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Freshwater Navigation Is Linked to Non-Native Species Distributions Across Spatial Scales

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ABSTRACT

Aim: Invasive species are among the most important drivers of native species declines, and cause serious economic and ecological costs. Globally, Europe is a hotspot for freshwater non-native species, especially among macroinvertebrates and fish, and inland navigation is thought to be a major driver of their spread. However, the degree to which different aspects of navigation (i.e., ship traffic vs. infrastructures) contribute to non-native species spread, establishment and distribution has not yet been quantified. Our study set out to determine the role that navigation plays in the distribution of Western European freshwater established non-native species, and which aspects of navigation are most responsible. Additionally, we aimed to identify the spatial scale at which these navigation pressures operate, and what ecological characteristics may influence species' response to navigation.

Location: Europe.

Methods: We extracted data from the Global Biodiversity Information Facility (GBIF) to identify occurrences of established non-native species in Europe from the past 30 years. Using over 500,000 occurrences, we mapped the coverage of over 250 established non-native species and paired this with pan-European data on inland ship traffic, navigation infrastructure and environmental data.

Results: We found that the greatest predictor of non-native species richness and occurrences was the presence of a shipping canal in the subcatchment. This held true for both fish and macroinvertebrates at fine and large spatial scales. Temperature was also an important predictor of non-native species distribution. We found these positive associations to be strongest for generalist fish species, molluscs and crustaceans.

Main Conclusions: Freshwater navigation, especially canals, is an important vector for non-native species establishment, and highlights the need for frequent monitoring and mitigation. Given that increased temperatures are associated with establishment success, climate change may also play an increased role in non-native species dispersal.

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1 | Introduction

The spread and proliferation of invasive species has major ecological, economic and societal costs (Pyšek et al. 2020; Diagne et al. 2021; IPBES 2023). Invasive species can cause depressions of fisheries and agricultural systems, extirpations of native species and sometimes permanently change the receiving ecosystems (Kimbro et al. 2009; Butchart et al. 2010; Vila et al. 2011). In freshwater systems, the colonisation of invasive species is widely cited as one of the main drivers of native biodiversity declines across taxonomic groups (Reid et al. 2019). For example, in North American lakes the introduction of the highly invasive zebra and quagga mussels (*Dreissena polymorpha* and *D. rostriformis bugensis*) via ballast water has led to decreases in local fish populations, increased water temperatures and decreased recreational and commercial fisheries (Higgins 2014; Karatayev and Burlakova 2022; Vanderploeg et al. 2002).

Europe is the global hotspot for freshwater established non-native species with the highest number of documented invasive fishes and macroinvertebrates—in particular crustaceans and molluscs (IPBES 2023). In central Europe between 2000 and 2018, non-native species richness increased 5-fold and their abundance 40-fold (Haubrock et al. 2023). Estimates suggest that 25% of non-native freshwater animal introductions into Europe are a result of boating and shipping (Gherardi et al. 2009). The vectors for introduction of non-native species include intentional releases for horticulture and aquaculture, accidental releases from ballast ship water, and the opening of new waterways (canals) that allow species spread (Nehring 2006; Leuven et al. 2009; Keller et al. 2011; Soto, Ahmed, Beidas, et al. 2023; Soto, Cuthbert, Ricciardi, et al. 2023; Soto, Cuthbert, Ahmed, et al. 2023). Shipping has also been identified as the pathway of introduction for certain highly invasive species, such as the zebra mussel (*Dreissena polymorpha*), silver carp (*Hypophthalmichthys molitrix*) and more, in the Mississippi and Illinois rivers in the USA (Jacobs and Keller 2017; Mills et al. 1993). The zebra mussel successfully invaded European waterways and North American inland lakes because veliger larvae of zebra mussels can survive long transport times in ballast water and are released at destination and adults can attach to ship objects (hulls, anchor chains, etc.) (Dalton and Cottrell 2013; McCartney and Mallez 2018; Pollux et al. 2010). Similarly, the wide invasion of the goby (*Noegobius melanostomus*) resulted from efficient transport of larvae by ships (Jacobs and Keller 2017) and ballast water (Nogueira Tavares et al. 2020). Navigation infrastructures also play an important role in invasion phenomena (as reviewed in Jeliazkov et al. 2024); for instance, boat ramps were identified as the main dispersal route for the highly invasive zebra mussel in Great Britain (Rodríguez-Rey et al. 2021), and lock operations favour the spread and residency of the big head carp (*Hypophthalmichthys nobilis*) and the silver carp (*H. molitrix*) (Fritts et al. 2024). While the causes of first arrival are often the focus of investigation, we lack a more quantified identification of the conditions that favour the success of establishment and proliferation of non-native species in these areas.

In an effort to reduce the carbon footprint of transports of goods, freshwater shipping has been identified as a promising solution. As such, the EU Green Deal in Europe plans to increase inland navigation by 25% by 2030 (INE 2020), additionally, the world's largest wetland in the tropics is threatened by a large-scale navigation project to transform the landscape and promote freshwater shipping (Wantzen et al. 2024). These projected increases, in concert with the well-known responsibility of maritime shipping for introducing non-native species (Costello et al. 2022; Keller et al. 2011; O'Brien et al. 2017), make it vital to gain a better understanding of how freshwater shipping may further impact freshwater ecosystems and non-native species spread.

While navigation has been documented to be an important driver of long-distance, non-native species introductions in both marine and freshwater systems, we have a more limited understanding regarding which aspects of navigation are most responsible for non-native species establishment and distribution, especially in freshwater systems (Keller et al. 2011). Navigation pressure includes ship traffic, canals to connect rivers and waterways, locks to allow ships to move through waterways that would be otherwise impassible, and ports to host ships at their destinations. These infrastructures have significant impacts on the landscape and can decrease biodiversity and reshuffle communities (Wolter 2001; Gabel et al. 2011; Chen et al. 2016). However, navigation is often considered in a hegemonic manner lumping together all these aspects in discussions of impact on biodiversity and non-native species expansions and distribution. It would be most useful to parse out these different aspects of the navigation industry to better understand which are most responsible for non-native freshwater species establishment to improve monitoring and mitigation efforts.

Furthermore, to properly monitor and manage the proliferation of non-native species, it is crucial to understand the spatial scale to which they associate with ship traffic and navigation infrastructure. For example, is the presence of a shipping port associated with increases in non-native species in the localised area, or across the entire watershed it is within? Understanding scale effects will help determine if policies should be coordinated at the watershed scale (e.g., synchronising lock operations) or should be focused at a finer scale on specific hotspots for example. Additionally, the promotion of inland navigation in the coming years will increase ship traffic on existing routes, but could also add new routes, ports, locks and canals (Wang et al. 2020), which could lead to wide ranging consequences.

Finally, it is also important to be able to identify the functional groups that are most strongly associated with shipping and infrastructures and may explain the success of non-native species establishment or proliferation, with the aim to adapt and improve our navigation management and policy development. Like in regard to the zebra mussels mentioned above, ballast water was found to be their main transportation mode, and thus, in 2017 the International Maritime Organisation adopted a legally binding ordinance for ships to manage their ballast water for aquatic organisms. Similar taxa-specific and navigation infrastructure-specific identification of non-native species spread would be valuable in mitigating the impacts of freshwater invasive species, at least in newly developed waterways such as canals. Additionally, there may be certain groups of non-native species that are not spreading via navigation, and so policies to target those species would be meaningless if focused on navigation. For example, previous work has shown ship traffic to be especially harmful for flow-specialist native fish species (Zajicek et al. 2018), therefore it may be that flow-specialist non-native fish species also exhibit negative associations with navigation.

Here we ask three central questions: Here we ask three central questions: (1) How do the different aspects of inland navigation (i.e., ship traffic vs. infrastructures) contribute to the occurrence and richness of Established Non-Native (ENN) freshwater species in Western Europe? (2) At which spatial scales do these contributions have the greatest influence on ENN occurrences and richness? and (3) What are the main functional groups of ENN species which show the strongest positive association with inland navigation traffic and infrastructure? We hypothesised that ship traffic (i.e., frequency of ships) would be the strongest determinant of ENN species occurrences and richness—especially at larger spatial scales. As shipping is spatially dynamic, and has the ability to move species long distances, we predicted that shipping would drive increases in ENN species at larger spatial scales. However, at a finer spatial scale, we hypothesised that navigation infrastructures play a larger role. At this finer spatial scale, we predicted ports to be especially important, as this is where ships are releasing their ballast water, and therefore where ENN species should be more prevalent. Finally, we hypothesised that ports and ship traffic would be favourable for less mobile species that disperse in ballast water or on ship hulls but would be less important for mobile species such as fish. For fish, and more mobile macroinvertebrates, we hypothesised that the presence of a canal would be a strong determinant of ENN species at multiple spatial scales.

We generated a pan-European database documenting the occurrences of more than 250 ENN freshwater fish and macroinvertebrate species over the past 30 years using data from the Global Biodiversity Information Facility (GBIF), combined with data on inland ship traffic, navigation infrastructure and environmental data. We focus our analyses & interpretation here on Western Europe, as this is where the most complete data are available on the GBIF platform. We then generated rarefied metrics of ENN species richness and number of occurrences across Europe and modelled them against our navigation and environmental data. Measuring both the species richness and occurrences of ENNs allowed us to determine if navigation was associated with increases in only a small number of prolific species (which would lead to increases in occurrences, but not as much in richness), or if multiple species were benefiting from navigation. Finally, we also included environmental conditions across our river systems to control for environmental heterogeneity across Western Europe, including temperature, elevation and discharge—all of which have been shown to be major drivers of freshwater species distributions.

