Inland navigation is a driver of freshwater biodiversity declines in Europe

Aaron Sexton (✉ aaron.niles.sexton@gmail.com)  
Fondation pour la Recherche sur la biodiversité  https://orcid.org/0000-0002-8926-3872

Jean-Nicolas Beisel  
Université de Strasbourg, ENGEES, CNRS, LIVE UMR 7362, F-67000 Strasbourg, France.

Cybill Staentzel  
Université de Strasbourg, ENGEES, CNRS, LIVE UMR 7362, F-67000 Strasbourg, France.

Christian Wolter  
Leibniz-Institute of Freshwater Ecology and Inland Fisheries

Evelyne Tales  
University of Paris-Saclay, INRAE, HYCAR, Antony, France.

Jérôme Belliard  
University of Paris-Saclay, INRAE, HYCAR, Antony, France.  https://orcid.org/0000-0001-8757-125X

Anthonie Buijse  
Stichting Deltares  https://orcid.org/0000-0002-9759-8189

Vanessa Martinez Fernández  
Departamento de Sistemas y Recursos Naturales, E.T.S. Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid.

Karl Wantzen  
UNESCO Chair “Fleuves et Patrimoine”, CNRS UMRS CITERES, Tours University, 37000 Tours, and CNRS UMR LIVE, Strasbourg University, France.

Sonja Jähnig  
Leibniz-Institute of Freshwater Ecology and Inland Fisheries  https://orcid.org/0000-0002-6349-9561

Carlos García de Leaniz  
Swansea University

Astrid Schmidt-Kloiber  
University of Natural Resources and Life Sciences  https://orcid.org/0000-0001-8839-5913

Peter Haase  
Senckenberg Research Institute and Natural History Museum Frankfurt  https://orcid.org/0000-0002-9340-0438

Marie Forio  
Ghent University

Gaët Archambaud  
INRAE, Aix Marseille Univ, RECOVER, Aix-en-Provence, France
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Abstract

Freshwater navigation is expected to increase in the coming years, being promoted as a low-carbon form of transport. However, we currently lack knowledge on how this will impact biodiversity at large scales and interact with existing stressors. We addressed this knowledge gap by analyzing fish and macroinvertebrate community time series spanning the last 30 years across large European rivers comprising 19,592 observations from 4,049 sampling sites. We found ship traffic to be associated with biodiversity declines, i.e. decreases in fish and macroinvertebrate taxonomic richness and diversity, and trait richness. Shipping was also associated with increases in taxonomic evenness, which, in concert with richness decreases, can likely be attributed to losses in rare/smaller populations. In particular, shipping was especially harmful for benthic taxa and those preferring slow flows. These effects were often dependent on local land use and degradation. In fish, the negative impacts of shipping were highest in urban and agricultural landscapes. Regarding navigation infrastructure, the negative impact of channelization on macroinvertebrates was only evident when riparian degradation was also high. Our results demonstrate the risk of increasing inland navigation on freshwater biodiversity. Integrative waterway management accounting for riparian and landscape characteristics could help to mitigate these impacts.

Introduction

Freshwater ecosystems are among the most diverse in the world (Reid et al. 2019) but populations of freshwater vertebrate species have declined globally by over 80% since 1970 (WWF 2018). In Europe and North America, freshwater fish extinction rates are over 100 times greater than natural extinction rates (Dias et al. 2017). Efforts are being made to halt these declines as freshwater ecosystems harbor vital ecological, economic, and cultural values. 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 water quality decline and the introduction of aquatic invasive species (Dudgeon et al. 2006). In general, local stressors like habitat loss, have appeared to be more important for freshwater biodiversity declines than regional drivers such as warming (Morris et al. 2022).

