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Multiple co-occurrent alien invaders constrain aquatic biodiversity in rivers

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Abstract. A greater understanding and effective management of biological invasions is a priority for biodiversity conservation globally. Many freshwater ecosystems are experiencing the colonization and spread of multiple co-occurrent alien species. Here the implications of both the relative abundance and richness of alien invaders on aquatic macroinvertebrate taxonomic and functional richness, ecosystem quality, and functional redundancy are assessed using long-term data from rivers in England. Based on the most common aquatic invaders, results indicated that their richness, rather than abundance, was the most important factor negatively affecting aquatic macroinvertebrate biodiversity. However, the response of functional redundancy was negatively affected by invader abundance at the river basin scale. The response of communities varied as the number of invading taxa increased, with the most marked reductions following the colonization of the first few invaders. Results indicate that different facets of multiple biological invasions influence distinct aspects of aquatic biodiversity. Preventing the establishment of new invaders and limiting invader taxa richness within a community should therefore be a conservation priority. These findings will assist river scientists in understanding mechanisms driving changes in biodiversity and facilitate the testing of ecological theories while also ensuring environmental managers and regulators can prioritize conservation / management opportunities.

Key words: alien species; bioassessment; biological invasions; freshwater biodiversity; functional diversity; invertebrates; multiple invasions.

Introduction

Biological invasions have been identified as one of the primary drivers of change in the natural environment (IPBES 2019), with the control and management of invasive alien species highlighted as a priority for biodiversity conservation and resource management globally (Pyšek et al. 2020). A growing number of new alien species have been identified worldwide and many biotic communities and ecosystems are already experiencing or are predicted to experience multiple invaders (Pyšek et al. 2020, Seebens et al. 2021). Inland freshwaters and rivers are particularly vulnerable to multiple invasions with potentially significant consequences for their long-term management and conservation (Preston et al. 2012, Gallardo and Aldridge 2015). Within freshwater ecosystems, the relative abundance (number of individuals) and relative richness (number of taxa) of alien invaders have been explored as measures to quantify and define biological pollution or "biocontamination" (Arbačiauskas et al. 2008). The relevance of these specific components in quantifying levels of biological invasion has also been recommended within other ecosystems to aid understanding of the "contribution" that alien species make to a community (Catford et al. 2012). A recent meta-analysis of terrestrial, marine, and freshwater research highlighted that the community response to invasion depended on the invasive species' abundance and trophic position (Bradley et al. 2019). Likewise, the probability of whether or not an alien species will successfully establish a population in a novel

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environment is often related to the number of individuals introduced (Cassey et al. 2018). Species richness and the number of organisms are among the most common variables used to describe biodiversity in ecological studies (e.g., Colwell 2009). Despite this, the effect of both abundance and richness of multiple co-occurrent invaders on community taxonomic and functional measures remains unclear and has barely been acknowledged in invasion biology or water resource management literature.

To advance knowledge and improve the global evidence base of understanding of biological invasion, there is a pressing need to explore the "biocontamination signal" using multiple taxa and long-term observational data (e.g., Matzek et al. 2015, Boon et al. 2020). This study aims to examine this research gap by (1) identifying the most common combination of co-occurrent invaders in temperate rivers and (2) exploring which biocontamination component exerts the greatest effect on measures of taxonomic and functional biodiversity at different spatial scales. Specifically, we aim to study the implications of varying gradients of abundance and richness of invader taxa on macroinvertebrate communities using long-term field data (>10 yr) from rivers in England. Deconstructing biocontamination into two components, (1) relative abundance and (2) relative richness of taxa, provides opportunities to identify specific pressures due to multiple co-occurring invaders and advance theoretical ecological understanding. This may help scientists and environmental managers to prioritize activities centered on conserving biodiversity through the management of invader abundance (e.g., by preventing population explosions and/or containing the most abundant taxa) or focusing on preventing the colonization and establishment of new invaders.

Methods

Biological data

Aquatic macroinvertebrate data and taxonomic metrics were obtained through standardized protocols from the Environment Agency, the statutory regulator within England responsible for monitoring the status of water bodies. Macroinvertebrates have been widely utilized in ecological research and environmental assessment (Buss et al. 2015), being pivotal components within lotic food webs and nutrient processing, with direct links to riparian and terrestrial ecosystems (Suter and Cormier 2015). A total of 1249 samples from 202 lotic sites (covering the period 2006–2019) were used in the analyses from central and southern England (mostly Rivers Trent and Thames basins, see Appendix S1: Table S1). The entire data set included ~1.8 million classified organisms and all samples comprised at least 80% of the taxa identified to genus or species level. The study area has been subject to multiple biological invasion events (e.g., Gallardo and Aldridge 2015) and sites are typical of many temperate river ecosystems. A total of 12 alien invertebrate taxa were considered to quantify the level of biocontamination (abundance contamination index [ACI] and richness contamination index [RCI] values) within the data set (four amphipods, two decapods, two bivalves, one gastropod, mysid, triclad, and terebellid; see taxonomic details in Appendix S1: Table S1), representing the most common and widely distributed invaders in European and British fresh waters (Gallardo and Aldridge 2013, UKTAG 2015). All taxa have previously been identified as invasive or potentially harmful in similar studies and are defined here as "invaders" (Gallardo and Aldridge 2013, Laverty et al. 2015). The 12 macroinvertebrate taxa (10 genera plus *Dugesia tigrina* and *Gammarus tigrinus*) reflect the dominance of Crustacea and Mollusca as the most common invertebrate invaders of fresh waters globally (Strayer 2010) and encompass diverse functional features covering varying body sizes, food preferences, and feeding habits (e.g., from filter feeders to predators, from size <10 to >80 mm). Using this list, two measures of biocontamination were calculated: an abundance contamination index (coded ACI) and a richness contamination index (coded RCI) (Arbačiauskas et al. 2008). Both were calculated as the proportion of the overall community in a sample, with values ranging from 0 to 1 with values closer to 1 indicating greater biocontamination. Four macroinvertebrate-based indices were calculated for each sample and examined in association with the abundance and richness biocontamination measures: (1) the Whalley, Hawkes, Paisley, and Trigg score (coded WHPT TOTAL; Paisley et al. 2014); (2) the number of taxa used to calculate the WHPT score (N_TAXA-WHPT; Paisley et al. 2014); (3) functional richness (FRich, following Villéger et al. 2008) and (4) functional redundancy (FRed, following Pillar et al. 2013). The WHPT score represents the abundance-based adaptation of the globally utilized Biological Monitoring Working Party index (Hawkes 1998) where taxa are scored according to their sensitivity to contamination (the greater their pollution tolerance, the lower the score). This is the biomonitoring scoring system used in UK to derive the official measures for ecological status assessment of rivers. Thus N_TAXA-WHPT provides a quantitative proxy of overall taxonomic richness at the family level, which is a widely applied metric in river biomonitoring procedures (Buss et al. 2015). Community functional approaches may improve understanding of associations between biodiversity and ecosystem properties (Gagic et al. 2015). Here we focused on two functional indices previously recognized as being sensitive to anthropogenic pressures and invasive species in rivers (Belmar et al. 2019, Guareschi et al. 2021*a*). FRich is defined as the volume of functional multidimensional space occupied by all species in a community (Villéger et al. 2008), while FRed reflects the degree to which species in a community share similar functional features (Hooper et al. 2005). The functional characteristics of the communities were characterized using biological traits describing life history, resilience or resistance features, reproduction strategy, respiration, feeding preferences, and feeding mode according to Tachet et al. (2010) and Schmidt-Kloiber and Hering (2015) at the genus level. This taxonomic level is widely utilized in research focused on functional diversity and the response of riverine communities to external stressors (Gutiérrez-Cánovas et al. 2019). The entire data set of biological traits was used to derive FRich while five “effect traits” (size, dispersal, mode of locomotion, food consumed, and feeding habits) were used to calculate FRed, following the approach used for alpine and temperate riverine communities previously (Bruno et al. 2019, