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Back to the future: Exploring riverine macroinvertebrate communities' invasibility

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Abstract

Riverine communities have been subject to numerous biological invasion events, with crustaceans among the most successful group of invasive animals worldwide. Understanding what makes a river system prone to invasion is of considerable interest to environmental regulators, resource managers, scientists and wider society globally. The Ponto-Caspian amphipod, *Dikerogammarus haemobaphes* (Crustacea: Gammaridae), is a hyper-successful invasive species that was first recorded in the UK in 2012. The use of contemporary distribution data for *D. haemobaphes* (2009–2020) from England provided a unique opportunity to study faunal community patterns and differences between sites that experienced invasion compared to those that have not. Macroinvertebrate community taxonomic, functional and phylogenetic features, as well as the presence of co-occurrent invaders and abiotic features of the river systems, were examined from sites before the invasion and compared to control sites that were not invaded during the study period. Sites that would later experience invasion by *D. haemobaphes* were characterized by higher abundances of other invaders (e.g., especially Ponto Caspian taxa), lower abundances of crustaceans and typically had greater channel width and water depth. These basic characteristics may help identify sites at risk of future invasion by *D. haemobaphes*. Most biomonitoring tools examined displayed no difference between control and pre-invaded samples, while both taxonomic and functional richness displayed higher values at sites that were subsequently invaded, questioning classic biological invasion hypotheses. Recognizing specific community characteristics that may be a precondition for subsequent invasion is essential for understanding and better predicting their future trajectories of change.

KEYWORDS
alien species, ecological indicators, freshwater, invasion biology, macroinvertebrates, precondition, river ecosystems

1 | INTRODUCTION

Freshwater ecosystems and particularly rivers are among the most endangered ecosystems globally, with biological invasions being highlighted as one of the greatest contemporary pressures on their biological communities (Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015; Moorhouse & Macdonald, 2015; Tickner et al., 2020). Most freshwater invaders are generally less visible and are poorly

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studied compared to their terrestrial counterparts. This raises a series of challenges and potential consequences if early detection and management are not possible (Moorhouse & Macdonald, 2015). Given that the eradication of invaders can be particularly complicated in riverine ecosystems (Simberloff, 2020), and prevention is widely accepted to be the best economic management option (Leung et al., 2002), it is critical that we improve our ability to predict taxa invasiveness. In addition, understanding what makes a community prone to invasion and what influences its "invasibility" (i.e., the susceptibility of communities to be invaded) is of considerable scientific interest for stakeholders including environmental regulators, river managers and academic scientists.

Maps obtained through species distribution models are often used to predict the potential invasive range of introduced species and help in early detection programmes (e.g., Barbet-Massin, Rome, Villemant, & Courchamp, 2018), but are typically developed using large scale variables (e.g., climate) which lack details at the local and community-scale. The availability of long-term observational field data (both biotic and abiotic information) provides the opportunity to take an additional step by predicting the invasibility of sites by specific invasive species and develop greater understanding regarding what makes some biological communities/sites susceptible to invasion compared to others at the community and ecosystem level (e.g., Cuthbert, Kotronaki, Dick, & Briski, 2020; Mathers et al., 2020). In addition, the exploration of long-term riverine community data facilitates the testing of key ecological concepts and hypotheses associated with biological invasion that have almost exclusively been developed using terrestrial ecosystems thus far (e.g., vegetation communities as model systems, Catford, Jansson, & Nilsson, 2009; Jeschke & Heger, 2018).

Crustaceans are among the most successful group of invasive animals worldwide with numerous examples recorded from riverine ecosystems (e.g., Oficialdegui, Sánchez, & Clavero, 2020; Strayer, 2010). In this research, we focus on *Dikerogammarus haemobaphes* (Eichwald, 1841) (Crustacea: Gammaridae) as a model organism, and an example of a successful invasive organism in UK rivers (Guareschi, Laini, England, Johns et al., 2021). This amphipod (hereinafter Dh) originates from the Ponto-Caspian region and was first recorded in the UK during 2012, subsequently spreading throughout rivers of central-south England (Johns, Smith, Homann, & England, 2018). *D. haemobaphes* displays a number of features that may promote its invasiveness, including its flexible feeding habit and high fecundity (Bacela-Spychalska & Van Der Velde, 2013). More recently it has been shown to have implications on leaf litter processing efficiency (Constable & Birkby, 2016), measures of macroinvertebrate community diversity and integrity (Guareschi, Laini, England, Johns, et al., 2021) also being potentially responsible for the introduction of pathogens within its invaded range (Bojko et al., 2018).

Using long term observational macroinvertebrate data from British rivers, we analysed the patterns of biomonitoring indices, functional, phylogenetic and biocontamination metrics, as well as abiotic information between sites with different invasion trajectories. Sites were examined before the arrival of Dh, specifically considering those sites that would be invaded in the future (locations invaded at some point during the study period) and control sites (not invaded during the study period) to investigate conditions favouring the arrival and establishment of the species. In addition, the use of long time-series allows the examination of hypotheses associated with the establishment of invasive species specifically considering lotic invertebrates within riverine ecosystems and using Dh as an example of a successful biological invasion process. For example, analysing biomonitoring indices and land use types facilitate the assessment of the "human activity" hypothesis (Jeschke & Heger, 2018; Leprieur, Beauchard, Blanchet, Oberdorff, & Brosse, 2008) and analysis of the co-occurrence of other invaders permits the examination of the "invasional meltdown" hypothesis (Simberloff & Von Holle, 1999, see Table 1).

In this study we aim (a) to identify specific biotic and abiotic conditions that make riverine ecosystems susceptible to Dh invasion; and (b) to explore the validity of some of the most popular concepts and hypotheses associated with biological invasions on riverine communities. Identifying specific community and environmental characteristics that may precondition them to subsequent successful invasion is essential for understanding their future trajectories of change and may help resource managers and agencies to manage and reduce the potential for future invasions.

2 | METHODS

2.1 | Macroinvertebrate data and dataset building

Biological data were obtained from the Environment Agency, the statutory regulator within England, who is responsible for monitoring the ecological quality of rivers, lakes and coastal waterbodies. All samples/sites used had not been subject to any other known disturbance events (e.g., pollution incidents) and had not been invaded by other *Dikerogammarus* species. All benthic invertebrate samples were collected using the same sampling protocol for river biomonitoring in the UK, comprising a 3-minute "kick- sample" using a standard pond-net (ISO 7828-1985) covering all available habitats in proportion to their occurrence, followed by a 1-min hand search (RIVPACS Macroinvertebrate Sampling Protocol, available at http://www.eu-star.at/frameset.htm). Macroinvertebrate data were largely recorded at species and genus level, while some Diptera larvae were resolved to family/subfamily level and some taxa such as Hydracarina and Oligochaeta were recorded as such.

Our research utilised a macroinvertebrate dataset covering a 12-year period (2009–2020 inclusive) encompassing the current regions where Dh has spread in England (details in Table S1 and Figure 1) trying to minimize climate, lithological and hydromorphological background variability. To achieve this the following steps were followed: (a) the most recent distribution information for Dh in England was used (up to 2020); for sites supporting Dh, the date of the first record was used as the date of the first occurrence; (b) community data up to 3 years prior the first record was extracted and used as "pre-invaded samples"; (c) we retained "control samples"

TABLE 1 List of all the variables and descriptors tested in the study divided in taxonomic metrics, functional descriptors and abiotic characteristics

Metric/variable	Definitions and details	References	Biological invasion hypothesis
Taxonomic metrics			
WHPT_TOTAL	WHPT total score (base for ecological status assessment)	Paisley, Trigg, and Walley (2014)	Human activity and Biotic resistance (Jeschke & Heger, 2018; Leprieur et al., 2008)
N_TAXA-WHPT	Number of taxa used for WHPT total calculation (proxy of family richness and ecological status assessment metric)	Paisley et al. (2014)	Human activity and Biotic resistance (Jeschke & Heger, 2018; Kennedy et al., 2002; Leprieur et al., 2008)
WHPT_ASPT	Average WHPT value (ecological status assessment metric)	Paisley et al. (2014)	Human activity (Leprieur et al., 2008)
PSI	Proportion of sediment-sensitive invertebrates (at family level)	Extence et al. (2013)	Human activity (Leprieur et al., 2008)
LIFE	Lotic invertebrate index for flow evaluation (at family level)	Extence, Balbi, and Chadd (1999)	Human activity (Leprieur et al., 2008)
EPT	Abundance of EPT taxa and richness of Ephemeroptera, Plecoptera, Trichoptera at family level (proxy of ecological conditions)	Kitchin (2005)	Human activity and Biotic resistance (Jeschke & Heger, 2018; Kennedy et al., 2002; Leprieur et al., 2008)
OCH	Abundance of Odonata, Coleoptera, Hemiptera (proxy of lentic habitats)	Bonada, Rieradevall, and Resh (2006)	Biotic resistance (Kennedy et al., 2002)
OH	Abundance of Oligochaeta and Hirudinea (proxy of tolerant taxa)	Chang, Lawrence, Rios-Touma, and Resh (2014)	Human activities and Biotic resistance (Leprieur et al., 2008)
RCI	Richness contamination index (based on 11 well-known invasive taxa)	Guareschi, Laini, England, Barrett, and Wood (2021)	Invasional meltdown (Simberloff & Von Holle, 1999)
ACI	Abundance contamination index (based on 11 well-known invasive taxa)	Guareschi, Laini, England, Barrett, and Wood (2021)	Invasional meltdown (Simberloff & Von Holle, 1999)
Abundance of Gammaridae	Number of organisms from the family Gammaridae (proxy of phylogenetic relatedness of invaders to native communities)	Tested in this study	Darwin's naturalization (Jeschke & Heger, 2018; Thuiller et al., 2010)
Abundance of Crustaceans	Number of organisms from the taxa Crustacea (proxy of phylogenetic relatedness of invaders to native communities)	Tested in this study	Darwin's naturalization (Jeschke & Heger, 2018; Thuiller et al., 2010)
Amount of Pontocaspian taxa	Richness and abundance of organisms from the taxa: *Hypania*, *Dreissena*, *Chelicorophium*, *Hemimysis*	Tested in this study	Invasional meltdown (Simberloff & Von Holle, 1999)
Functional descriptors			
Functional richness	Hypervolume enclosing the functional space filled by the community (using 11 biological traits)	Villéger, Mason, and Mouillot (2008)	Human activity and Biotic resistance (Jeschke & Heger, 2018; Leprieur et al., 2008)
Functional evenness	Measure of regularity of the distribution in the functional space	Villéger et al. (2008)	Human activity and Biotic resistance (Leprieur et al., 2008)
Functional redundancy	Degree to which species in a community share similar functional features (using 5 biological traits)	Pillar et al. (2013)	Human activity and Biotic resistance (Leprieur et al., 2008)
Presence of predators (feeding habitat modality)	Richness and abundance of organisms with main feeding habitat coded as predator or piecer	Tested in this study (from Schmidt-Kloiber & Hering, 2015)	Darwin's naturalization (Jeschke & Heger, 2018; Thuiller et al., 2010)
Abiotic characteristics			
†Fine substrate (%)	Percentage of fine sediments in the riverbed	Tested in this study	—
†Coarse substrate (%)	Percentage of course sediments in the riverbed	Tested in this study	—

(Continues)

TABLE 1 (Continued)

Metric/variable	Definitions and details	References	Biological invasion hypothesis
†River depth	Average channel depth in the reach (cm)	Gallardo and Aldridge (2018)	—
†River width	Average channel width in the reach (m)	Gallardo and Aldridge (2018)	—
Land use1: Artificial	Artificial surface in 1 km radius buffer (km^2)	Laini et al. (2018)	Human activity (Leprieur et al., 2008)
Land use2: Agriculture	Agricultural land in 1 km radius buffer (km^2)	Monteagudo, Moreno, & Picazo (2012)	Human activity (Leprieur et al., 2008)
Land use3: Forested and near-natural	Forested and near-natural surface in 1 km radius buffer (km^2)	Tested in this study	—
Land use4: Wetlands and water bodies	Waterbodies surface in 1 km radius buffer (km^2)	Tested in this study	—

Note: Codes, definitions, references and specific biological invasion hypothesis (when pertinent) are also provided. Abiotic descriptors labelled with † were measured in the field.

sites present within the same basins and covering the same time period that had not been invaded by Dh (at least until 2020). Following these screening steps, there were no records of Dh in the pre-invaded or control datasets. Knowing in advance the future trajectory of pre-invaded site communities enables them to be considered sites vulnerable to colonisation and invasion of Dh. The selection of 3 years (1,095 days) prior to the first detection of the species was used as this provided a large and well-balanced dataset comprising 649 biological samples for analysis: 355 samples classified as pre-invaded and 294 as control samples from 173 sites (100 pre-invaded and 73 control/never invaded). Biocontamination metrics (see Table 1) were calculated and compared only for samples where the taxonomic resolution was at the genus level for more than 75% of the entire community (n total samples = 389). This avoided mismatches due to the potential presence of invasive and native taxa within the same family.

2.2 | Taxonomic, phylogenetic, and functional descriptors

A wide range of taxonomic (13), phylogenetic (2) and functional (5) descriptors were calculated and compared between pre-invaded and control samples (full details and references in Table 1). The indices comprised those routinely used by the Environment Agency for general (WHPT_TOTAL, N_TAXA-WHPT, WHPT_ASPT) and stressor-specific ecological assessments (PSI and LIFE for sediment and flow evaluation, respectively). Similar or derivate indices are widely used in river biomonitoring programs internationally (Buss et al., 2015). The communities were further characterised using the abundance and richness of EPT (Ephemeroptera, Plecoptera, Trichoptera) at family level (proxy of ecosystem conditions), abundance of Odonata, Coleoptera, Hemiptera (proxy of lentic habitats) and abundance of Oligochaeta and Hirudinea (proxy of pollution tolerant taxa).

The level of biocontamination (presence of invasive species) was explored using both the Richness Contamination Index (coded RCI) and Abundance Contamination Index (coded ACI) (Arbačiauskas et al., 2008) and the richness and abundance of other Ponto Caspian species (originating from the same geographical region as Dh, Table 1). A total of 11 alien macroinvertebrate taxa were considered to quantify both ACI and RCI within the data set (three amphipods, two decapods, two bivalves, one gastropod, mysid, triclad and terebellid; full taxonomic details in Table S2), representing the most common and widely distributed macroinvertebrate invaders in European and British fresh waters (e.g., Gallardo & Aldridge, 2013; Guareschi, Laini, England, Barrett, & Wood, 2021). The abundance of Crustacea and of organisms belonging to the family Gammaridae were also used as proxy of phylogenetic relatedness of Dh to local communities.

Functional measures were characterized using the macroinvertebrate biological traits proposed by Schmidt-Kloiber and Hering (2015) and Tachet, Bournaud, Richoux, and Usseglio-Polatera (2010) at the genus level. Taxa resolved to species level were aggregated to genus to be consistent with current trait classifications while data resolved to family level were assigned values based on the average for the different genera. Functional community responses were investigated by calculating the metrics: (a) functional richness (FRich); (b) functional evenness (FEve); (c) functional redundancy (FRed). These metrics have previously been identified as being sensitive to different anthropogenic pressures in lotic ecosystems (Belmar et al., 2019; Mathers et al., 2020). Gower dissimilarity matrices (adapted for fuzzy-coded traits, Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009) using all 11 biological traits (63 modalities) were used to calculate FRich and FEve following Villéger et al. (2008). To derive FRed, five "effect traits" (i.e., features that directly influence a specific ecosystem function: size, mode of dispersal, mode of locomotion, food consumed and feeding habits) were selected based on the review of Hevia et al. (2017) and previously tested by Laini et al. (2019).

Two further specific functional descriptors, based on the feeding habits of Dh, were also determined: number and abundance of predators. These were used to explore if the presence of invertebrate taxa

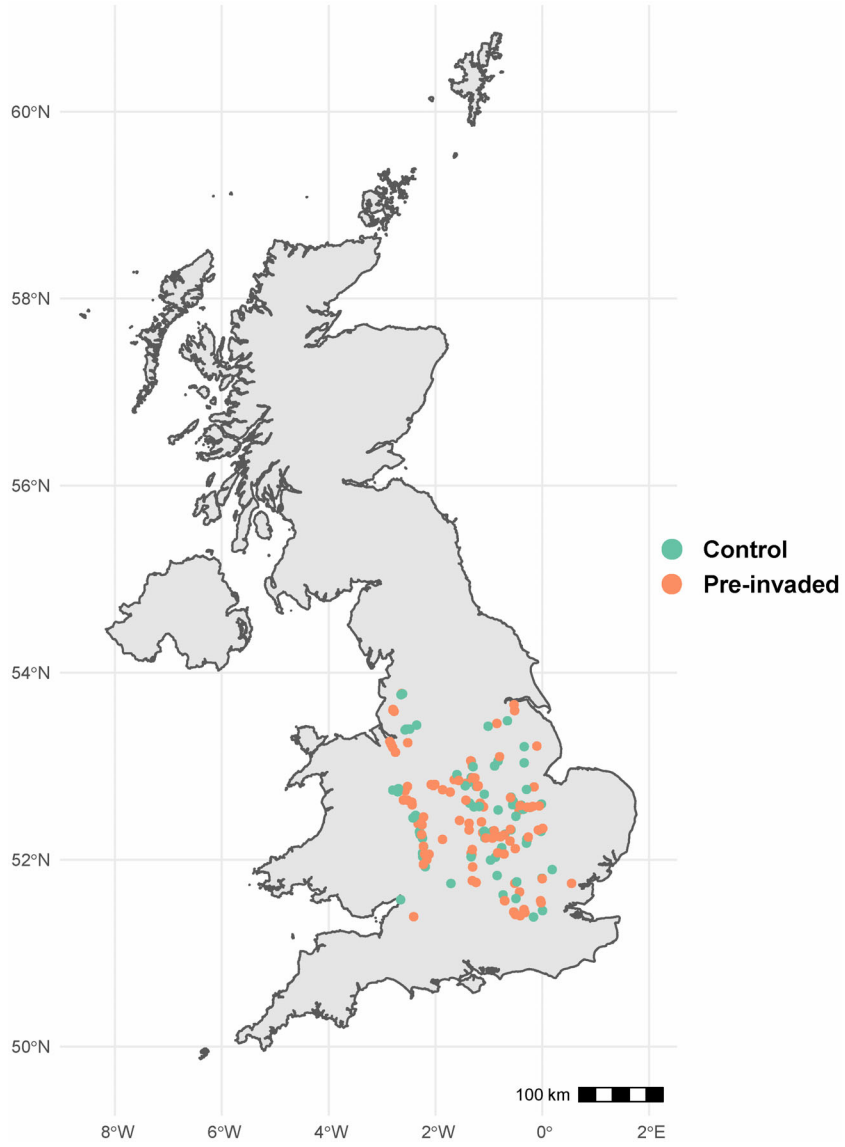

FIGURE 1 Map of study sites employed in the present research (England, UK). Control and pre-invaded are labelled in different colour

with specific feeding habits in the recipient community influenced the future invasibility by Dh. A taxon was considered as a predator when it was coded at least 0.5 out of 1 for its feeding habit "predator" or "piecer" within the biological traits' dataset proposed by Schmidt-Kloiber and Hering (2015).

2.3 | Abiotic descriptors

Riverine abiotic conditions were assessed by measuring four physical descriptors at each sample site: percentage of fine sediment (the proportion of clay, silt, sand), percentage of coarse sediment, the average channel width and average water depth. These latter data were available for 615 and 608 samples respectively. In addition, a buffer of 1 km-radius centred on each studied site was used to describe the local land use surface using four classes (artificial—including urban, agriculture, forested and semi-natural, wetlands and water bodies) based on the CORINE land cover dataset (using 2012 as the census year, source: https://land.copernicus.eu/pan-european/corine-land-cover). A similar approach was applied by Laini et al. (2018) and Monteagudo et al. (2012) to detect the influence of land use on macroinvertebrate community and quality status of rivers. Land use analysis was performed at the site level ($n = 173$) within the programme QGIS (2021); this assumed that land use remained constant throughout the study period.

2.4 | Biological invasion hypotheses tested

The comparison between pre-invaded samples and control (never invaded samples) enabled the examination of four ecological hypotheses related to biological invasions: (a) Human activity, (b) Biotic resistance, (c) Invasional meltdown and (d) Darwin's naturalization. This allowed these theories to be tested using riverine invertebrate communities for the first time in the majority of instances. The "human activity" hypothesis (also named "disturbance" hypothesis) argues

that anthropogenic activities facilitate the establishment of non-native species by disturbing natural environments (Jeschke & Heger, 2018; Leprieur et al., 2008). Similarly, measuring the taxonomic and functional richness values of both control and pre-invaded sites allows the "biotic resistance" hypothesis (also called diversity-invasibility theory) to be tested. This predicts that species-rich communities should prevent or limit the establishment of new non-native species (e.g., Kennedy et al., 2002). Analysing the co-occurrence of other invaders (e.g., through considering the biocontamination signal and the presence of co-occurrent Ponto-Caspian species) allowed the examination of the "invasional meltdown" hypothesis which predicts that if multiple new species invade the same site/habitat, they may help facilitate each other's establishment (Simberloff & Von Holle, 1999). Finally, focussing on the presence and abundance of closely related species in the recipient community (e.g., number of crustacean, organisms from Gammaridae family) provided the opportunity to examine "Darwin's naturalization conundrum" that proposes that taxa with high levels of phylogenetic relatedness with invaders would reduce their chances of successful invasions (Thuiller et al., 2010).

2.5 | Statistical analysis

To determine the effect of the sample condition (control or pre-invaded) on the pool of biological metrics and descriptors, a mixed model framework was used to analyse the data. Biomonitoring and functional metrics, as well as average channel width and water depth were explored using linear mixed models (LMM; package "lmerTest" Kuznetsova, Brockhoff, & Christensen, 2017). LMMs are powerful and robust tools for analysing complex datasets with multiple or clustered observations (Schielzeth et al., 2020) and were performed considering the sample condition as a fixed factor and sampling site (repeated along the temporal period) as a random factor.

Generalized linear mixed models (GLMM, glmer function) were used for variables derived from count data (e.g., abundance of crustacean, gammarids, Ponto Caspian taxa and the abundance-based metrics: EPT, OCH, OH) with a negative binomial distribution to control for over-dispersion. The percentage of riverbed substrate type, being expressed as fine or coarse (with total value equal to 100%) was examined using GLMM using a binomial distribution. Models were validated by checking the graphical distribution of residuals as well as for overdispersion (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) using the "DHARMa" (Hartig, 2021) and "predictmeans" (Luo, Ganesh, & Koolaard, 2021) packages.

To investigate differences in land use typologies, models with and without spatial correlation were assessed and the final model selection performed using Akaike's information criterion. Spatial correlation was then modelled using generalized least squares and a Gaussian correlation structure. All statistical analyses were performed using R statistical software v. 4.1.1 (R Core Team, 2021) and scripts used to calculate functional indices are available at https://github.com/alexology/biomonitoR.

3 | RESULTS

More than 650,000 organisms were identified in the dataset used in this research. A summary of all variables analysed is presented in Table 2 for pre-invaded and control groups (including mean, *SD*, median and maximum values).

Results from the mixed model analysis identified that many variables did not display any statistical differences between pre-invaded and control samples (e.g., LIFE, PSI, WHPT_ASPT and EPT values). Four biomonitoring and functional metrics displayed similar values but were significantly higher in pre-invaded samples compared to control samples—WHPT_TOTAL, N_TAXA-WHPT, FRich and Fred (Figure 2, Table 3). RCI values were significantly higher for pre-invaded samples (Table 3 and Figure 3) illustrating the importance of the contemporary presence of other invaders. Similarly, the number and abundance of other alien Ponto-Caspian taxa were significantly higher at sites that were subsequently invaded than control sites (Tables 2–4). This pattern was confirmed for almost all river catchments considered (Figure 4). In contrast, control sites (not invaded by Dh) appeared to support higher abundances of crustaceans (proxy of phylogenetic related taxa with Dh, see Tables 2 and 4).

Land uses did not differ among the 2 groups (artificial surfaces t-value 1.43, p-value = .15; agriculture surfaces t value = 0.73, p-value = .46, results from other typologies not shown: no value in up to 140 sites). Finally, sites that were subsequently invaded by Dh were significantly wider and deeper compared to control sites, although there were no differences associated with fine- or coarse-grained riverbed sediments (Table 5). Overall, there were few strong associations with classic biological invasion hypotheses, although supporting evidence was observed for the "invasional meltdown" and "Darwin's naturalization conundrum" (see Section 4.2 below).

4 | DISCUSSION

4.1 | Lessons from the past: Preconditions of invasibility

The analysis of multiple community and environmental features has been recommended to better understand the observed changes associated with biological invasion (e.g., Alahuhta et al., 2019). In the current research we integrated taxonomic, phylogenetic, and functional measures of ecosystem integrity and biodiversity, as well as physical characteristics of the sites in a multidimensional approach. When these variables were analysed over the long-term study period it facilitated the comparison between the two groups of samples (pre-invaded and control) located within the same geographical river catchments, but subject to different trajectories of changes (the colonisation and invasion by Dh or—control sites).

Samples from sites that were subsequently invaded by *D. haemobaphes* were characterized by the presence of a higher abundance of other invaders compared to control sites (e.g., Richness Contamination Index values). This was especially evident when focussing

TABLE 2 Mean, *SD*, median, maximum values of the variables tested in the study divided between pre-invaded and control samples (total = 649)

	Pre-invaded samples				Control samples			
Variable	**Mean**	***SD***	**Median**	**Max**	**Mean**	***SD***	**Median**	**Max**
WHPT_TOTAL	118.3	38.8	118.1	212.5	107.3	41.8	105.1	224.8
WHPT_ASPT	4.9	0.75	4.9	6.8	4.9	0.9	5	7.2
N_TAXA-WHPT	23.6	5.8	24	39	21.3	6	21	41
PSI	35.3	20.1	34.7	79	42.3	21.8	45.4	90
LIFE	6.7	0.6	6.7	8.5	6.8	0.7	7	8.5
EPT abun	202.1	271	111	1894	165.4	236.2	80	1912
EPT richness	6.8	3.6	7	16	6.4	3.8	6	16
OCH abun	43.6	57	19	331	51.7	81.3	18	540
OH abun	103.8	273.6	40	3,846	99	252.7	50	3,831
RCI	0.08	0.06	0.07	0.33	0.06	0.04	0.05	0.19
ACI	0.1	0.1	0.06	0.82	0.08	0.1	0.04	0.67
Gammarids abun	104.2	350.7	13	5,000	285.3	1,162.1	41	15,784
Crustacean abun	172.6	367.96	61	5,004	364.9	1,166.3	100	15,789
Ponto Caspian abun	9.3	51	0	800	0.02	0.2	0	3
Ponto Caspian rich	0.3	0.6	0	3	0.01	0.14	0	2
FRich	0.06	0.05	0.06	0.25	0.05	0.05	0.04	0.37
FEve	0.51	0.08	0.51	0.75	0.50	0.09	0.49	0.72
FRed	0.24	0.05	0.24	0.51	0.22	0.06	0.23	0.37
Predator abun	40.7	44	27	282	45.8	67.7	26	497
Predator richness	6.1	3.4	6	18	6	3.5	5	24
Total fines	38	32.7	28	100	42	32.1	34	100
Total coarse	62	32.7	77	100	58	32.1	66	100
Channel depth	92.3	85.1	50	500	43.5	44.2	30	300
Channel width	19.6	17	15	70	7.7	10	3.9	60
Land use 1	0.97	0.96	0.61	3.13	0.85	0.96	0.5	3.13
Land use 2	2	1	2.1	3.13	2.1	1	2.4	3.13

Note: Details, definitions and references in Table 1.

Abbreviations: Abun, abundance; ACI, Abundance Contamination Index; EPT, Ephemeroptera, Plecoptera, Trichoptera; FEve, functional evenness; FRed, functional redundancy; FRich, functional richness; RCI, Richness Contamination Index.

on taxa derived from the same native range as Dh (Ponto Caspian species). The importance of the Ponto Caspian Region as source of alien/invasive amphipod taxa of riverine systems has been stressed at global scale (Cuthbert et al., 2020). This has been particularly evident at the European and UK scale, with invasion and dispersal largely facilitated by the interconnection of river basins via anthropogenic canals and intentional introductions (Bij de Vaate, Jazdzewski, Ketelaars, Gollasch, & Van der Velde, 2002; Gallardo & Aldridge, 2015; Labat, Piscart, & Fontan, 2011). In addition, sites that would later experience the arrival of Dh were characterized by channels that were typically wider and deeper compared to control sites, highlighting that larger rivers were more susceptible to Dh colonisation. This supports previous research indicating large rivers act as hotspot of biological invasion within Europe (Leuven et al., 2009) and especially for invasive amphipods (e.g., Labat et al., 2011). This probably reflects propagule pressures (i.e., measure of introduction effort) that are difficult to quantify (e.g., mode of artificial transport or intentional introductions) as well as specific habitat modifications, landscape position and inter-basin water transfers that may facilitate the range expansion following colonization.

Sites that subsequently experienced the arrival of Dh had higher values of some biomonitoring metrics (e.g., N_TAXA-WHPT) and for other single pressure metrics there were no observable differences (e.g., LIFE and PSI). These results indicate that there is not a simple association between Dh and degraded sites/communities because invasion was more likely at higher scoring sites. Similarly, none of the functional measures nor the feeding habit descriptor were significantly lower within samples prior to the invasion. This highlights that it is extremely difficult to predict and detect the arrival of new invaders purely utilising current biomonitoring and biological metrics. Variables quantifying the biocontamination signal (e.g., RCI) or specific measures based on the co-occurrence of invaders that share the

geographical and evolutionary range provided a better indication of conditions that would favour the colonisation and invasion of Dh. Research undertaken using post invasion data, for the same areas of England, has demonstrated that different facets of biocontamination may affect a range of metrics and that an increase in the relative richness of invasive species (RCI) had a negative effect on the trajectories of multiple biomonitoring measures (Guareschi, Laini, England, Barrett, & Wood, 2021). The utility of RCI makes it a potentially important tool that scientists and natural resource managers can use to obtain a better understanding and assessment of biological invasion events, although a finer taxonomic resolution of faunal data should be used where possible (e.g., genus rather than family). Future applications in research and testing of ecological theories should explicitly incorporate both alien taxa abundance (ACI) and richness (RCI) as proxies for invasive taxa effects.

4.2 | Exploring biological invasion hypotheses applied to Dh

The dataset and analyses performed in this research allowed the consideration of several biological invasion hypotheses which have not been commonly tested using riverine invertebrates.

The "human activity" hypothesis would predict lower biomonitoring metric values and more intensive anthropogenic land-use

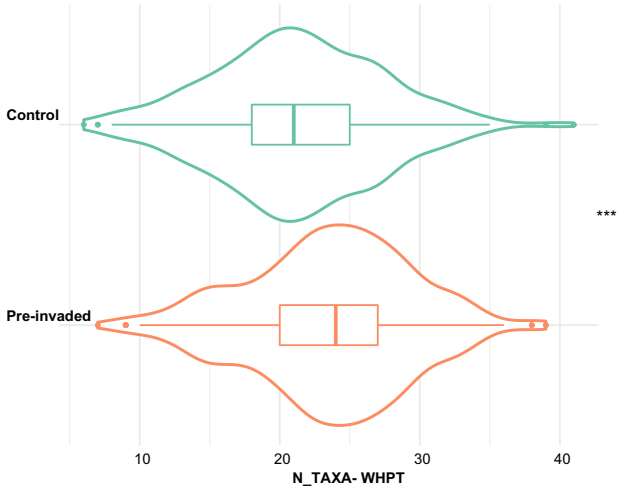

FIGURE 2 Violin plots showing the behaviour of the taxonomic metric N_TAXA-WHPT (definitions and values in Tables 1 and 2) in the two pools of samples analysed in the study ($n = 649$). Vertical bold line represents the median. Control and pre-invaded samples are displayed before the arrival of *Dikerogammarus haemobaphes*. ***$p < .001$

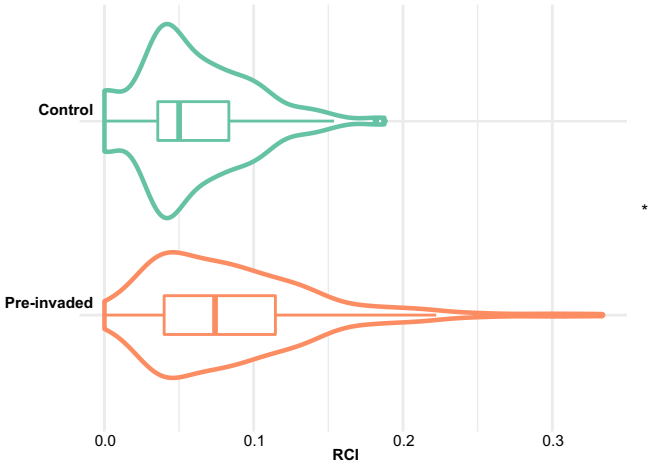

FIGURE 3 Violin plots showing the behaviour of the biocontamination metric RCI (Richness Contamination Index, see definitions in Table 1) in the two pools of samples analysed in the study. Vertical bold line represents the median. Control and pre-invaded samples are displayed before the arrival of *Dikerogammarus haemobaphes*. *$p < .05$

TABLE 3 Linear mixed model results for biomonitoring, functional and biocontamination metrics

Variable	Estimates	*SE*	*df*	*t* value	*p*-value
WHPT_TOTAL	15.033	5.438	167.2	2.765	.006**
WHPT_ASPT	0.126	0.120	171.7	1.047	.297
N_TAXA_WHPT	2.846	0.804	153.8	3.538	.00053***
PSI	−3.621	3.062	170.2	−1.182	.239
LIFE	−0.020	0.094	171.8	−0.211	.833
FRich	0.034	0.014	153.1	2.411	.017*
FRed	0.026	0.006	152.1	4.265	.00003***
FEve	0.007	0.009	151.7	0.771	.442
ACI sqrt	0.001	0.020	92.9	0.500	.618
RCI sqrt	0.038	0.015	117.9	2.441	.016*

Note: See Table 1 for details and definition. ACI and RCI were sqrt-transformed.
Abbreviations: ACI, Abundance Contamination Index; FEve, functional evenness; FRed, functional redundancy; FRich, functional richness; RCI, Richness Contamination Index.
***$p < .001$. **$p < .01$. *$p < .05$.

TABLE 4 Generalized linear mixed model results for all biological metrics based on count data

Variable	Estimates	*SE*	*z*-value	*p*-value
Crustacean abundance	−0.396	0.188	2.109	.035*
Gammarids abundance	−0.534	0.390	−1.368	.171
Ponto Caspian abundance	4.003	1.391	2.88	.0040**
Ponto Caspian richness	3.074	0.593	5.185	2.16e−07***
EPT abundance	0.393	0.202	1.95	.051
EPT richness	0.165	0.085	1.955	.051
OCH abundance	0.018	0.242	0.074	.941
OH abundance	−0.217	0.157	−1.382	.167
Predator abundance	−0.062	0.137	−0.454	.650
Predator richness	0.058	0.075	0.775	.438

Note: See Table 1 for details and definition.
***$p < .001$. **$p < .01$. *$p < .05$.

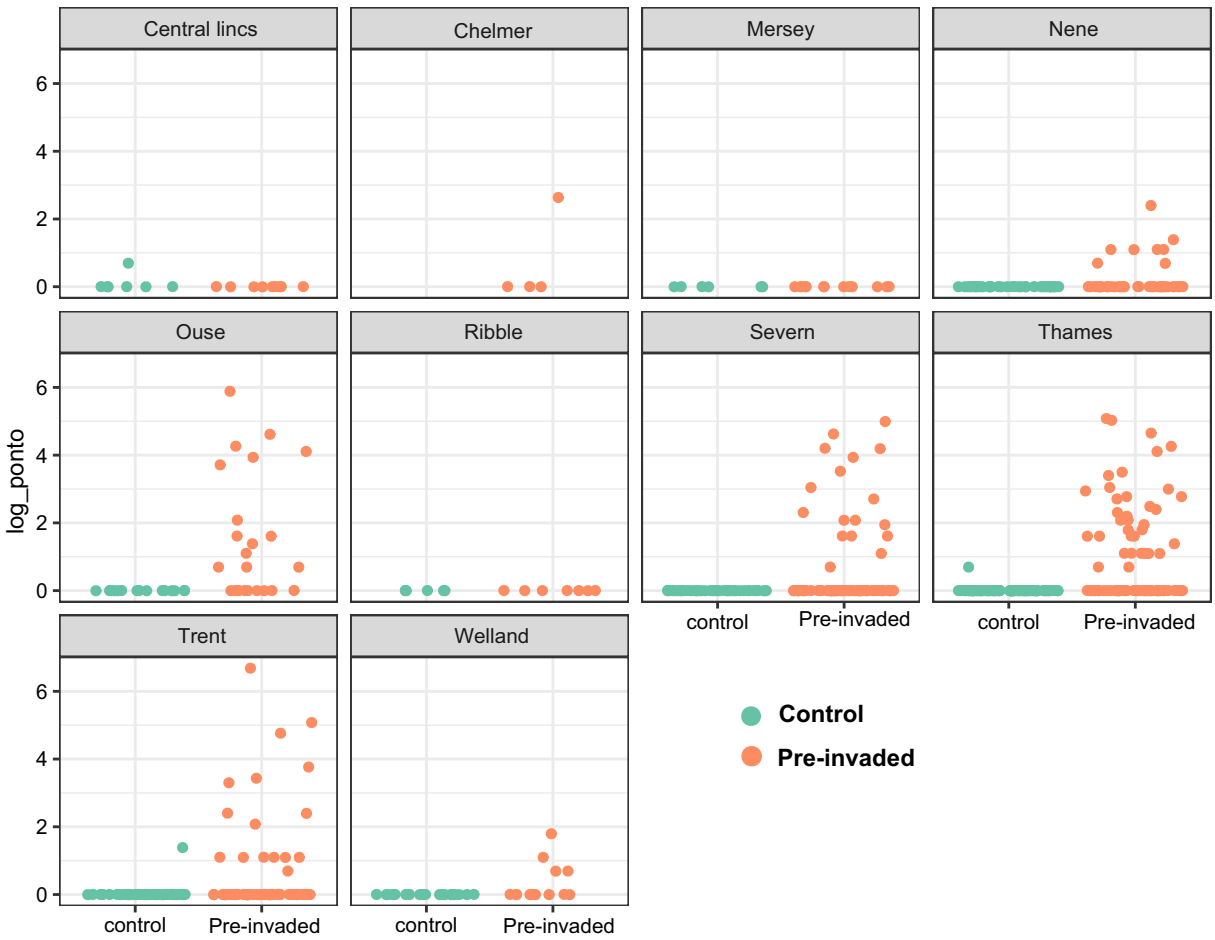

FIGURE 4 Abundance values of Ponto Caspian taxa (from genus: *Hypania*, *Dreissena*, *Chelicorophium*, *Hemimysis*) separated by river catchment. Data are log transformed (natural ln plus one) for increase plot readability

at sites that will experience subsequent invasion. However, our results did not support these predictions, with no differences when considering land use and higher biomonitoring metric values at sites prior to invasion. Similarly, both taxonomic and functional richness displayed higher values at sites that were subsequently invaded (compared to never invaded sites) raising doubts regarding the "biotic resistance" hypothesis and in agreement with the findings of Leprieur et al. (2008) and Henriksson, Yu, Wardle, and Englund (2015) who considered freshwater fish communities in the river and lacustrine environments, respectively. Evidence supporting the "biotic resistance" hypothesis is

TABLE 5 Results for the abiotic descriptor models

Variable	Estimates	*SE*	*z*-value	*p*-value
Total fines	−0.026	0.371	−0.069	.945
Total coarse	0.026	0.371	0.069	.945
Variable	**Estimates**	***SE***	***t* value**	***p*-value**
Average channel depth	0.746	0.126	5.913	1.9e−08***
Average channel width	1.076	0.143	7.522	3.04e−12***

Note: Total fines and total coarse (% riverbed sediment) were modelled with GLMM, while average depth and average width with LMM after log transformation (width: *df* 169.1; depth: *df* 163.8).
Abbreviations: GLMM, generalized linear mixed models; LMM, linear mixed models.
***$p < .001$.

mixed depending on the experiment/habitat studied (Jeschke & Heger, 2018); with clearer patterns reported primarily from terrestrial ecosystems (e.g., plant communities: Beaury, Finn, Corbin, Barr, & Bradley, 2020).

The last two hypotheses considered, the "invasional meltdown" and "Darwin's naturalization," were partially supported by the findings of our research. The presence of other co-occurring invaders (RCI and Ponto Caspian taxa presence) was significantly higher at sites that subsequently experienced the arrival of Dh supporting the prediction of the "invasional meltdown" hypothesis. It has been proposed that "invasional meltdown" is more likely with species from the same native biogeographical region that have co-evolved under similar environmental conditions and have developed strategies that may facilitate their coexistence (Ricciardi, 2001). For example, it has been argued that the presence of *Dreissena polymorpha*, a habitat-forming bivalve, co-occurring with Dh in their native range, may help it establish stable populations in newly invaded areas (Kobak & Kakareko, 2009).

Our simple measures of phylogenetic relatedness provided some support of the "Darwin's naturalization conundrum" indicating how related taxa (belonging to the same sub-phylum and family) were less abundant at sites that subsequently experienced invasion by Dh. The reduced abundance of crustacean and gammarids (although the latter was not significant) may favour the successful colonisation of Dh due to limited niche overlap and competition (e.g., De Gelder et al., 2016 for species displacements). Further studies would be required to confirm these observations (and to validate the others) due to the relatively weak associations recorded, the limited knowledge regarding Dh/resident fauna interactions (both alien and native), and the heterogeneity of results reported in the wider scientific literature (Jeschke & Heger, 2018). A global literature review found that support for major biological invasion hypotheses is uneven across taxonomic groups and habitats, although the "invasional meltdown" hypothesis was better supported by empirical evidence than other hypothesis including "biotic resistance" (Jeschke et al., 2012).

It may be possible that the successful spread of Dh is also related to other features, pathways and behaviours, not considered or quantified in the present study (e.g., presence of aquatic vegetation and specific waterway uses). Indeed, indirect measures of propagule pressure such as socio-economic activities (e.g., international cargo trade and transport) and societal awareness and lifestyles (e.g., recreational boating and fishing) as well as specific inter-basin transfers may have accidentally enhanced the rapid regional dispersal of Dh.

4.3 | Final remarks and opportunities

The detailed examination of sites prior to the invasion of Dh allowed the identification of key biotic and abiotic characteristics that may help in identifying sites at future risk of invasion by this highly successful amphipod. Sites that would be invaded by Dh in the future were characterized by higher abundances of other pre-exiting invaders, lower abundances of other crustaceans and the sites typically had a greater channel width and water depth. Sites sharing these features could be monitored in the future, in England and elsewhere where Dh has been widely recorded (e.g., Labat et al., 2011), to accurately monitor and if possible prevent its future range extension. Recognizing specific abiotic and biotic characteristics that may precondition a site/community for subsequent successful invasion is essential for understanding and better predicting the future trajectories of community change.

Overall, our findings, using Dh as model organism, provided evidence to support the "invasional meltdown" and, at least partially, "Darwin's naturalization conundrum" based on the variables analysed. However, biological invasions within riverine ecosystems are still less studied compared to other ecosystems and the challenges of working in water (where most organism cannot be readily observed) make them more difficult to detect and to develop generalizable concepts. Traditional ecological theories are a crucial starting point for data analysis, and riverine systems will benefit from further hypothesis assessment (both experimental and observational) in the field of biological invasion (e.g., multiple co-occurrent invaders) as well as new context-specific approaches specifically designed to consider freshwater ecosystems and the communities they support.