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 practiced for centuries but is expected to increase by 50% in Europe by 2050 as it is being touted as a carbon-friendly mode of transport (INE 2020). This rise in shipping will not only mean more ship traffic, but will also require the modification of navigation infrastructures (e.g., heavier embankments, larger locks and ports, additional waterways) that will impact freshwater ecosystems in ways which are difficult to predict (He et al. 2021). In contrast to global change stressors, inland navigation and its infrastructures have largely been investigated as being vectors for invasive species spread, and not nearly as much for their direct impact on facets of native biodiversity such as richness, evenness and functional trait responses (Leuven et al. 2009; Hanafiah et al. 2013; Nunes et al. 2015). Additionally, with few exceptions (Zajicek et
al. 2018; Zajicek and Wolter 2019), most research in inland navigation has been conducted at the local scale, examining the effects of a specific lock, river or catchment (e.g., Bergman et al. 2022; Xiong et al. 2021; Jackson and Grey 2013; Huckstorf et al. 2011). These studies have shown that inland navigation constitutes a significant pressure on freshwater biodiversity. Specifically, these local studies have shown navigation to decrease fish abundances and reproduction, especially that of limnophilic fish (Xiong et al. 2021; Huckstorf et al. 2011), reduce fisheries and other riverine ecosystem services.

Given that most studies have addressed different navigation-related effects, taxa, and local contexts, drawing generalizations on the overall effect of inland navigation at a large scale is fraught with uncertainty. This endeavor is particularly challenged by the potential context-dependency of navigation-biodiversity relationships. For example, the landscape (e.g. urban vs. agricultural areas) and natural habitat conditions (channelized rivers which may have a disconnect to the floodplain) are both known to be important determinants of freshwater communities (Brink et al. 1996; Décamps 2011; Manfrin et al. 2020). Therefore, analyses of fine-scale observations across multiple land use contexts are required to assess whether the impact of inland navigation is consistent across catchments, and if this impact interacts with other known local and landscape contextual stressors.

To address these knowledge gaps, we analyzed how inland navigation impacts taxonomic and trait, or functional, richness, diversity, and evenness of freshwater fish and macroinvertebrate communities, as well as the prevalence of invasive taxa, using several local biodiversity datasets. Additionally, we tested how navigation stressors (ship traffic, density of ports and locks, and degree of river channelization) interact with land use and riparian degradation. We hypothesized a consistently negative effect of ship traffic on taxonomic and functional richness and diversity. Additionally, in ports, where ships are docking and in close contact, the prevalence of invasive taxa would be highest, as has been documented in marine and estuarine systems (Keller et al. 2011). Moreover, we aimed to evaluate how land use and riparian degradation would alter the effects of navigation. We hypothesized that navigation's negative impact would be lessened in highly degraded landscapes. This hypothesis rests on the assumption that when degradation is high, an additional stressor of ship traffic would exert a similar pressure on these communities, thereby hampering its effect or detection. Alternatively, land use and riparian degradation could aggravate the effect of inland navigation, such that in areas with a higher fraction of anthropogenic land use and riparian degradation the effect is stronger than in in more natural areas. This follows what has been documented in other studies when stressors such as organic and inorganic pollution, land use changes, and water abstraction are combined – their cumulative effects on biodiversity are much greater than the sum of each individual stressor (e.g. Navarro-Ortega et al. 2015).

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 spanning the last 32 years. 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 diversity, and functional richness of both fish and macroinvertebrates (Fig. 2, Supplemental Table 1). Additionally, for both fish and macroinvertebrates, ship traffic was positively associated with the prevalence of invasive species and taxonomic evenness. For all models other than invasive species, ship traffic was the term in the model with the largest effect size, indicating strong effects throughout.

In addition to shipping's direct impacts, we also found significant interactions between the effect of ship traffic on fish communities and the degree of riparian degradation and agricultural and urban land cover. Shipping's negative association with fish richness and diversity and the positive association with evenness was magnified in areas of increased agricultural and urban land use with relatively no impact in areas of low agricultural and urban cover (Fig. 3, Supplemental Table 1). Shipping's impact of increased prevalence of invasive fishes was magnified in highly urbanized areas (Fig. 2). Regarding local scale riparian degradation, we found shipping to be negatively associated with fish taxonomic richness regardless of the riparian area but the magnitude of this negative effect decreased as riparian degradation increased (Fig. 3). Similarly, while shipping had a positive effect on taxonomic evenness, the magnitude of this effect decreased as riparian degradation increased (Fig. 3, Supplemental Table 1).

For macroinvertebrates, urban land cover modulated the effect of shipping (Fig. 3). Shipping's negative impact on richness was strongly negative in areas of low urban cover, but minimal in areas of high urban cover. Shipping's positive effect on taxonomic evenness was only observed in areas of low to moderate urban cover, and was only negative in areas of high riparian degradation.

The effects of channelization were also context-dependent. For macroinvertebrates, taxonomic and 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). Additionally, when riparian degradation was high, channelization was associated with significant increases in invasive species prevalence. In areas of low to moderate riparian degradation, the effect of channelization had no impact on studied metrics.

Locks were weakly associated with increases in fish taxonomic richness and functional diversity, and a decrease in invasive prevalence, and with slight decreases in functional diversity for macroinvertebrates. Ports were associated with slight increases in taxonomic and functional richness for both fish and macroinvertebrates.

**Traits involved in navigation-biodiversity relationships**
To better understand the types of species responding to navigation, we analyzed the relationships between traits and navigation pressures via an RLQ-Fourth Corner analysis. We found strong significant relations between the navigation gradients (linear combination of navigation pressures) and species trait syndromes (a linear combination of several traits) in both fish (Fig. 4, Supplemental Table 2) and macroinvertebrates (Fig. 5, Supplemental Table 2).

In fish, the first navigation axis was driven by increases in shipping intensity, and the second axis was driven largely by an increase in the number of ports. We found that the first navigation axis (shipping intensity) was positively correlated with the first trait axis, and the second navigation axis (ports) was positively associated with the second trait axis. Traits positively associated with axis one (shipping) included pelagic environment, planktivorous feeding, and diadromous migration, whereas limnophilic species tended to decrease. On axis two (the port axis), traits positively associated included planktivorous and detritivorous feeding, and lithophilic reproduction.

For macroinvertebrates, like in fish, both the first and second navigation and trait axes were positively associated (Fig. 5). The first axis of navigation pressures for macroinvertebrates was also driven by an increase in shipping intensity and the second dimension of variation was driven by infrastructures (Fig. 5, normed scores in Supplemental Table 2). For the traits, increased shipping was primarily and significantly associated with declines in passive aquatic dispersers and interstitial/crawling species versus increases in aerial passive dispersers, aquatic active dispersers and locomotive swimmers. Increased infrastructure was associated with increases in active aerial dispersal, free eggs, and those inhabiting gravel, sandy, and silty substrates.

To identify how landscape and local degradation mediated navigations impact on traits, we ran additional RLQ-Fourth Corner analyses using subsets of sites with the highest degree of anthropogenic land use cover and riparian degradation (top 25% of sites with each land cover class). In fish, we found degradation did not change the impact of navigation on traits. The same traits that expressed negative or positive associations with shipping intensity were maintained as such in highly urban or agricultural sites (Extended Data Fig. 2, Supplemental Table 3). In macroinvertebrates, this held true for agricultural sites, but not for urban sites. For example, in the full dataset, burrowing species and those laying clutches in terrestrial sites had positive associations to shipping, but in highly urbanized sites these traits had a strongly negative association to shipping (Extended Data Fig. 2, Supplemental Table 3).

**Discussion**

At the European scale, inland shipping has negative impacts on freshwater biodiversity. This confirms findings from previous studies at finer spatial scales reporting negative impacts of navigation on freshwater fish and macroinvertebrate communities. This study goes beyond existing local studies in showing that inland navigation threatens biodiversity of multiple taxa across a large spatial scale, affecting the whole 35,000 km European inland waterway network. In particular, we found negative responses to ship traffic of both fishes and macroinvertebrates, at both taxonomical and trait/functional
levels, and increases in the prevalence of invasive species. Ship traffic causing a decrease in richness and increase in evenness can likely be explained by losses in the smallest populations, rarer and specialists species with would decrease richness but also even out the community. To check for this, we conducted a follow-up analysis and found strong correlations between taxonomic evenness and the abundances and occurrences of rare taxa for both fish and macroinvertebrates (Supplemental File 2, Extended Data Fig. 3), which supports this hypothesis that ship traffic is driving losses in rare populations.

These impacts on biodiversity facets can be partially explained by trait shifts in both fish and macroinvertebrate communities. In particular we see navigation showing the most negative impacts for species inhabiting the river bed (benthic taxa) and those with low flow preference (limnophilic). Navigation was positively associated with traits such as pelagic environment, generalist water flow preference, egg clutches fixes to substrates, and a negative selection for fish whose eggs are suspended in the current and that prefer lower flow (i.e., limnophilic). Together these traits likely reflect selection by vessel-induced strong waves and return currents, which negatively impact survival and reproduction in species with these traits (Zajicek and Wolter 2019; Gabel et al. 2017). Additionally, ship waves cause erosion and sediment resuspension, which degrades the littoral habitat for both fish and macroinvertebrates (Gabel et al. 2011). Commonly used heavy embankments to prevent bank erosion pose a significant impact on littoral habitats in all navigated rivers, and have been shown to reduce fish diversity (Wolter, 2001). Finally, areas of intense ship traffic often require fairway dredging of the river bottom to maintain navigable water depth (Grygoruk et al. 2015). These known effect of ship traffic and navigation maintenance helps explain the particularly negative association with benthic species we observed.

The community shifts described above are confirmed by the positive association we found between ship traffic and taxonomic evenness in both fish and macroinvertebrates, and the loss in rare species. Shipping may favor the most tolerant, generalist and abundant/ubiquitous taxa and eliminate rarer (less abundant) species, resulting in a more even community. This might have consequences at the ecosystem level given the role that these rarer species play in ecological function and stability (Hooper et al. 2005).

In fish communities, we saw that the negative impact of ship traffic was magnified in more degraded landscapes. In highly urban and agricultural areas, decreases in richness and diversity were greater. These interactions demonstrate that land use can modify the effects of shipping and can create environments where few taxa can persist. This follows research at similar scales that has shown that multiple stressors like pollution, land use, and water use can interact to negatively affect freshwater ecosystem services (Elmhagen et al 2015; Wen et al. 2017). It may be the case that many freshwater fish species that live in large rivers are able to tolerate some level of degradation, via agricultural or urban pollution and habitat modifications, but when an additional stressor such as shipping is added, the environment becomes too degraded for these species to persist.

There was also an aggravating effect of channelization’s impact on macroinvertebrate communities in areas of high riparian degradation and agricultural cover. We saw that channelization only decreased
Fish richness tended to be higher in river segments with a higher number of locks. Although locks do not support directed migration, they seemingly fragment rivers less compared to e.g. dams and weirs. For the latter, numerous studies have evidenced negative consequences of such river infrastructures such as to fragment rivers (Nilsson et al. 2005; Belletti et al. 2020). However, it is likely that locks are not a primary
cause of fragmentation. Some studies have found that locks can increase connectivity for certain species in highly fragmented rivers, as lock operation draws in water and can allow for passage of species that cannot pass through other ways such as fish ladders (Lin et al. 2013; Vergeynst et al. 2021). Additionally, locks are areas where river flow is disrupted, and so there is a creation of lentic habitats, which could allow for a wider diversity of species to be found in these locations. Further research is needed to elucidate how locks can be best managed to ensure they are not fragmenting rivers, and that native fish populations are able to navigate through, especially in rivers that have high lock densities. This is especially important at large (continental-wide) scales to build coordinated and transboundary management policies.

Richness values of both fish and macroinvertebrates were slightly higher in areas near ports. Two factors may help explain this result: the creation of novel habitats, and ballast water. Ports alter the physical environment of lowland rivers by increasing depth, providing pools of standing water, and a buildup of sediments (Samsami et al. 2022). Our trait analyses found macroinvertebrates living in sandy and gravel substrates to be positively associated with ports – both of which tend to build up in ports and towards the end of the river continuum where ports are often found (Keller et al. 2011). Additionally, the mixing and releasing of ballast water that occurs in port areas is known to transport species (Costello et al. 2022). Finally, it should be noted that while statistically significant, the effect sizes were quite small – an order of magnitude smaller than the negative effect sizes of shipping intensity.

**Conclusion**

Together our findings highlight the need for large-scale and internationally organized management and mitigation practices around inland navigation. This mode of transport is commonly supported as the most carbon-friendly; however, its impacts on freshwater biodiversity are usually not considered, although extremely relevant. We show inland navigation to be a driver of freshwater biodiversity declines across multiple watersheds. This pressure should be increasingly considered when restoring ecosystems and seeking to identify multiple stressor effects. Weighing the carbon benefits of freshwater navigation against the costs such as hydromorphological modifications and loss of floodplain connection must be an important assessment in any future planning. Additionally, we were able to show, for the first time at this scale, the effects of specific navigation infrastructures, and aid in the identification of management actions on the most problematic infrastructures without requiring an extreme reduction of navigation activities. Locks, for example, if operated to support fish migration may not negatively affect diversity or hinder connectivity. In general our findings indicate that the effects of inland navigation on freshwater biodiversity are complex and transcend those derived merely from the spread of aquatic invasive species.

An increase in shipping intensity could have serious negative consequences for Europe’s freshwater biodiversity – decreasing diversity across multiple taxa, with significant losses in rare species/populations and benthic taxa. Identifying the drivers behind navigation and land use interactions is important to mitigating massive losses in stressful habitats such as urban or agricultural areas. More work is needed to better understand how inland navigation could be sustainably promoted, if at all
possible. In particular, further research into how to mitigate navigation's impacts on native biodiversity directly, and not simply the spread of invasive species, is warranted in freshwater systems. For example, at the local scale our findings can be applicable as we show that the inclusion of riparian vegetation can offset some negative effects of navigation, and should therefore be integrated into any mitigation or management efforts.

Methods

**Fish & Macroinvertebrate Biodiversity**

We combined data from locally collected datasets and monitoring programs of fish and macroinvertebrate 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. (2023) relevant for our study. Specifically, we defined a “large river” as having a Strahler order of five or greater (based on the HydroSHEDS database: www.hydrosheds.org/). This ensured we focused only on navigated and navigable waterways and did not include data from smaller rivers that have markedly different biotic and abiotic conditions. By not including these smaller rivers we avoid over-estimating the impact of navigation by ensuring we are not linking river size to navigation (additionally, we avoid this by including Strahler order as a term in our model, fully outlined later). We used data from 1992 to 2021, as the opening of the Main-Danube canal in 1992 began the subsequent spread of freshwater invasive species (Leuven et al. 2009). During this time period the total amount of goods transported by commercial navigation has remained rather constant, which indicates that shipping intensity remained relatively consistent across time (see next section) and allowed for spatial-temporal comparisons. One ecological community dataset consisted of presences-absence data which was only used in the taxonomic richness model; all other included datasets consisted of abundance data for multiple taxa at specific locations with spatial coordinates, years and sampling effort included.

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

Additionally, we calculated the relative abundance of invasive taxa, and total relative abundance of the community. 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, 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 species 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.info trait database. Flow preference traits followed the FAME consortium (EU FP5), fish community traits of sensitivity according to van Treeck et al. (2020), of Fish Region Index (FRI) and its variation of FRI ($S^2_{FRI}$) based on Wolter et al. (2021). Macroinvertebrate traits were obtained from the Tachet database (Tachet et al. 2010). Linking these species traits to our community data, we calculated the metrics functional richness, diversity, and evenness using the {mFD} package in R (Magneville et al. 2021). The traits we use here are ecological traits, and not strictly only functional traits according to (Violle et al. 2007). Therefor 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 relates to their interactions with the abiotic and biotic environments (as defined in Magneville et al. 2021).