2 | Methods

2.1 | Taxa Selection

We compiled lists of non-native species across European freshwaters, then trimmed this list to only established taxa. For macroinvertebrate taxa selection, we built on previous work that aimed to identify all exotic aquatic invertebrates worldwide (Dobrzycka-Krahel 2023). Taxa were extracted from the Global Register of Introduced and Invasive Species (Pagad et al. 2022) considering all possible ecosystems worldwide (https://griis.org/). To restrict ourselves to freshwater taxa and Europe, we first removed marine and terrestrial species and merged synonymous taxa. We then added missing taxa based on publications reporting first records of established, non-native species in each of the 41 European countries considered. This allowed us to create 'species × country' pairs to clearly define species deemed 'established' in a country where it is considered to be non-native (File S1). Fish taxa were obtained from FishBase (https://fishbase.mnhn.fr/search.php), only including freshwater taxa listed as established and non-native in a given European country, that is, taxa 'introduced but not established' or 'status unknown' categories were removed. This taxa definition allowed us to focus on species that have escaped their natural range and become established in a new area, with the potential to cause harm on their new ecosystem, and is stricter than including all taxa deemed non-native but less cumbersome to define in space and time than strictly 'invasive' (Soto et al. 2024). This selection generated 153 macroinvertebrate and 106 fish species, each paired with the countries it has been identified as ENN in.

2.2 | Data Extraction and Refining in Five Steps

2.2.1 | Step 1. GBIF Extraction

We queried all occurrences of our selected 259 ENN species on the platform since 1992. The year 1992 was selected because this was the opening of the Rhine-Main-Danube Canal, which marked the beginning of the modern era of European inland navigation, linking Eastern and Western Europe. This opening has since been linked to numerous subsequent species invasions (Bij de Vaate et al. 2002; Leuven et al. 2009). We extracted occurrence records as individual observations made by one or more individuals at a particular place and time. We removed all observations that were outside of mainland Europe, and within one kilometre of the coast, removed observations with missing names, coordinates, and/or duplicate rows, maintained only the records categorised as 'Human Observation', 'Occurrence' or 'Observation' and removed all other observation categories, which include fossil, museum and preserved specimens, and machine observations. This generated 41,105,824 macroinvertebrate occurrences covering Porifera (112,099 occ.), Cnidaria (217,948 occ.), Bryozoa (87,980 occ.), Platyhelminthes (96,611 occ.), Nematoda (1425 occ.), Annelida (724,300 occ.), Mollusca (2,533,818 occ.) and Arthropoda (37,331,643 occ.). The Actinopterygii class was retained for fish (2,774,077 occ.). All extractions were conducted in May 2023, and a synoptic figure visualising data extraction steps is provided in File S2. We ran the GBIF extractions with R (version 4.1.2; R Core Team 2021; code and data will be made publicly available on Zenodo upon acceptance of this manuscript).

2.2.2 | Step 2. Select Publishers Along a Confidence Level

To maintain only observations with a high degree of confidence, only publishers corresponding to observations made by scientists and organisations, and by, or confirmed by, naturalists (e.g., a 'research grade' iNaturalist observation), were used.

This meant 742 (94%) publishers for macroinvertebrates and 308 (73%) publishers for fish were used, totalling 1,822,684 observations. The final list of data publishers is provided in File S3.

2.2.3 | Step 3. Select Only Established Non-Native 'Species × Country' Pairs From Lists

Once all occurrences of ENN species were obtained from GBIF, we had to then determine which observations were within the species home range, and which were within the range they have been deemed non-native and established. We trimmed our list of 1,822,684 global observations to only those which corresponded to those observations where a species was listed at ENN in each country (e.g., for a species which is native to Hungary, but ENN in France, all Hungary observations were dropped), as defined in the Taxa Selection section above. This retained a total of 366,107 macroinvertebrate ENN and 200,362 fish ENN occurrences. While we included species lists for all European countries, our emphasis remains on Western Europe, as that is where high quality data currently exists.

2.2.4 | Step 4. Subcatchment Mapping and Observation Rarefaction

Using the HydroBASINS database from HydroSHEDS (Lehner and Grill 2013), grouping of observations was performed at six spatial grains, from 'Pfafstetter' level 6 (representing a larger grain—average size of 79,072 km^2) up to level 12 (the finest subcatchment delineation grain—average size of 129 km^2) – histograms of all subcatchment sizes are provided in File S4. Within each subcatchment we calculated the richness of ENN species and the number of their occurrences (e.g., for a given species recorded more than once in a given subcatchment, these were recorded as multiple occurrences).

Because data were not evenly distributed across Europe, ENN species richness and occurrences were rarefied using the Menhinick diversity metric, which is a commonly applied tactic when using GBIF data (e.g., Enquist et al. 2019). The formula for Menhinick diversity metric is as follows:

$$S_{\text{Menhinick}} = S_{\text{non-native}} / \sqrt{N_{\text{all occurrences}}}$$

$$O_{\text{Menhinick}} = O_{\text{non-native}} / \sqrt{N_{\text{all occurrences}}}$$

where $S_{\text{non-native}}$ represents the number of ENN species observed in each subcatchment, $O_{\text{non-native}}$ represents the number of ENN occurrences observed in each subcatchment, and $N_{\text{all occurrences}}$ represents the total number of occurrences in each subcatchment. To obtain $N_{\text{all occurrences}}$ we extracted all freshwater observations on GBIF from our list of 742 macroinvertebrate and 308 fish publishers. This included native and ENN observations from our list of high confidence publishers, which gives a fuller assessment of sampling effort in each subcatchment than if we were to only include ENN observations which would miss a large proportion of GBIF observations and potentially over- or underestimate sampling effort in certain regions. Additionally, by only using data from our selected publishers we exclude non-relevant terrestrial taxa and observations. We elected to use the Menhinick diversity metric as it is a more conservative estimate of higher species richness estimates. Alternatively, the Margalef diversity metric is a more liberal estimate of higher species richness as it assumes a logarithmic rarefaction function instead of a square root function. To test if using the Menhinick or Margalef diversity metric would influence our results, we calculated both metrics for each subcatchment at all spatial grains (formulas and model coefficients from both Menhinick and Margalef models are provided in File S5).

2.2.5 | Step 5. Navigation and Environmental Metrics

To quantify navigation intensity, we collected data on four metrics of inland navigation: ship traffic, presence of navigation canals, density of inland shipping ports and density of locks (Figure 1). Ship traffic was obtained from Marine Traffic (https://www.marinetraffic.com/) and compiled as the number of ships per-month passing through 30 km river stretches in 2019. A spatial grain size of 30 km was selected as it is well-aligned with the Water Framework Directives River Basin Management Plans, and a finer spatial grain would have been irrelevant for the linear flow of ship traffic, as it would have generated several repeating values in a river stretch. Ship traffic values were then clipped to the extent of the European Waterway Network (https://unece.org/DAM/trans/main/sc3/AGN_map_2018.pdf) to exclude maritime ship traffic. The locations of canals were obtained from the EU Hydro database (https://land.copernicus.eu/en/products/eu-hydro), which constituted 'an artificial waterway with no flow, or a controlled flow, usable or built for navigation'. The location of 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 (Figure 1). Within each subcatchment at all six Pfafstetter levels, we calculated the average number of ships per month, the number of ports and locks, and the presence or absence of a shipping canal. Environmental variables were obtained from the HydroATLAS database (https://www.hydrosheds.org/hydroatlas), which provides environmental data at a 15 arc sec resolution. For each subcatchment, at each scale, we obtained the average annual temperature (°C), the elevation (m) and annual discharge (m^3) (File S6) (Hijmans et al. 2005; Robinson et al. 2014; Döll et al. 2003). These three environmental metrics were chosen as they are important determinants of freshwater fish and macroinvertebrate communities, often used to model non-native species distributions (e.g., Rodriguez-Rey et al. 2019; Markovic et al. 2014).

2.2.6 | Step 6: Functional Approach

Both fish and macroinvertebrates were split into functional groups that incorporate several important ecological traits that are responsive to navigation pressures, such as dispersal, sensitivities & reproduction (Sexton et al. 2024). This functional group approach allows for a simple integrative approach that is well suited to our wide taxonomic dataset. Macroinvertebrates were split into Insects, Crustaceans and Molluscs, which follows the classification level commonly used when studying non-native species (IPBES 2023). These classes represent differences in dispersal capabilities, which

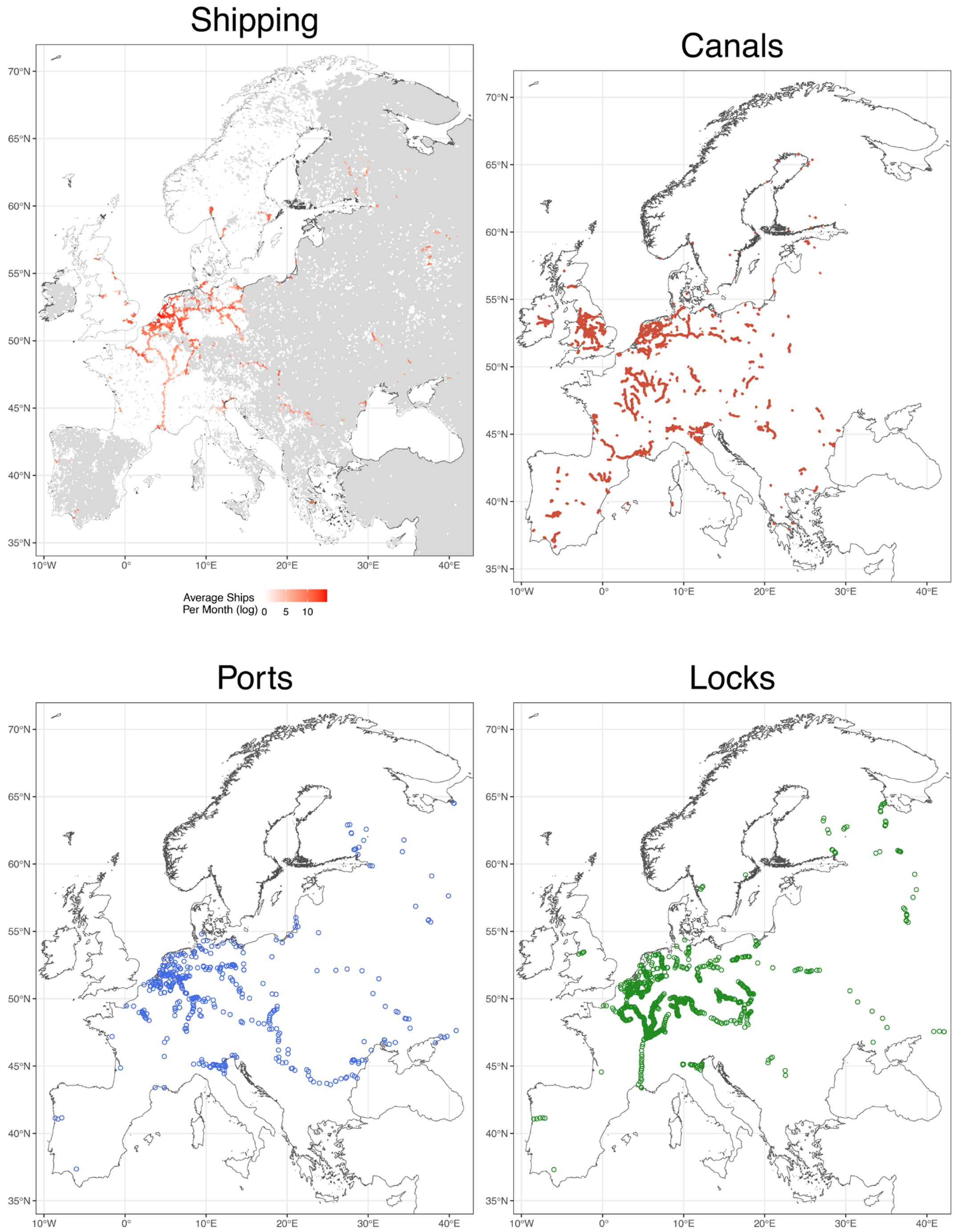

FIGURE 1 | Maps of the navigation metrics used in our analyses: Shipping (log average number of ships per month within 30 km^2 cells); Canals (linear elements); Ports (point elements); Locks (point elements). In the shipping panel, white cells indicate a confirmed value of no ship traffic, while grey cells indicate no data.

is an important determinant of sensitivity to habitat modifications (Mondy and Usseglio-Polatera 2014) and previous work at the European scale has shown that ship traffic can have disproportionately negative effects on low mobility macroinvertebrates (passive dispersers) (Sexton et al. 2024). Fish were split into three modalities based on their spawning habitat: (i) euryoparous: generalists, with no clear spawning habitat preferences, (ii) limnoparous: preference to spawn in slow or stagnant waters and (iii) rheoparous: preference to spawn in running waters. Spawning preference was chosen because it indicates habitat type usage and swimming performance, both of which have been shown to be responsive to navigation pressures (Wolter and Arlinghaus 2003). Fish traits were obtained from the freshwaterecology.info trait database (https://www.freshwaterecology.info/).

2.2.7 | Step 7: Statistical Models

To quantify the effects of navigation and environmental variables on freshwater ENN species richness and occurrences, we used generalised linear mixed models (GLMs). The model structure was as follows: Response (either $S_{\text{Menhinick}}$

or $O_{\text{Menhinick}}$) ~ Ship traffic + Canal presence + Port density + Lock density + Temperature + Elevation + Discharge. All predictor variables were scaled and centered (to an average of 0 and standard deviation of ±1). Because our data were continuous with high degree of zero-inflation, we ran a 'Tweedie' distribution model, a type of step-model, which model residuals showed to perform much better than a classic 'Gaussian' model (model residuals of both Tweedie and Gaussian models shown in File S7).

To determine the scale-dependencies of navigation's impact, we ran the same GLM at all six watershed subcatchment size classes (Pfafstetter levels) for all four response metrics (ENN fish and macroinvertebrate richness and occurrences). To account for differences in sample sizes due to scale change (17,000+ subcatchments with data at Pfafstetter level 12 compared to 714 subcatchments at level 6), we applied a bootstrapping approach. At each grain, we randomly selected 700 subcatchments to run a model, and this was repeated 999 times (with replacement of extracted rows each time) to obtain an average and standard deviation of effect sizes for each predictor. Bootstrapping minimised spatial autocorrelation issues as each subcatchment was chosen at random, limiting spatial clumping of the data. To check for potential spatial auto-correlation issues, we calculated Moran's index for our models at the finest spatial grain (where spatial autocorrelation is usually expected to be the strongest [Jelinski and Wu 1996]) and found very low levels of spatial autocorrelation (average $I = 0.06$ for macroinvertebrate models, and 0.11 for fish; File S8). To confirm that bootstrapping did not affect interpretations of the model, additional models were run without bootstrapping, using all subcatchments, which confirmed mirroring trends in both bootstrapped and non-bootstrapped models (i.e., same predictors increasing or decreasing response metrics) (File S9). Collinearity between our fixed effects was checked via their variance inflation factor (VIF) scores and all were below two, indicating the model was acceptable (Lüdecke et al. 2021). A conservative estimate of significance was determined if the standard deviation of the model estimate did not overlap with zero. Model estimates, standard deviations and 95% confidence intervals are provided in File S10.

The same models were used with the occurrence and richness metrics within functional groups as responses but were run at the finest subcatchment size class (Pfafstetter level 12) only. This made sure to maintain the finest degree of spatial accuracy to the original data points available while avoiding bootstrapping, which would have caused greater zero-inflation than was present in the full dataset (as the data were divided by taxa in this approach). GBIF data were extracted using the 'rnaturalearth', 'readr', 'readxl', 'rgbif', 'sf', 's2', 'tidyverse' and 'data.table' packages; models were run using the 'glmmTMB' and 'car' packages; and figures were made using the 'ggplot2', 'ggpubr', 'sf' and 'rphylopic' packages (South 2017; Wickham et al. 2022; Dowle and Srinivasan 2021; Fox and Weisberg 2019; Brooks et al. 2017; Kassambara 2020; Pebesma 2018; Gearty and Jones 2023; Wickham 2016).

3 | Results

Our data refining process generated over 500,000 ENN species occurrences (366,107 macroinvertebrates and 200,362 fish), covering 259 species (153 macroinvertebrates and 106 fish species). At the finest spatial grain (Pfafstetter level 12) our data covered 22,109 subcatchments for macroinvertebrates and 17,029 for fish (Figure 2).

Increases in ENN species richness and occurrences of both fish and macroinvertebrates at all spatial grains were positively associated with the presence of a shipping canal across Western Europe (Figure 3, statistics in File S10). For ENN fish occurrences, the effect size was largest at the largest spatial grain (Pfafstetter level), with a 3-fold increase in effect sizes with scale. For all other metrics, the effect size remained relatively constantly positive across spatial grains (Figure 3b). Ship traffic exhibited positive correlations with ENN fish and macroinvertebrate occurrences (Figure 3b,d respectively) across spatial grain, though the effect sizes were roughly 10 times smaller than those of canals and showed a negative correlation with fish richness at the largest spatial grain (Figure 3a). Port density exhibited the same positive association with ENN occurrences as ship traffic did at large spatial grains, but no significant associations on any metric at finer grains (95% confidence intervals of model estimates overlapped with zero). Lock density exhibited a positive association with macroinvertebrate richness, double that of ship traffic and port density, but not for fish richness. For both taxa, locks followed the same pattern as ports with a significantly positive association at the largest spatial grain, but no significant relationship at smaller grains.

Increased temperature was also associated with ENN richness and occurrences in both taxa, with the largest model estimates for macroinvertebrate richness at a small Pfafstetter level and all other metrics remaining consistent across grains (Figure 3). Elevation had a negative relationship with ENN macroinvertebrates (Figure 3c,d), but a positive relationship with ENN fish richness (Figure 3a). Discharge showed a marginally negative association with ENN occurrences and no relationship with ENN richness.

Canals still represented the most important navigation metric across functional groups, associated with increases in both the richness and occurrences of all functional groups except for the occurrences of highly mobile macroinvertebrates—insects (Figure 4). Temperature also maintained a positive association with all functional groups for both richness and occurrences. Ship traffic was associated with increases in ENN richness and occurrences of molluscs, crustaceans and occurrences of euryoparous and limnoparous fish, but decreases in the richness and occurrences of rheoparoud fish. Ports and locks both had positive associations with mollusc and crustacean richness and limnoparous fish occurrences. Additionally, ports had a positive association with limnoparous richness and locks had a positive association with euryoparous richness. Elevation followed the same pattern as the upstream-downstream river continuum that is observed in native species (rheoparous upstream and eury/limno taxa downstream).

Coefficients from the models using the Menhinick and Margalef diversity metrics mirrored each other, showing consistent positive or negative associations with ENN distributions (File S5). In the Margalef models, canals showed stronger positive associations with ENN richness and occurrences than in the Menhinick

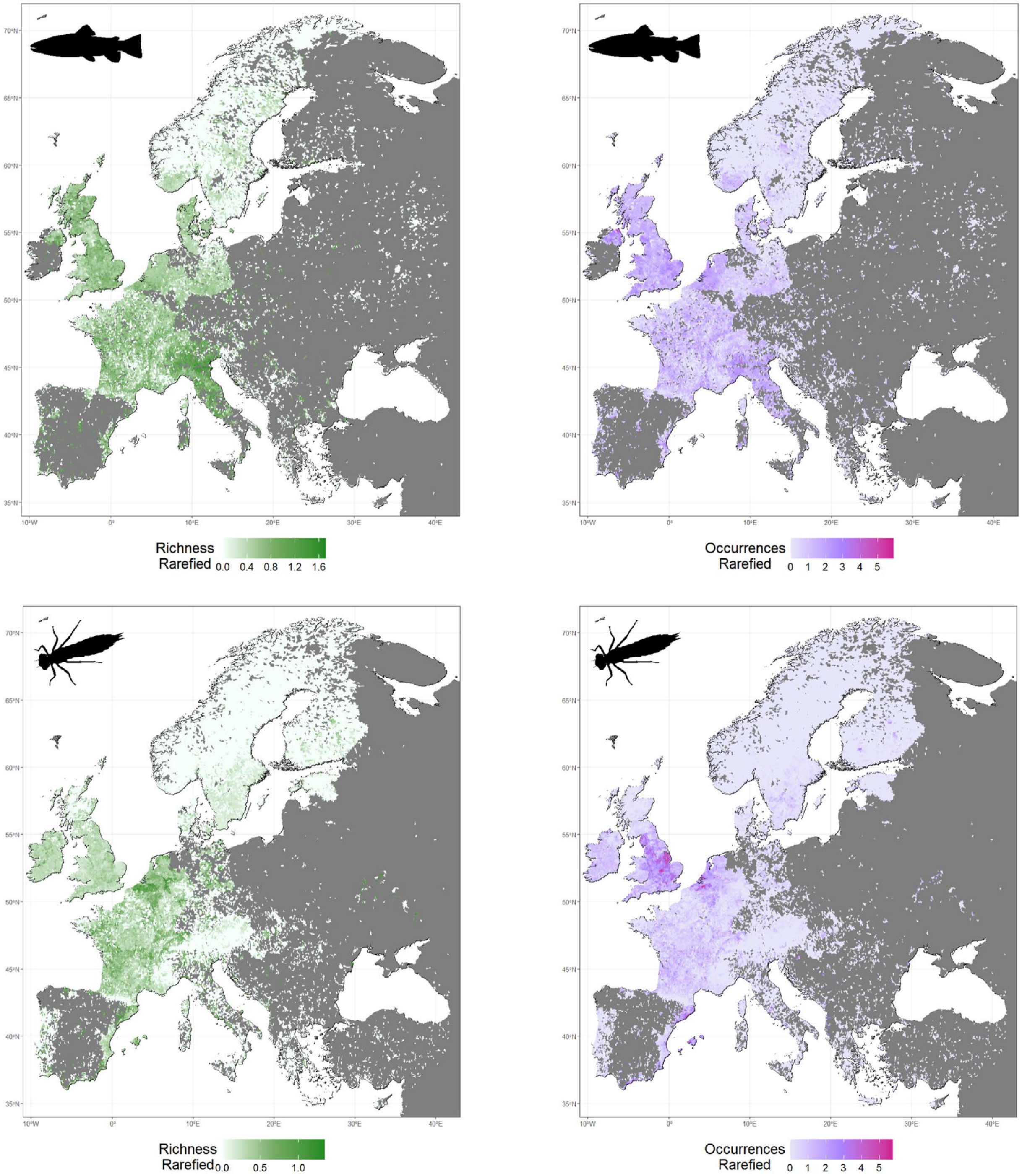

FIGURE 2 | Maps of freshwater established non-native (ENN) fish and macroinvertebrate distributions. The two left panels show the ENN species rarefied richness in our subcatchments at the finest spatial grain—Pfafstetter level 12, and the panels on the right show the rarefied number of ENN species occurrences, with fish on the top row and macroinvertebrates on the bottom. All values are rarefied via the Menhinick diversity metric, and have been square root converted for improved visualisation. Grey subcatchments indicate no data.

models, indicating that the association between canals and ENN species is even stronger in areas of particularly high richness values.

4 | Discussion

Our study set out to determine how the different aspects of navigation are associated with the occurrence and richness of ENN species, at what scale, and for which functional groups of ENN species the association is greatest across Western Europe. We found that all aspects of navigation, especially the presence of a canal, but also ship traffic and locks, are associated with increases in ENN species distributions. While we had hypothesised ship traffic and ports to be the navigation aspects most responsible for ENN species distribution, our results show that canals were the strongest predictor of ENN species, across subcatchment size classes.

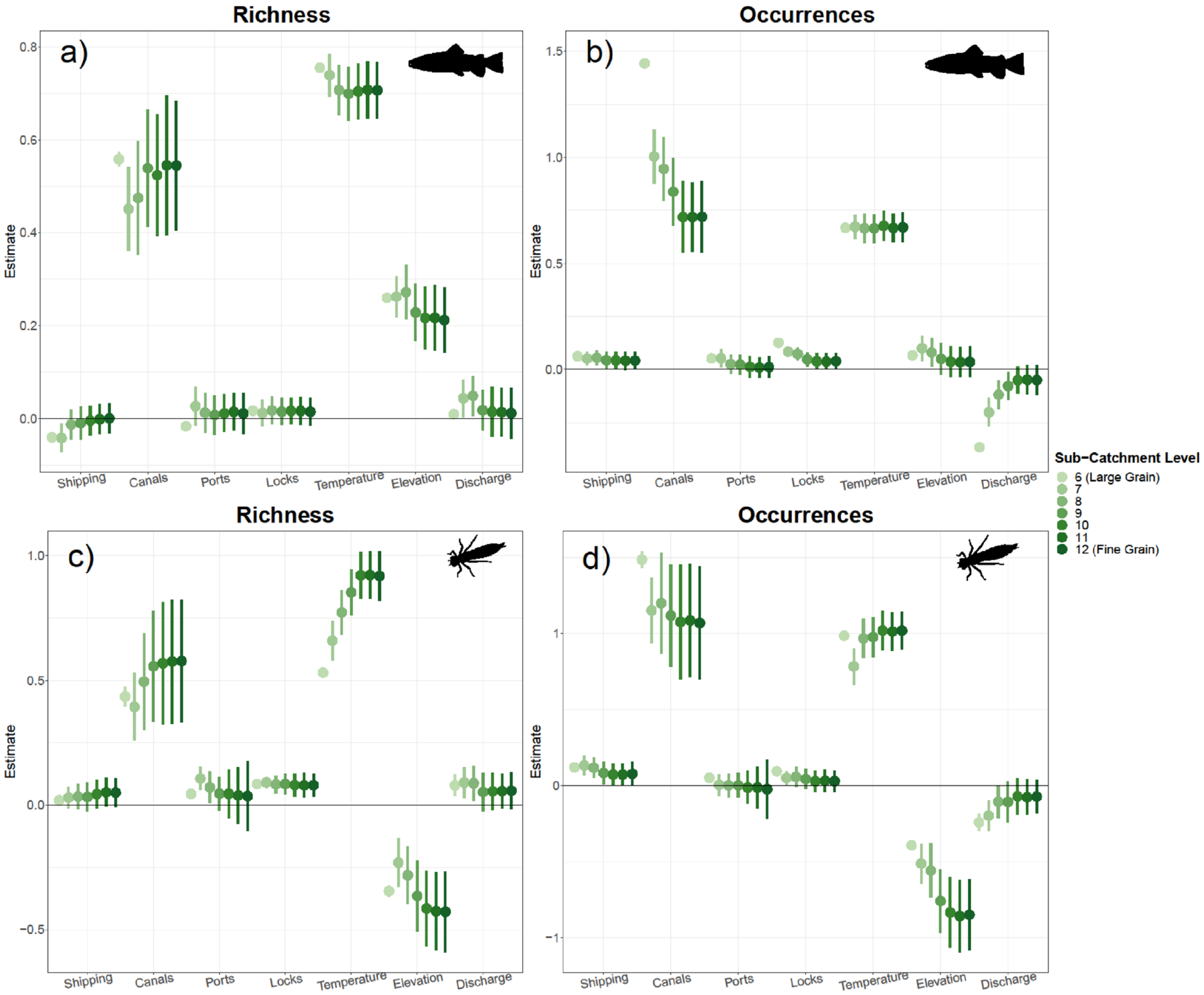

FIGURE 3 | Model estimates of how navigation and environmental variables predict the Menhinick richness and occurrences of established non-native (ENN) species. Dots represent the average model estimate for each term and bars represent the standard deviation of model estimates across the 999 iterations of the models with ENN species richness (panels on the left) or occurrences (panels on the right). Dot and line colour represent the spatial grain the model was run at, from a large grain (Pfafstetter level 6) in pale green to a fine/small grain (Pfafstetter level 12) in dark green.

4.1 | Effects of Canals & Temperature on ENN Species Distributions

Several processes can explain this positive association of ENN species with canals. First, canals, especially new connection channels, can act as routes allowing for non-native species colonisation of formerly disconnected watersheds (e.g., Manné et al. 2013; Zvezdin et al. 2021). Second, because channelisation implies habitat degradation/destruction, canals can also play a role as suitable habitats for new species that arrive, encounter no or few competitors due to their extirpation after disturbance, and thus can easily establish and rapidly proliferate (e.g., Bernauer and Jansen 2006; Graf et al. 2015). Indeed, previous work has shown that invasive species such as Caspian crustaceans (e.g., *Dikerogammarus villosus*, *Limnomysis benedeni*, *Hemimysis anomala* and *Katamysis warpachowskyi*) and gobiid fish species (e.g., *Proterorhinus semilunaris*, *Ponticola kessleri*, *Babka gymnotrachelus* and *Neogobius fuviatilis*) benefit from the artificial embankments therein and are able to reproduce prolifically in these habitats (Borza et al. 2017; Borza 2014; Soto, Cuthbert, Ahmed, et al. 2023; Grabowska et al. 2023). Canals lack the morphological heterogeneity of natural rivers that create various flow, temperature and depth conditions required by native species for diverse shelter and nursing habitats—making native species less competitive in the face of invasions. For example, Brabender et al. (2016) found modifications made to shorelines to support navigation led to a nine-fold decrease in native macroinvertebrate species reproduction and increases in non-native species reproduction. In smaller rivers it has been shown that channelisation and reduction of river-braiding significantly reduces the hydraulic conditions favourable for native juvenile fish and fish larvae (Sukhodolov et al. 2009). Finally, we observed a positive relationship between fish ENN richness and elevation, a result that is likely not linked to navigation, but instead other non-native species introduction pathways. It is likely that this result arises from the historical and ongoing stocking practices in recreational reservoirs and impounded sections upstream. This practice would explain why we observed an increase in ENN fish, but not macroinvertebrates, as there is no common stocking practices of aquatic macroinvertebrates.

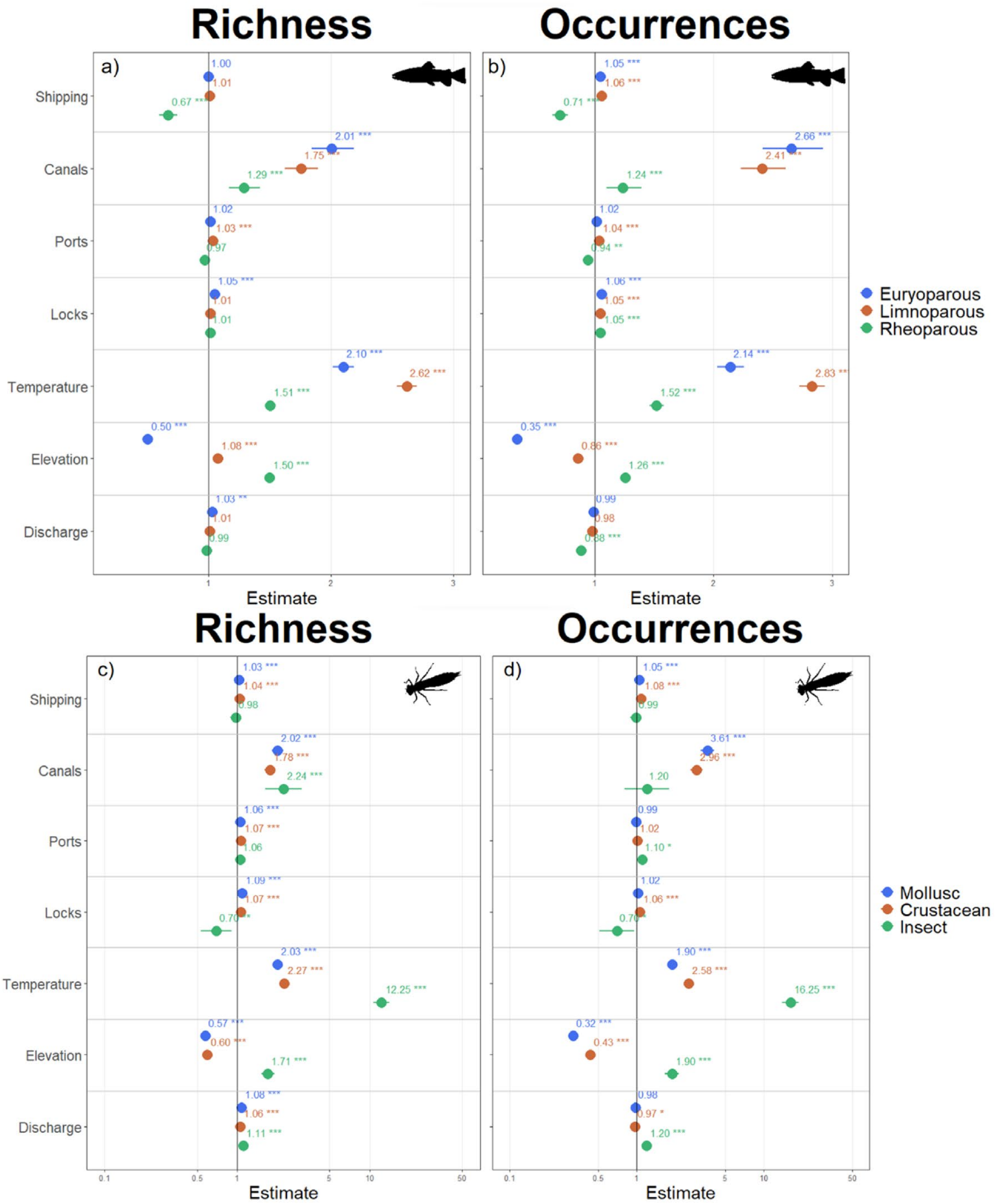

FIGURE 4 | Functional group model results. Dots represent the regression coefficient of the model term, and the bars represent the 90% confidence interval. Asterisks show significance values (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$). On the top row are fish values, split into the three functional groups (euryoparous, limnoparous and rheoparous), and the bottom are macroinvertebrates, split into their functional groups (molluscs, crustaceans, insects).

It is also important to note that canals were associated with increases in both ENN species richness and occurrences, as well as across functional groups, indicating that the relationship is consistent across diversity metrics, taxa, and subcatchment size classes. Additionally, as canals had their strongest association with ENN taxa at the largest Pfafstetter level, this suggests that the presence of a shipping canal can lead to the proliferation and establishment of non-native species across an entire watershed. This follows the findings mentioned above whereby the opening of a significant canal, such as the RMD led to dramatic increases in ENN species across Central and Western Europe (Soto, Ahmed, Beidas, et al. 2023). Our findings suggests that canals play a large, generalised role in the establishment success of non-native freshwater species in Western Europe and should be a focus for monitoring and management efforts in the years to come.

Temperature also had strongly positive associations with ENN species across Pfafstetter levels. This suggests that rising temperatures may increase non-native species' spread in coming years, and follows concerns highlighted in Kernan (2015; Rahel and Olden 2008). In Europe, freshwater systems are experiencing temperature increases at faster rates than the global average (van Vliet et al. 2013), and rising temperatures have already shown to facilitate species invasions by increasing interspecific competition and the virulence of certain diseases (Rahel and Olden 2008). Non-native species, such as the prolific/invasive *D. villosus* mentioned above, have been shown to increase their predation pressure on native species in warmer temperatures (Pellan et al. 2016).

The combined pressures of climate change and navigation could interact to further promote the spread of ENN species. With increasing temperatures and drought, waterways will have to be intensively managed to maintain a deep enough draft for ships to pass through, which will require dredging of riverbeds and manipulations of flow rates (Dahl et al. 2018; Guerrero et al. 2013). As freshwater navigation has already been shown to negatively impact benthic species (Sexton et al. 2024), increased riverbed dredging with climate change may exacerbate these impacts. Rising temperatures and management will have direct negative impacts on native species, but our results now also suggest that they may support the establishment of non-native species in the coming years, thus amplifying the overall pressure on native biodiversity. Finally, new canals opening novel avenues of species movement could generate significant increases in species invasions coverage in coming years, and foster climate migrations of new species that previously could not survive low temperatures. For instance, navigation experts have begun planning for increases in the Northern Sea, and arctic sea routes (Mahmoud et al. 2024). Initial models have suggested that this could lead to significant increases in non-native species introductions into previously semi-pristine arctic regions (Ware et al. 2014), and our results here support these findings and suggest caution in this regard.

4.2 | Scale-Dependent Effects of Navigation

Ship traffic's association with ENN species distributions showed to be scale-dependent, such that ship traffic was associated with increases in ENN species occurrences at large Pfafstetter levels, but the effect became insignificant at smaller Pfafstetter levels. While ports and ship traffic have been shown to be among the most important spreaders of species invasions in marine systems (Costello et al. 2022; Keller et al. 2011; O'Brien et al. 2017), here we see that their association is not as strong as the presence of a canal. This is likely due to the fact that marine traffic connects habitats from different continents that are naturally isolated by sea and become connected by ballast ship water. Additionally, in freshwater navigation, inland vessels generally transport ballast water from within the same river system, which makes their impact from ENN species very little. Maritime ships are also significantly larger than inland ships, holding larger ballast water tanks (up to 30× larger), which will pick up and transport a greater amount of organisms. Finally, our analyses do not include maritime ports or ships—only freshwater ports. Therefore it is possible that ENN species, especially those that can tolerate brackish water (Paiva et al. 2018), may still proliferate in maritime ports, which we did not consider here. Regarding ship traffic's lack of a strong effect, previous work on fish and macroinvertebrate communities has shown ship traffic to decrease freshwater diversity (Arlinghaus et al. 2002; Huckstorf et al. 2011; Wolter 2001; Wolter and Arlinghaus 2003; Zajicek et al. 2018; Zajicek and Wolter 2019; Sexton et al. 2024). Ship traffic may likewise be harmful for non-native species, and not only native species, which would explain the lack of a strongly positive association we found. For example, we found that ship traffic had a strongly negative association with rheoparous species, which follows findings in native fish communities showing that ship waves and ship traffic are disproportionately negative for these species (Gabel et al. 2017; Gabel et al. 2011).

4.3 | Functional Group Associations With Navigation

We observed relatively consistent patterns across functional groups. Canals maintained their strong association with ENN richness and occurrences, with the exception of insect occurrences. Canals and euryoparous fish exhibited the strongest positive association. This observation aligns with ecological logic, as these species are generalists, able to tolerate wide ranges of flow rates, making them well-equipped to tolerate these artificial waterways. Previous research has found generalist fish species to be more resilient to turbulent and degraded environments than specialists (Vanderpham et al. 2013). We also saw that ports had a positive association with the richness and occurrences of low-flow species, and a negative association with high-flow species. This is likely due to the creation of stagnant water habitats in ports, which may allow these species to proliferate, and follows previous findings that ports are often associated with non-native species introductions into lentic environments (Holeck et al. 2004). High-flow specialists, rheoparous fish, also showed a strongly negative association with ship traffic which follows findings from native fish communities, whereby these flow specialists were disproportionally negatively impacted by ship-induced waves (Wolter and Arlinghaus 2003). This strong negative association could in-part explain the negative association between ship traffic and fish richness observed in the full-dataset analysis. Finally, elevation was associated with a shift in the fish community, from euryoparic species in low elevations, towards rheoparic species in higher elevation, which also follows ecological patterns broadly and findings from other modified rivers (Göthe et al. 2019).

4.4 | Study Limitations and Future Perspectives

One limitation of our analysis is that our focus is on the distribution of ENN species, not directly their mode of transport or first occurrence. There is a strong body of previous work focused on narratively identifying the record of first occurrences of individual species, and localities, as mentioned above. Our work builds on this knowledge of ENN species biology by showing the distribution and hotspots of ENN species in European waterways and the environmental conditions that favour them. We are also only focused here on the navigation industry, however other industries, such as aquaculture, are known to play an important role in ENN distributions and could benefit from a similar quantitative analysis. An additional limitation of our study is that, due to the nature of the distribution of GBIF data, we are not able to cover the entirety of Europe, and in particular we have more missing data in Eastern Europe, including the Danube river, which is regionally important for navigation. As such, our results are best interpreted to understand non-native species distributions in Western Europe particularly. However, as has been documented by others, the flow of non-native freshwater species has mainly been from Eastern to Western Europe in the past century (bij de Vaate et al. 2002; Leuven et al. 2009; Soto, Ahmed, Beidas, et al. 2023), and our data effectively capture this extent. Of course, GBIF data suffers from sampling bias with uneven sampling effort, beyond the Eastern/Western Europe divide we mention here, and while we partially mitigate for this with rarefaction our approach is still limited by this bias. Additional studies on the linear flow of ship traffic to identify directionality in ENN species distributional shifts would be beneficial and could help identify specific shipping routes that may contribute disproportionally to this issue. Nonetheless, our large-scale approach allowed us to disentangle different aspects of navigation, which could not have been achieved with an experimental design or local-scale approach, and this large-scale approach avoided major correlation issues between environmental variables such as temperature and elevation as we include climatically different regions such as Scandanavia, the Alps, and the Mediterranean deltas. Future investigations into species-specific temperature relationships, and changes in biodiversity-temperature gradients would improve our broad-scale findings here. Additional studies investigating the differences between established and non-established non-native species at this extent could also be a valuable future research direction. Finally, as our study focuses on Western Europe, we are unable to make concrete predictions about how new developments into more pristine areas may influence freshwater communities. In the tropical wetland mentioned above slated to be developed for navigation (the Pantanal), the effects of navigation have the potential to be more wide-ranging than what we observe here. Similarly, a recently proposed law in Brazil intended to divert water from previously isolated water basins is projected to lead to a proliferation in non-native species, and ecological homogenisation (Daga et al. 2020). Investigation into such novel projects may highlight differing impacts than what we observe here, and these time-sensitive impacts should be considered. For example, the development of a new port may see greater increases in non-native species than we predict here as our observations are related to pre-existing ports. Nonetheless, as we show here canals to have such a strong impact on established non-native species distributions across spatial scales, we would argue that the conservation implications for future development of navigation in areas such as the tropics are major and concerning. The development of new canals and shipping routes has the potential to unleash non-native and potentially invasive species into areas with relatively less invasive species pressure as compared to the highly navigated Western Europe.

5 | Conclusion

Identifying the spread of non-native freshwater species and the drivers of their establishment is crucial to manage and reduce their negative impacts on native biodiversity. Here, we underline that in freshwater systems canals play a crucial role in ENN species distribution and are more important than other navigation-related facets such as ship traffic or ports. In light of these results, we recommend that management efforts, traditionally mainly focused on ports and ballast water, could be adapted by including more canal-focused considerations in freshwater systems. Canals provide an opportunity for early detection and management of non-native species, and especially for blocking their movement at critical points, for examples, locks. Additionally, we show this effect to be strong at large watershed subcatchment size classes, and so the construction of new canals and connections to new shipping routes could lead to widespread non-native species establishments. Therefore, this potential for harm should be strongly considered in any future development plans.

In addition to monitoring, these canals, which must be ecologically improved according to the European WFD, could be structurally enhanced by the construction of heterogeneous habitats and natural substrates, which could mitigate the prevalence of many ENN species. Increasing habitat heterogeneity and adding areas of flow variation could allow a wider array of native species to potentially habitat in the canals themselves and be able to compete with the ENN species that currently dominate. Previous research has shown that the preservation of riparian buffers alongside artificial waterways can mitigate the spread of invasive species and lessen the loss of native species (Sexton et al. 2024). Renaturalisation and rehabilitation efforts could support native biodiversity and allow native species to compete with the ENN generalists that are currently able to dominate in these artificial waterways.

Finally, by using over 500,000 ENN species occurrences over the past three decades, we highlight the hotspots of Western European freshwater xenodiversity and among a suite of variables, the presence of artificial waterways and elevated temperatures are the strongest predictors of these hotspots. In the coming decades, navigation and global change have the potential to interact and influence non-native species distributions significantly. With rising temperatures and a reliance on these artificial waterways, the threat for future proliferation of ENN species is high. Monitoring and rehabilitation efforts could be targeted in these hotspots, in hopes to reduce the negative impact of these ENN species and support native biodiversity.

Author Contributions

All authors contributed to the conception of this research, via the NAVIDIV working group; A.N.S., C.S., A.J., N.C. and J.-N.B. conducted data collection and analyses; A.N.S., C.S., A.J. and J.-N.B. wrote the original manuscript, and all authors contributed to editing and revising the manuscript.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

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

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ddi.70204.

References

Arlinghaus, R., C. Engelhardt, A. Sukhodolov, and C. Wolter. 2002. "Fish Recruitment in a Canal With Intensive Navigation: Implications for Ecosystem Management." *Journal of Fish Biology* 61, no. 6: 1386–1402. https://doi.org/10.1006/jfbi.2002.2148.

Bernauer, D., and W. Jansen. 2006. "Recent Invasions of Alien Macroinvertebrates and Loss of Native Species in the Upper Rhine River, Germany." *Aquatic Invasions* 1, no. 2: 55–71.

Bij de Vaate, A., K. Jazdzewski, H. A. Ketelaars, S. Gollasch, and G. Van der Velde. 2002. "Geographical Patterns in Range Extension of Ponto-Caspian Macroinvertebrate Species in Europe." *Canadian Journal of Fisheries and Aquatic Sciences* 59, no. 7: 1159–1174.

Borza, P. 2014. "Life History of Invasive Ponto-Caspian Mysids (Crustacea: Mysida): A Comparative Study." *Limnologica* 44: 9–17. https://doi.org/10.1016/j.limno.2013.06.001.

Borza, P., T. Huber, P. Leitner, N. Remund, and W. Graf. 2017. "Current Velocity Shapes Co-Existence Patterns Among Invasive Dikerogammarus Species." *Freshwater Biology* 62, no. 2: 317–328. https://doi.org/10.1111/fwb.12869.

Brabender, M., M. Weitere, C. Anlanger, and M. Brauns. 2016. "Secondary Production and Richness of Native and Non-Native Macroinvertebrates Are Driven by Human-Altered Shoreline Morphology in a Large River." *Hydrobiologia* 776: 51–65.

Brooks, M. E., K. Kristensen, K. J. van Benthem, et al. 2017. "glmmTMB Balances Speed and Flexibility Among Packages for Zero-Inflated Generalized Linear Mixed Modeling." *R Journal* 9, no. 2: 378–400.

Butchart, S. H. M., M. Walpole, B. Collen, et al. 2010. "Global Biodiversity: Indicators of Recent Declines." *Science* 328, no. 5982: 1164–1168. https://doi.org/10.1126/science.1187512.

Chen, J. H., X. Zeng, and Y. B. Deng. 2016. "Environmental Pollution and Shipping Feasibility of the Nicaragua Canal." *Marine Pollution Bulletin* 113, no. 1–2: 87–93. https://doi.org/10.1016/j.marpolbul.2016.08.074.

Costello, K. E., S. A. Lynch, R. McAllen, R. M. O'Riordan, and S. C. Culloty. 2022. "Assessing the Potential for Invasive Species Introductions and Secondary Spread Using Vessel Movements in Maritime Ports." *Marine Pollution Bulletin* 177: 113496. https://doi.org/10.1016/j.marpolbul.2022.113496.

Daga, V. S., V. M. Azevedo-Santos, F. M. Pelicice, et al. 2020. "Water Diversion in Brazil Threatens Biodiversity." *Ambio* 49: 165–172.

Dahl, T. A., A. D. Kendall, and D. W. Hyndman. 2018. "Impacts of Projected Climate Change on Sediment Yield and Dredging Costs." *Hydrological Processes* 32, no. 9: 1223–1234.

Dalton, L. B., and S. Cottrell. 2013. "Quagga and Zebra Mussel Risk via Veliger Transfer by Overland Hauled Boats." *Management of Biological Invasions* 4: 129–133. https://doi.org/10.3391/mbi.2013.4.2.05.

Diagne, C., B. Leroy, A. C. Vaissière, et al. 2021. "High and Rising Economic Costs of Biological Invasions Worldwide." *Nature* 592, no. 7855: 571–576.

Dobrzycka-Krahel, A. 2023. "Movement of Southern European Aquatic Alien Invertebrate Species to the North and South." *Water* 15, no. 14: 2598.

Döll, P., F. Kaspar, and B. Lehner. 2003. "A Global Hydrological Model for Deriving Water Availability Indicators: Model Tuning and Validation." *Journal of Hydrology* 270: 105–134.

Dowle, M., and A. Srinivasan. 2021. "Data.table: Extension of 'Data.frame'." R package version 1.14.2. https://CRAN.R-project.org/package=data.table.

Enquist, B. J., X. Feng, B. Boyle, et al. 2019. "The Commonness of Rarity: Global and Future Distribution of Rarity Across Land Plants." *Science Advances* 5, no. 11: eaaz0414. https://doi.org/10.1126/sciadv.aaz0414.

Fox, J., and S. Weisberg. 2019. *An R Companion to Applied Regression*. Third ed. Sage. https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fritts, A. K., D. K. Gibson-Reinemer, B. C. Knights, et al. 2024. "Upstream Experience and Experimental Translocation of Invasive Bigheaded Carps Results in Increased Upstream Passage Success at a Navigation Lock in a Large River." *River Research and Applications* 40, no. 4: 575–586. https://doi.org/10.1002/rra.4253.