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AUTHORS' CONTRIBUTIONS

Simone Guareschi: Conceived the idea and designed methodology; data analysis; led the writing – manuscript; **Alex Laini**: Conceived the

idea and designed methodology; data analysis; **Judy England**: Provided the raw data; results interpretations – management perspective; **Jon Barrett**: Provided the raw data; results interpretations – management perspective; **Paul J. Wood**: Results interpretations – management perspective. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Site details and biological data are available via Environment Agency 'Ecology and Fish Data Explorer' at https://environment.data.gov.uk/ecology/explorer/ selecting 'invertebrates' and using the site codes (SITE_ID) found in first column of the Supplementary Material S1.

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REFERENCES

Alahuhta, J., Erös, T., Kärnä, O. M., Soininen, J., Wang, J., & Heino, J. (2019). Understanding environmental change through the lens of trait-based, functional, and phylogenetic biodiversity in freshwater ecosystems. *Environmental Reviews*, *27*(2), 263–273. https://doi.org/10.1139/er-2018-0071

Arbačiauskas, K., Semenchenko, V., Grabowski, M., Leuven, R. S. E. W., Paunović, M., Son, M. O., … Panov, V. E. (2008). Assessment of biocontamination of benthic macroinvertebrate communities in European inland waterways. *Aquatic Invasions*, *3*(2), 211–230. https://doi.org/10.3391/ai.2008.3.2.12

Bacela-Spychalska, K., & Van Der Velde, G. (2013). There is more than one "killer shrimp": Trophic positions and predatory abilities of invasive amphipods of Ponto-Caspian origin. *Freshwater Biology*, *58*(4), 730–741. https://doi.org/10.1111/fwb.12078

Barbet-Massin, M., Rome, Q., Villemant, C., & Courchamp, F. (2018). Can species distribution models really predict the expansion of invasive species? *PLoS One*, *13*(3), 1–14. https://doi.org/10.1371/journal.pone.0193085

Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology Letters*, *23*(3), 476–482. https://doi.org/10.1111/ele.13446

Belmar, O., Bruno, D., Guareschi, S., Mellado-Díaz, A., Millán, A., & Velasco, J. (2019). Functional responses of aquatic macroinvertebrates to flow regulation are shaped by natural flow intermittence in Mediterranean streams. *Freshwater Biology*, *64*(5), 1064–1077. https://doi.org/10.1111/fwb.13289

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H. A. M., Gollasch, S., & Van der Velde, G. (2002). Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, *59*(7), 1159–1174. https://doi.org/10.1139/f02-098

Bojko, J., Stentiford, G. D., Stebbing, P. D., Hassall, C., Deacon, A., Cargill, B., … Dunn, A. M. (2018). Pathogens of *Dikerogammarus haemobaphes* regulate host activity and survival, but also threaten native amphipod populations in the UK. *Diseases of Aquatic Organisms*, *136*, 63–78. https://doi.org/10.3354/dao03195

Bonada, N., Rieradevall, M., & Resh, V. H. (2006). Benthic macroinvertebrate assemblages and macrohabitat connectivity in Mediterranean-climate streams of northern California. *Journal of the North American Benthological Society*, *25*(1), 32–43.

Buss, D. F., Carlisle, D. M., Chon, T. S., Culp, J., Harding, J. S., Keizer-Vlek, H. E., … Hughes, R. M. (2015). Stream biomonitoringusing macroinvertebrates around the globe: a comparison of large-scaleprograms. *Environ Monit Assess*, *187*, 4132. https://doi.org/10.1007/s10661-014-4132-8

Catford, J. A., Jansson, R., & Nilsson, C. (2009). Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, *15*(1), 22–40. https://doi.org/10.1111/j.1472-4642.2008.00521.x

Chang, F. H., Lawrence, J. E., Rios-Touma, B., & Resh, V. H. (2014). Tolerance values of benthic macroinvertebrates for stream biomonitoring: Assessment of assumptions underlying scoring systems worldwide. *Environmental Monitoring and Assessment*, *186*(4), 2135–2149. https://doi.org/10.1007/s10661-013-3523-6

Constable, D., & Birkby, N. J. (2016). The impact of the invasive amphipod *Dikerogammarus haemobaphes* on leaf litter processing in UKrivers. *Aquatic Ecology*, *50*(2), 273–281. https://doi.org/10.1007/s10452-016-9574-3

Cuthbert, R. N., Kotronaki, S. G., Dick, J. T. A., & Briski, E. (2020). Salinity tolerance and geographic origin predict global alien amphipod invasions. *Biology Letters*, *16*, 2–7. https://doi.org/10.1098/rsbl.2020.0354

De Gelder, S., Van der Velde, G., Platvoet, D., Leung, N., Dorenbosch, M., Hendriks, H. W. M., & Leuven, R. S. E. W. (2016). Competition for shelter sites: Testing a possible mechanism for gammarid species displacements. *Basic and Applied Ecology*, *17*(5), 455–462.

Extence, C. A., Balbi, D. M., & Chadd, R. P. (1999). River flow indexing using British benthic macroinvertebrates: A framework for setting hydroecological objectives. *River Research and Applications*, *15*(6), 545–574. https://doi.org/10.1002/(sici)1099-1646(199911/12)15:6<545::aid-rrr561>3.0.co;2-w

Extence, C. A., Chadd, R. P., England, J., Dunbar, M. J., Wood, P. J., & Taylor, E. D. (2013). The assessment of fine sediment accumulation in rivers using macro-invertebrate community response. *River Research and Applications*, *29*, 17–55. https://doi.org/10.1002/rra.1569

Gallardo, B., & Aldridge, D. C. (2013). Priority setting for invasive species management: Risk assessment of Ponto-Caspian invasive species into Great Britain. *Ecological Applications*, *23*(2), 352–364. https://doi.org/10.1890/12-1018.1

Gallardo, B., & Aldridge, D. C. (2015). Is Great Britain heading for a Ponto-Caspian invasional meltdown? *Journal of Applied Ecology*, *52*(1), 41–49. https://doi.org/10.1111/1365-2664.12348

Gallardo, B., & Aldridge, D. C. (2018). Inter-basin water transfers and the expansion of aquatic invasive species. *Water Research*, *143*, 282–291. https://doi.org/10.1016/j.watres.2018.06.056

Guareschi, S., Laini, A., England, J., Barrett, J., & Wood, P. J. (2021). Multiple co-occurrent alien invaders constrain aquatic biodiversity in rivers. *Ecological Applications*, *31*(6), e02385. https://doi.org/10.1002/eap.2385

Guareschi, S., Laini, A., England, J., Johns, T., Winter, M., & Wood, P. J. (2021). Invasive species influence macroinvertebrate biomonitoring tools and functional diversity in British rivers. *Journal of Applied Ecology*, *58*(1), 135–147. https://doi.org/10.1111/1365-2664.13795

Hartig, F. (2021). DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R Package Version 0.4.4. Retrieved from http://florianhartig.github.io/DHARMa/.

Havel, J. E., Kovalenko, K. E., Thomaz, S. M., Amalfitano, S., & Kats, L. B. (2015). Aquatic invasive species: Challenges for the future. *Hydrobiologia*, *750*(1), 147–170. https://doi.org/10.1007/s10750-014-2166-0

Henriksson, A., Yu, J., Wardle, D. A., & Englund, G. (2015). Biotic resistance in freshwater fish communities: Species richness, saturation or species

identity? *Oikos*, *124*(8), 1058–1064. https://doi.org/10.1111/oik.01700

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., & González, J. A. (2017). Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. *Ecology and Evolution*, *7*(3), 831–844. https://doi.org/10.1002/ece3.2692

Jeschke, J., Gómez Aparicio, L., Haider, S., Heger, T., Lortie, C., Pyšek, P., & Strayer, D. (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota*, *14*, 1–20. https://doi.org/10.3897/neobiota.14.3435

Jeschke, J. M., & Heger, T. (2018). *Invasion biology: Hypotheses and evidence. CABI invasives series 9* (p. 177). Boston, MA: CAB International.

Johns, T., Smith, D. C., Homann, S., & England, J. A. (2018). Time-series analysis of a native and a non-native amphipod shrimp in two English rivers. *BioInvasions Records*, *7*(2), 101–110. https://doi.org/10.3391/bir.2018.7.2.01

Kennedy, T. A., Naeem, S., Howe, K. M., Knops, J. M., Tilman, D., & Reich, P. (2002). Biodiversity as a barrier to ecological invasion. *Nature*, *417*, 636–638. https://doi.org/10.1016/j.mehy.2012.01.005

Kitchin, P. L. (2005). Measuring the amount of statistical information in the EPT index. *Environmetrics*, *16*(1), 51–59. https://doi.org/10.1002/env.670

Kobak, J., & Kakareko, T. (2009). Preferences of the Ponto-Caspian amphipod *Dikerogammarus haemobaphes* for living zebra mussels. *Journal of Zoology*, *279*, 229–235. https://doi.org/10.1111/j.1469-7998.2009.00610.x

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest package: Tests in linear mixed effects models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Labat, F., Piscart, C., & Fontan, B. (2011). First records, pathways and distributions of four new Ponto-Caspian amphipods in France. *Limnologica*, *41*(4), 290–295. https://doi.org/10.1016/j.limno.2010.12.004

Laini, A., Bolpagni, R., Cancellario, T., Guareschi, S., Racchetti, E., & Viaroli, P. (2018). Testing the response of macroinvertebrate communities and biomonitoring indices under multiple stressors in a lowland regulated river. *Ecological Indicators*, *90*, 47–53. https://doi.org/10.1016/j.ecolind.2018.02.051

Laini, A., Viaroli, P., Bolpagni, R., Cancellario, T., Racchetti, E., & Guareschi, S. (2019). Taxonomic and functional responses of benthic macroinvertebrate communities to hydrological and water quality variations in a heavily regulated river. *Water*, *11*(7), 1478. https://doi.org/10.3390/w11071478

Leprieur, F., Beauchard, O., Blanchet, S., Oberdorff, T., & Brosse, S. (2008). Fish invasions in the world's river systems: When natural processes are blurred by human activities. *PLoS Biology*, *6*(2), 404–410. https://doi.org/10.1371/journal.pbio.0060028

Leung, B., Lodge, D. M., Finnoff, D., Shogren, J. F., Lewis, M. A., & Lamberti, G. (2002). An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B: Biological Sciences*, *269*(1508), 2407–2413. https://doi.org/10.1098/rspb.2002.2179

Leuven, R. S. E. W., van der Velde, G., Baijens, I., Snijders, J., van der Zwart, C., Lenders, H. J. R., & bij de Vaate, A. (2009). The river Rhine: A global highway for dispersal of aquatic invasive species. *Biological Invasions*, *11*(9), 1989–2008. https://doi.org/10.1007/s10530-009-9491-7

Luo, D., Ganesh, S., & Koolaard, J. (2021). Predictmeans: Calculate predicted means for linear models. R Package Version 1.0.6. Retrieved from https://CRAN.R-project.org/package=predictmean.

Mathers, K. L., White, J. C., Guareschi, S., Hill, M. J., Heino, J., & Chadd, R. (2020). Invasive crayfish alter the long-term functional biodiversity of lotic macroinvertebrate communities. *Functional Ecology*, *34*, 2350–2361. https://doi.org/10.1111/1365-2435.13644

Monteagudo, L., Moreno, J. L., & Picazo, F. (2012). River eutrophication: Irrigated vs. non-irrigated agriculture through different spatial scales. *Water Research*, *46*(8), 2759–2771. https://doi.org/10.1016/j.watres.2012.02.035

Moorhouse, T. P., & Macdonald, D. W. (2015). Are invasives worse in freshwater than terrestrial ecosystems? *WIREs Water*, *2*(1), 1–8. https://doi.org/10.1002/wat2.1059

Oficialdegui, F. J., Sánchez, M. I., & Clavero, M. (2020). One century away from home: How the red swamp crayfish took over the world. *Reviews in Fish Biology and Fisheries*, *30*(1), 121–135. https://doi.org/10.1007/s11160-020-09594-z

Paisley, M. F., Trigg, D. J., & Walley, W. J. (2014). Revision of the biological monitoring working party (BMWP) score system: Derivation of present-only and abundance-related scores from field data. *River Research and Applications*, *30*, 887–904. https://doi.org/10.1002/rra.2686

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: Application for improving the measurement of functional diversity. *Oikos*, *118*(3), 391–402. https://doi.org/10.1111/j.1600-0706.2009.16668.x

Pillar, V. D., Blanco, C. C., Müller, S. C., Sosinski, E. E., Joner, F., & Duarte, L. D. S. (2013). Functional redundancy and stability in plant communities. *Journal of Vegetation Science*, *24*(5), 963–974. https://doi.org/10.1111/jvs.12047

QGIS. (2021). *QGIS geographic information system*. QGIS Association Retrieved from http://www.qgis.org

R Core Team. (2021). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org

Ricciardi, A. (2001). Facilitative interactions among aquatic invaders: Is an "invasional meltdown" occurring in the Great Lakes? *Canadian Journal of Fisheries and Aquatic Sciences*, *58*(12), 2513–2525. https://doi.org/10.1139/cjfas-58-12-2513

Schielzeth, H., Dingemanse, N. J., Nakagawa, S., Westneat, D. F., Allegue, H., Teplitsky, C., … Araya-Ajoy, Y. G. (2020). Robustness of linear mixed-effects models to violations of distributional assumptions. *Methods in Ecology and Evolution*, *11*, 1141–1152. https://doi.org/10.1111/2041-210x.13434

Schmidt-Kloiber, A., & Hering, D. (2015). Www.freshwaterecology.info—an online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, *53*, 271–282. https://doi.org/10.1016/j.ecolind.2015.02.007

Simberloff, D. (2020). Maintenance management and eradication of established aquatic invaders. *Hydrobiologia*, *5*, 2399–2420. https://doi.org/10.1007/s10750-020-04352-5

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species. *Biological Invasions*, *1*(1), 21–32.

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Tachet, H., Bournaud, M., Richoux, P., & Usseglio-Polatera, P. (2010). *Invertébrés d'eau douce: Systématique, Biologie, Écologie* (p. 607). Paris: CNRS Editions.

Thuiller, W., Gallien, L., Boulangeat, I., de Bello, F., Münkemüller, T., Roquet, C., & Lavergne, S. (2010). Resolving Darwin's naturalization conundrum: A quest for evidence. *Diversity and Distributions*, *16*(3), 461–475. https://doi.org/10.1111/j.1472-4642.2010.00645.x

Tickner, D., Opperman, J. J., Abell, R., Acreman, M., Arthington, A. H., Bunn, S. E., … Young, L. (2020). Bending the curve of global freshwater biodiversity loss: An emergency recovery plan. *Bioscience*, *70*(4), 330–342. https://doi.org/10.1093/biosci/biaa002

Villéger, S., Mason, N. W. H., & Mouillot, D. (2008). New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, *89*(8), 2290–2301. https://doi.org/10.1890/07-1206.1

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer. https://doi.org/10.1007/978-0-387-87458-6

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