**Navigation & Infrastructures**

Ship traffic, i.e. vessel counts were obtained from Marine Traffic (https://www.marinetrack.com/) and compiled as the number of ships passing through 30 km stretches of river per-month over the course of 2019 (this scale was chosen following discussions with the data providers). To confirm that 2019 was a representative timestamp for ship traffic, we compared these data 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. (2018). This comparison showed ship traffic from 1992 to 2015 to be rather consistent (Supplemental Fig. 1). The location of all inland ports and locks was obtained via direct communication with a UNECE officer, and is sourced from the UNECE Inventory of Main Standards and Parameters of the Waterway Network. We then counted the number of ports and locks within a 5 km buffer (consistent with the scale of land usage) around each biodiversity sampling site. Finally, channelization cover was obtained via the Open Street Map database (https://openstreetmap.org/). We defined the rate of river channelization as the total length of channelized river within each 30 km-stretch. While channelization has been implemented for several reasons over the course of human history, some related to navigation and some not, (e.g. manipulation of floodplain for agriculture) this a good metric of riverine modifications required for navigation that has been practiced in almost all of Europe's navigated rivers (Petts et al. 1989).

**Local and landscape land use**

To identify how landscape and local level characteristics moderate navigation's impact, we collected data on the land use and riparian degradation surrounding each biodiversity sampling site.
For land use, we collected data at the landscape scale, to identify how the two main forms of land use degradation in Europe (urbanization and agriculture) moderate navigation’s impact. For this, 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 to get a large-scale understanding of land-use effects. While additional research is needed to elucidate the spatial scale at which land use influences aquatic taxa, studies have shown that a scale between 1–5 km is appropriate (Wang et al. 2001; Bergerot et al. 2013). We found strong correlations between land use at 1 km and 5 km across our sites (Supplemental Fig. 2). Within these buffers, we obtained surfaces of surrounding urban and agricultural land uses for each site. To prevent collinearity issues between the two land use variables (Pearson's correlation test significant between urban and agricultural land use), we conducted a PCA on these values and then used the first two Principal Components that were associated with each land use type (Supplemental Table 4).

To obtain finer-scale information on habitat structure, we characterized riparian degradation at the scale of 1 km. To do so, we used the Green Arteries database from CORINE (Weissteiner et al. 2016). Within a 1 km radius buffer around our biodiversity sampling sites, we clipped the “Potential Riparian Extent” (PRZ) as modeled based on hydrologic and geomorphologic characteristics, and the “Actual Riparian Extent” (ARZ) as informed with the 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 chose to use the subcatchment size (Pfaffstetter level) that was the best predictor of taxonomic richness at our sites, i.e. at which Pfaffstetter level taxonomic richness was correlated with size, in our case level six, which was an average of size of 7,972.7 m^2 (code provided in Supplemental File 1).

**Statistical Analyses**

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

\[
\text{Biodiversity Response} \sim \text{Ship Traffic} + \text{Ports} + \text{Locks} + \text{Channelization} + \text{Riparian Degradation} + \text{Agriculture} + \text{Urban} + \text{Ship:Riparian} + \text{Ship:Agriculture} + \text{Ship:Urban} + \text{Channelization:Riparian} + \text{Channelization:Agriculture} + \text{Channelization:Urban} + \text{Subcatchment Size} + \text{Strahler order} + (1|\text{Study/Year}).
\]

For macroinvertebrates, we found an effect of year on taxonomic richness – an increase in richness from 2000–2010, followed by a decrease from 2010–2020. So to control for this difference in diversity across years, we included an additional term to the macroinvertebrate models of: + (poly(yr_scaled, 2). This term was added as a polynomial effect due to the nature of year’s non-linear impact on richness. Plot’s
showing the year effect on macroinvertebrates and fish are visualized in Supplemental Fig. 3. Finally, for the invasive abundance model for both fish and macroinvertebrates, we included an offset term of total community abundance (log transformed) to control for large samples.

This structure allowed us to test the effect of navigation and associated infrastructures, their interaction with local and landscape stressors while controlling for hydrotopographic factors (Strahler oder, subcatchment size), differences in collection methods/efforts across different studies and years across the same study (Study/Year), and changes in biodiversity patterns across years driven by factors such as climate warming, El Nino, etc. Collinearity between our fixed effects was checked via their Variable Inflation Factors (VIF) scores and all were below two, indicating the model was acceptable (e.g. Graham 2003; Supplemental Table 1). All predictor terms were scaled to an average value of 0 and a standard deviation of +/- 1. Scatterplots of pairwise comparisons of predictor values in Supplemental Fig. 4. Identifying the marginal effects of shipping at various levels of landscape degradation was obtained using the ‘margins’ and ‘cplot’ functions in the {margins} R package and the ‘interact_plot’ function in the {interactions} R package (Leeper 2021; Long 2019). Figures were produced using the {ggplot} and {ggpubr} R packages (Wickham 2016; Kassambara 2020).

To better understand the types of species responding to navigation, we analyzed the relationships between functional traits and navigation pressures via an RLQ-Fourth Corner analysis (Dray et al. 2014) and identified specific ecological traits that positively or negatively responded to navigation and navigation infrastructures. This multivariate approach analyses the links between the environmental variables (ship traffic, count of ports and locks, and rate of channelization) at sites (R), the species abundances at these sites (L) and the species traits (Q) to create a “fourth corner” (M) that is an environmental-trait relationship matrix. This was conducted using the {ade4} R package (Dray et al. 2007), applying a Correspondence analysis to the species table, a principal component analysis to the environmental and trait tables, and then the function ‘rlq’ was run on these ordinations to join the three “corners”. A permutation test (n = 999 permutations) was conducted to test global significance of the traits-environment relationships, using the function ‘fourthcorner.rlq’, following Dray 2014 (Supplemental Table 2).

**Declarations**

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References


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**Figures**

![Figure 1](image1)

**Figure 1**

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

**Inland navigation and other stressor effects on biodiversity.** Model estimates from the GLMMs. Each column represents the response metric of a model run, with predictors of the model as rows. Red cells indicate a negative impact and blue cells represent a positive impact, with color intensity representing the magnitude of effect. Non-significant effects are blank cells (Std. Errors reported in Supplemental Table 1).

**Figure 3**
Context-dependent effect of ship traffic. Effects of shipping across varying degrees of landscape degradation. Panel a) shows marginal effects (i.e., changes in slope) of the relationship between shipping and taxonomic richness and evenness as urban land, agricultural land or riparian degradation increases. Negative marginal effects indicate a negative relationship between shipping and the diversity metrics, a value at zero indicates no relationship (i.e., slope = 0), and a positive value indicates a positive relationship. Panel b) shows the predicted values of taxonomic richness and evenness as shipping increases in intensity in areas of relatively low, medium and high degrees of urban cover. For both panels fish are on the top row and macroinvertebrates are on the bottom.

Figure 4

Fish trait responses to navigation. RLQ-Fourth corner relationships between fish traits (in colored boxes) and navigation variables (in bold green text). Traits are facet wrapped into their respective trait groups. The grid in the bottom right corner visualizes the statistical significance between the navigation and trait axes of the RLQ test analysis.
Figure 5

Macroinvertebrate trait responses to navigation. RLQ-Fourth corner relationships between macroinvertebrate traits (in colored boxes) and navigation variables (in bold green text). Traits are facet wrapped into their respective trait groups. The grid in the bottom right corner visualizes the statistical significance between the navigation and trait axes of the RLQ test analysis.

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- SupplementalTable1SynthNatEcoEvoforsubmission.xlsx
- SupplementalTable2SynthNatEcoEvoforsubmission.xlsx
- SupplementalTable3RLQsubsetsNatEcoEvoforsubmission.xlsx
- SupplementalTable4SynthNatEcoEvoforsubmission.xlsx
- SupplementalFigure1SynthNatEcoEvowithcaption.docx
- SupplementalFigure2SynthNatEcoEvo.png
- SupplementalFigure3Fish.png
- SupplementalFigure3Inverts.png
- SupplementalFigure4Fish.png
- SupplementalFigure4Inverts.png