riparian degradation and agricultural land use. A negative value on the y-axis indicates a negative impact of channelization on said metric (for example a decrease in taxonomic richness), and a value at 0 (grey horizontal line) indicates a null effect. Left panel shows the relationships of taxonomic richness and right panel shows the prevalence of invasive taxa. Predictors were standardized to zero mean and a SD of ±1.

https://doi.org/10.1038/s41559-024-02414-8



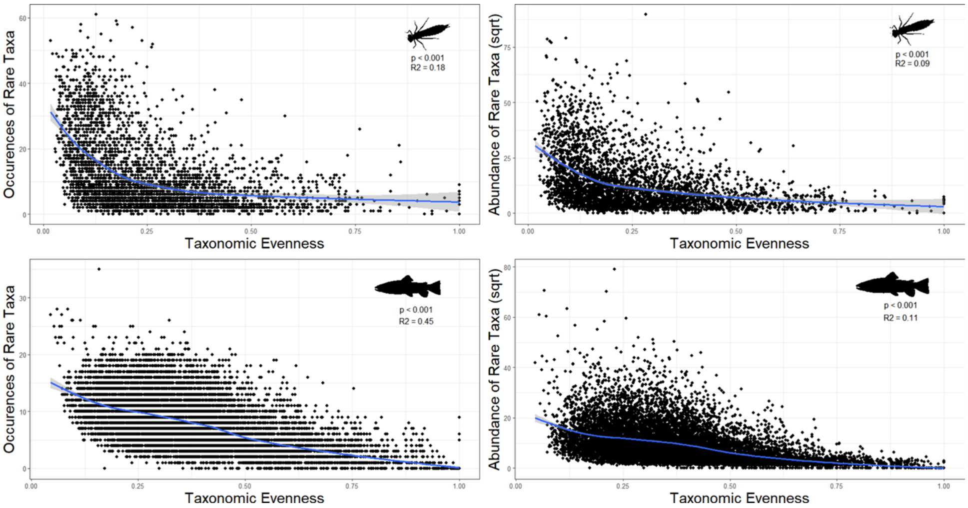
Macroinvertebrate Trait Associations with Ship Traffic Across Land Use Scenarios

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

Extended Data Fig. 2 | Fish and macroinvertebrate trait relationships with ship traffic across different land use scenarios. Trait scores associated with the environmental axis of heightened ship traffic in the RLQ analysis are shown in the 'Full Dataset' column, and are the values shown in the ordination of Figs. 4 and 5. Columns two and three of each table show the trait associations with heightened ship traffic when the RLQ is re-run in highly agricultural sites (those with the top 25% of agricultural cover across the datasets) and in highly urbanized sites.



Extended Data Fig. 3 | Relationships between taxonomic evenness and the abundance and occurrences of rare species in fish and macroinvertebrates. We defined a rare species as a species whose abundance accounting for less than 25% of the total community abundance (see Supplementary File 2 for details). Blue line represents the model regression and the area in grey surrounding the line represented the 95% confidence interval.

nature portfolio

Corresponding author(s): Aaron N. Sexton

Last updated by author(s): Apr 8, 2024

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our Editorial Policies and the Editorial Policy Checklist.

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	Data were collected and analysed using R version 4.1.2.
Data analysis	Data were collected and analysed using R version 4.1.2.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our policy

All data and R code used in this study are available in an open-source repository (https://github.com/aaronsexton/Sextonetal_Navigation_Biodiversity_Supplementals).

Research involving human participants, their data, or biological material

Policy information about studies with human participants or human data. See also policy information about sex, gender (identity/presentation), and sexual orientation and race, ethnicity and racism.

Reporting on sex and gender	This information has not been collected.
Reporting on race, ethnicity, or other socially relevant groupings	This information has not been collected.
Population characteristics	This information has not been collected.
Recruitment	This information has not been collected.
Ethics oversight	This information has not been collected.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Analysis of fish and macroinvertebrate communities in European rivers over 32 years shows that inland ship traffic is associated with declining taxonomic richness, diversity and trait richness, and increased taxonomic evenness
Research sample	Freshwater fish and macroinvertebrate communities in large European rivers. 19,592 observations from 4,049 sampling sites. These communities were selected to determine the impact of navigation on biodiversity, as previous studies have shown these taxa to be responsive to degradation and navigation, and the data on them were well dispersed across Europe.
Sampling strategy	Sampling was conducted by individual researchers, and design followed pre-determined strategies commonly used in their resepective fields (freshwater fish and macroinvertebrate ecology).
Data collection	Fish and macroinvertebrates were collected in the field, with exact locations recorded, and data were compiled afterwards.
Timing and spatial scale	1992-2022 in large European rivers. 1992 was the opening of the Main-Danube canal, which began the modern era of European Freshwater navigation, and only large rivers can be navigated.
Data exclusions	No data were excluded.
Reproducibility	Data and code used to run these analyses are all publicly available at the corresponding's author GitHub, and have been archived on Zenodo.
Randomization	Organisms were classified taxonomically, observations were grouped by the data provider to maintain consistency in collection methods. Data provider was included as a random effect in the models, as was year
Blinding	Blinding was not possible, because we needed to ensure that data remained grouped by data provider, as this was a random effect in our models.

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☐	☒ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern
☒	☐ Plants

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Animals and other research organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research, and Sex and Gender in Research

Laboratory animals	Study did not include laboratory animals.
Wild animals	Fish were caught in the wild and immediately released following idenfication. Macroinvertebrates were collected in the field and identified in the lab after being killed. This was necessary to provide proper identification to genus or species level.
Reporting on sex	Information has not been collected.
Field-collected samples	Study did not include laboratory samples.
Ethics oversight	No ethics approval was needed, as all field collected data had already been conducted before our work on this publication/analysis began.

Note that full information on the approval of the study protocol must also be provided in the manuscript.

Plants

Seed stocks	*Report on the source of all seed stocks or other plant material used. If applicable, state the seed stock centre and catalogue number. If plant specimens were collected from the field, describe the collection location, date and sampling procedures.*
Novel plant genotypes	*Describe the methods by which all novel plant genotypes were produced. This includes those generated by transgenic approaches, gene editing, chemical/radiation-based mutagenesis and hybridization. For transgenic lines, describe the transformation method, the number of independent lines analyzed and the generation upon which experiments were performed. For gene-edited lines, describe the editor used, the endogenous sequence targeted for editing, the targeting guide RNA sequence (if applicable) and how the editor was applied.*
Authentication	*Describe any authentication procedures for each seed stock used or novel genotype generated. Describe any experiments used to assess the effect of a mutation and, where applicable, how potential secondary effects (e.g. second site T-DNA insertions, mosiacism, off-target gene editing) were examined.*