Gabel, F., S. Lorenz, and S. Stoll. 2017. "Effects of Ship-Induced Waves on Aquatic Ecosystems." *Science of the Total Environment* 601: 926–939. https://doi.org/10.1016/j.scitotenv.2017.05.206.

Gabel, F., S. Stoll, P. Fischer, M. T. Pusch, and X. F. Garcia. 2011. "Waves Affect Predator-Prey Interactions Between Fish and Benthic Invertebrates." *Oecologia* 165, no. 1: 101–109. https://doi.org/10.1007/s00442-010-1841-8.

Gearty, W., and L. A. Jones. 2023. "Rphylopic: An R Package for Fetching, Transforming, and Visualising PhyloPic Silhouettes." *bioRxiv*. https://doi.org/10.1101/2023.06.22.546191.

Gherardi, F., S. Gollasch, D. Minchin, S. Olenin, and V. E. Panov. 2009. "Alien Invertebrates and Fish in European Inland Waters." In *Handbook of Alien Species in Europe. Invading Nature - Springer Series in Invasion Ecology*, vol. 3. Springer. https://doi.org/10.1007/978-1-4020-8280-1_6.

Göthe, E., E. Degerman, L. Sandin, J. Segersten, C. Tamario, and B. G. McKie. 2019. "Flow Restoration and the Impacts of Multiple Stressors on Fish Communities in Regulated Rivers." *Journal of Applied Ecology* 56, no. 7: 1687–1702. https://doi.org/10.1111/1365-2664.13413.

Grabowska, J., D. Blonska, M. Ondracková, and T. Kakareko. 2023. "The Functional Ecology of Four Invasive Ponto-Caspian Gobies." *Reviews in Fish Biology and Fisheries* 33, no. 4: 1329–1352. https://doi.org/10.1007/s11160-023-09801-7.

Graf, W., P. Leitner, and F. Pletterbauer. 2015. "Short Overview on the Benthic Macroinvertebrate Fauna of the Danube River." In *The Danube River Basin, The Handbook of Environmental Chemistry*, edited by I. Liska, vol. 39, 287–316. Springer.

Guerrero, M., M. Re, L. D. Kazimierski, Á. N. Menéndez, and R. Ugarelli. 2013. "Effect of Climate Change on Navigation Channel Dredging of the Parana River." *International Journal of River Basin Management* 11, no. 4: 439–448.

Haubrock, P. J., R. N. Cuthbert, and P. Haase. 2023. "Long-Term Trends and Drivers of Biological Invasion in Central European Streams." *Science of the Total Environment* 876: 162817.

Higgins, S. N. 2014. “Meta-Analysis of Dreissenid Effects on Freshwater Ecosystems.” In *Quagga and Zebra Mussel: Biology, Impacts, and Control*, 2nd ed., 487–494. CRC Press.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. “Very High Resolution Interpolated Climate Surfaces for Global Land Areas.” *International Journal of Climatology* 25, no. 15: 1965–1978.

Holeck, K. T., E. L. Mills, H. J. MacIsaac, M. R. Dochoda, R. I. Colautti, and A. Ricciardi. 2004. “Bridging Troubled Waters: Biological Invasions, Transoceanic Shipping, and the Laurentian Great Lakes.” *Bioscience* 54, no. 10: 919–929.

Huckstorf, V., W. C. Lewin, T. Mehner, and C. Wolter. 2011. “Impoverishment of YOY-Fish Assemblages by Intense Commercial Navigation in a Large Lowland River.” *River Research and Applications* 27, no. 10: 1253–1263. https://doi.org/10.1002/rra.1420.

INE. 2020. *Naiades, Inland Navigation Europe [WWW Document]*. Inland Navigation Europe. http://www.inlandnavigation.eu/news/policy/naiades-programme-for-post-covid-growth.

IPBES. 2023. *Thematic Assessment Report on Invasive Alien Species and Their Control of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*, edited by H. E. Roy, A. Pauchard, P. Stoett, and T. Renard Truong. IPBES Secretariat. https://doi.org/10.5281/zenodo.7430682.

Jacobs, A. I., and R. P. Keller. 2017. “Straddling the Divide: Invasive Aquatic Species in Illinois and Movement Between the Great Lakes and Mississippi Basins.” *Biological Invasions* 19, no. 2: 635–646.

Jeliazkov, A., V. Martínez-Fernández, V. Y. Altanov, et al. 2024. “A Global Systematic Map of Knowledge of Inland Commercial Navigation Effects on Freshwater Ecosystems.” *Journal of Environmental Management* 370: 122474.

Jelinski, D. E., and J. Wu. 1996. “The Modifiable Areal Unit Problem and Implications for Landscape Ecology.” *Landscape Ecology* 11, no. 3: 129–140.

Karatayev, A. Y., and L. E. Burlakova. 2022. “What We Know and Don't Know About the Invasive Zebra (*Dreissena polymorpha*) and Quagga (*Dreissena rostriformis bugensis*) Mussels.” *Hydrobiologia* 852: 1029–1102.

Kassambara, A. 2020. “ggpubr: ‘ggplot2’ Based Publication Ready Plots.” R package version 0.4.0. https://CRAN.R-project.org/package=ggpubr.

Keller, R. P., J. M. Drake, M. B. Drew, and D. M. Lodge. 2011. “Linking Environmental Conditions and Ship Movements to Estimate Invasive Species Transport Across the Global Shipping Network.” *Diversity and Distributions* 17, no. 1: 93–102. https://doi.org/10.1111/j.1472-4642.2010.00696.x.

Kernan, M. 2015. “Climate Change and the Impact of Invasive Species on Aquatic Ecosystems.” *Aquatic Ecosystem Health & Management* 18, no. 3: 321–333.

Kimbro, D. L., E. D. Grosholz, A. J. Baukus, et al. 2009. “Invasive Species Cause Large-Scale Loss of Native California Oyster Habitat by Disrupting Trophic Cascades.” *Oecologia* 160, no. 3: 563–575. https://doi.org/10.1007/s00442-009-1322-0.

Lehner, B., and G. Grill. 2013. “Global River Hydrography and Network Routing: Baseline Data and New Approaches to Study the World's Large River Systems.” *Hydrological Processes* 27, no. 15: 2171–2186. https://doi.org/10.1002/hyp.9740.

Leuven, R., G. van der Velde, I. Baijens, et al. 2009. “The River Rhine: A Global Highway for Dispersal of Aquatic Invasive Species.” *Biological Invasions* 11, no. 9: 1989–2008. https://doi.org/10.1007/s10530-009-9491-7.

Lüdecke, D., M. S. Ben Shachar, I. Patil, and P. Waggoner. 2021. “Performance: An R Package for Assessment, Comparison and Testing of Statistical Models.” *Journal of Open Source Software* 6, no. 60: 3139. https://doi.org/10.21105/joss.03139.

Mahmoud, M. R., M. Roushdi, and M. Aboelkhear. 2024. “Potential Benefits of Climate Change on Navigation in the Northern Sea Route by 2050.” *Scientific Reports* 14, no. 1: 2771.

Manné, S., N. Poulet, and S. Dembski. 2013. “Colonisation of the Rhine Basin by Non-Native Gobiids: An Update of the Situation in France.” *Knowledge and Management of Aquatic Ecosystems* 411: 1–17.

Markovic, D., S. Carrizo, J. Freyhof, et al. 2014. “Europe's Freshwater Biodiversity Under Climate Change: Distribution Shifts and Conservation Needs.” *Diversity and Distributions* 20: 1097–1107. https://doi.org/10.1111/ddi.12232.

McCartney, M. A., and S. Mallez. 2018. “The Role of Waterway Connections and Downstream Drift of Veliger Larvae in the Expanding Invasion of Inland Lakes by Zebra Mussels in Minnesota, USA.” *Aquatic Invasions* 13, no. 3.

Mills, E. L., J. H. Leach, J. T. Carlton, and C. L. Secor. 1993. “Exotic Species in the Great Lakes: A History of Biotic Crises and Anthropogenic Introductions.” *Journal of Great Lakes Research* 19, no. 1: 1–54.

Mondy, C. P., and P. Usseglio-Polatera. 2014. “Using Fuzzy-Coded Traits to Elucidate the Non-Random Role of Anthropogenic Stress in the Functional Homogenisation of Invertebrate Assemblages.” *Freshwater Biology* 59, no. 3: 584–600.

Nehring, S. 2006. “The Ponto-Caspian Amphipod *Obesogammarus obesus* (Sars, 1894) Arrived the Rhine River via the Main-Danube Canal.” *Aquatic Invasions* 1, no. 3: 148–153.

Nogueira Tavares, C., M. Brauns, S. Hille, et al. 2020. “Tracing the Colonization Process of non-Native Gobies into a Large River: The Relevance of Different Dispersal Modes.” *Biological Invasions* 22: 2421–2429. https://doi.org/10.1007/s10530-020-02281-x.

O'Brien, C. E., M. W. Johnston, and D. W. Kerstetter. 2017. “Ports and Pests: Assessing the Threat of Aquatic Invasive Species Introduced by Maritime Shipping Activity in Cuba.” *Marine Pollution Bulletin* 125, no. 1–2: 92–102. https://doi.org/10.1016/j.marpolbul.2017.07.071.

Pagad, S., S. Bisset, P. Genovesi, et al. 2022. “Country Compendium of the Global Register of Introduced and Invasive Species.” *Scientific Data* 9, no. 1: 391.

Paiva, F., A. Barco, Y. Chen, et al. 2018. “Is Salinity an Obstacle for Biological Invasions?” *Global Change Biology* 24, no. 6: 2708–2720.

Pebesma, E. 2018. “Simple Features for R: Standardized Support for Spatial Vector Data.” *R Journal* 10, no. 1: 439–446. https://doi.org/10.32614/RJ-2018-009.

Pellan, L., V. Médoc, D. Renault, T. Spataro, and C. Piscart. 2016. “Feeding Choice and Predation Pressure of Two Invasive Gammarids, *Gammarus tigrinus* and *Dikerogammarus villosus*, Under Increasing Temperature.” *Hydrobiologia* 781, no. 1: 43–54. https://doi.org/10.1007/s10750-015-2312-3.

Pollux, B. J. A., G. van der Velde, and A. bij de Vaate. 2010. “A Perspective on Global Spread of Dreissena Polymorpha: A Review on Possibilities and Limitations.” In *The Zebra Mussel in Europe*, edited by van der Velde G., Rajagopal S., and A. bij de Vaate, 45–58. Backhuys Publishers.

Pyšek, P., P. E. Hulme, D. Simberloff, et al. 2020. “Scientists' Warning on Invasive Alien Species.” *Biological Reviews* 95, no. 6: 1511–1534.

R Core Team. 2021. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing. https://www.R-project.org/.

Rahel, F. J., and J. D. Olden. 2008. “Assessing the Effects of Climate Change on Aquatic Invasive Species.” *Conservation Biology* 22, no. 3: 521–533.

Rahel, F. J., and J. D. Olden. 2008. "Assessing the Effects of Climate Change on Aquatic Invasive Species." *Conservation Biology* 22, no. 3: 521–533. https://doi.org/10.1111/j.1523-1739.2008.00950.x.

Reid, A. J., A. K. Carlson, I. F. Creed, et al. 2019. "Emerging Threats and Persistent Conservation Challenges for Freshwater Biodiversity." *Biological Reviews* 94, no. 3: 849–873. https://doi.org/10.1111/brv.12480.

Robinson, N., J. Regetz, and R. P. Guralnick. 2014. "EarthEnv-DEM90: A Nearly-Global, Void-Free, Multi-Scale Smoothed, 90m Digital Elevation Model From Fused ASTER and SRTM Data." *ISPRS Journal of Photogrammetry and Remote Sensing* 87: 57–67. https://doi.org/10.1016/j.isprsjprs.2013.11.002.

Rodriguez-Rey, M., S. Consuegra, L. Borger, and C. Garcia de Leaniz. 2019. "Improving Species Distribution Modelling of Freshwater Invasive Species for Management Applications." *PLoS One* 14, no. 6: e0217896. https://doi.org/10.1371/journal.pone.0217896.

Rodríguez-Rey, M., S. Consuegra, L. Börger, and C. Garcia de Leaniz. 2021. "Boat Ramps Facilitate the Dispersal of the Highly Invasive Zebra Mussel (*Dreissena polymorpha*)." *Biological Invasions* 23, no. 5: 1487–1496.

Sexton, A. N., J. N. Beisel, C. Staentzel, et al. 2024. "Inland Navigation and Land Use Interact to Impact European Freshwater Biodiversity." *Nature Ecology & Evolution* 8: 1098–1108. https://doi.org/10.1038/s41559-024-02414-8.

Soto, I., D. A. Ahmed, A. Beidas, et al. 2023. "Long-Term Trends in Crayfish Invasions Across European Rivers." *Science of the Total Environment* 867: 161537. https://doi.org/10.1016/j.scitotenv.2023.161537.

Soto, I., P. Balzani, L. Carneiro, et al. 2024. "Taming the Terminological Tempest in Invasion Science." *Biological Reviews* 99: 1357–1390.

Soto, I., R. N. Cuthbert, D. A. Ahmed, et al. 2023. "Tracking a Killer Shrimp: Dikerogammarus Villosus Invasion Dynamics Across Europe." *Diversity and Distributions* 29, no. 1: 157–172. https://doi.org/10.1111/ddi.13649.

Soto, I., R. N. Cuthbert, A. Ricciardi, et al. 2023. "The Faunal Ponto-Caspianization of Central and Western European Waterways." *Biological Invasions* 25, no. 8: 2613–2629. https://doi.org/10.1007/s10530-023-03060-0.

South, A. 2017. "Rnaturalearth: World Map Data From Natural Earth." R package version 0.1.0. https://CRAN.R-project.org/package=rnaturalearth.

Sukhodolov, A., W. Bertoldi, C. Wolter, N. Surian, and M. Tubino. 2009. "Implications of Channel Processes for Juvenile Fish Habitats in Alpine Rivers." *Aquatic Sciences* 71, no. 3: 338–349. https://doi.org/10.1007/s00027-009-9199-x.

van Vliet, M. T. H., W. H. P. Franssen, J. R. Yearsley, et al. 2013. "Global River Discharge and Water Temperature Under Climate Change." *Global Environmental Change-Human and Policy Dimensions* 23, no. 2: 450–464. https://doi.org/10.1016/j.gloenvcha.2012.11.002.

Vanderpham, J. P., S. Nakagawa, and G. P. Closs. 2013. "Feeding Ability of a Fluvial Habitat-Specialist and Habitat-Generalist Fish in Turbulent and Still Conditions." *Ecology of Freshwater Fish* 22: 596–606. https://doi.org/10.1111/eff.12064.

Vanderploeg, H. A., T. F. Nalepa, D. J. Jude, et al. 2002. "Dispersal and Emerging Ecological Impacts of Ponto-Caspian Species in the Laurentian Great Lakes." *Canadian Journal of Fisheries and Aquatic Sciences* 59, no. 7: 1209–1228. https://doi.org/10.1139/f02-087.

Vila, M., J. L. Espinar, M. Hejda, et al. 2011. "Ecological Impacts of Invasive Alien Plants: A Meta-Analysis of Their Effects on Species, Communities and Ecosystems." *Ecology Letters* 14, no. 7: 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x.

Wang, Y., X. Chen, A. G. Borthwick, et al. 2020. "Sustainability of Global Golden Inland Waterways." *Nature Communications* 11, no. 1: 1553.

Wantzen, K. M., M. L. Assine, I. M. Bortolotto, et al. 2024. "The End of an Entire Biome? World's Largest Wetland, the Pantanal, Is Menaced by the Hidrovia Project Which Is Uncertain to Sustainably Support Large-Scale Navigation." *Science of the Total Environment* 908: 167751.

Ware, C., J. Berge, J. H. Sundet, et al. 2014. "Climate Change, Non-Indigenous Species and Shipping: Assessing the Risk of Species Introduction to a High-Arctic Archipelago." *Diversity and Distributions* 20, no. 1: 10–19.

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

Wickham, H., J. Hester, and J. Bryan. 2022. "readr: Read Rectangular Text Data." R package version 2.1.2. https://CRAN.R-project.org/package=readr.

Wolter, C. 2001. "Conservation of Fish Species Diversity in Navigable Waterways." *Landscape and Urban Planning* 53, no. 1–4: 135–144. https://doi.org/10.1016/s0169-2046(00)00147-x.

Wolter, C., and R. Arlinghaus. 2003. "Navigation Impacts on Freshwater Fish Assemblages: The Ecological Relevance of Swimming Performance." *Reviews in Fish Biology and Fisheries* 13, no. 1: 63–89. https://doi.org/10.1023/a:1026350223459.

Zajicek, P., J. Radinger, and C. Wolter. 2018. "Disentangling Multiple Pressures on Fish Assemblages in Large Rivers." *Science of the Total Environment* 627: 1093–1105. https://doi.org/10.1016/j.scitotenv.2018.01.307.

Zajicek, P., and C. Wolter. 2019. "The Effects of Recreational and Commercial Navigation on Fish Assemblages in Large Rivers." *Science of the Total Environment* 646: 1304–1314. https://doi.org/10.1016/j.scitotenv.2018.07.403.

Zvezdin, A. O., A. V. Kucheryavyy, A. V. Kolotei, N. V. Polyakova, and D. S. Pavlov. 2021. "Invasion of the European River Lamprey *Lampetra fluviatilis* in the Upper Volga." *Water* 13, no. 13: 1825.

Supporting Information

Additional supporting information can be found online in the Supporting Information section. **File S1:** Species by country pairs dataset which defines species deemed 'established' in a country where it is considered to be non-native. Fish taxa were obtained from FishBase (https://fishbase.mnhn.fr/search.php), only including freshwater taxa listed as established and non-native in a given European country, that is, taxa 'introduced but not established' or 'status unknown' categories were removed. **File S2:** Data and workflow for the extraction and rarefaction of the invasive species observations. Briefly, we collected the observations of 259 invasive species from the Global Biodiversity Information Facility (GBIF), kept only the publishers with high confidence values, identified where those observations were invasive or non-invasive, summed occurrences and richness of invasive species in nested subcatchments across Europe while rarefying these values based on total freshwater occurrences across catchment scales, and finally modelled their response to a suite of navigation and abiotic, or environmental metrics. To better identify the functional groups of taxa being spread via freshwater navigation, we divided our taxa into six groups—three macroinvertebrates and three fish. **File S3:** List of GBIF publishers from which we used data (identified by a fish or macroinvertebrate dataset provider). To maintain only observations +with a high degree of confidence, only publishers corresponding to observations made by scientists and organisations (Value of '1' in the 'confidence_level' column) and by, or confirmed by, naturalists, for example, a 'research grade' iNaturalist observation (Value of '2' in the 'confidence_level' column), were used. **File S4:** Histograms of all subcatchment sizes by Pfafstetter levels. **File S5:** Formulas and model coefficients from both Menhinick and Margalef models and calculations. **File S6:** Maps of average annual temperature (°C), the elevation (m) and annual discharge (m^3) in our study region. **File S7:** Model residuals of both Tweedie and Gaussian models to show the better fit of the Tweedie model, which was used for our full analyses. **File S8:** Moran's index histograms for models run at the finest spatial scale (Pfafstetter level 12). To check for potential spatial auto-correlation issues, we calculated Moran's index for our models at the finest spatial grain (where spatial autocorrelation is usually expected to be the strongest [Jelinski and Wu 1996]) and found very low levels of spatial autocorrelation (average $I = 0.06$ for macroinvertebrate models, and 0.11 for fish). **File S9:** Model outputs from both using a bootstrapping approach (top row) and no bootstrapping (bottom row). **File S10:** Model outputs including model estimates from the bootstrapped models, standard deviation of the estimate and 95% confidence intervals.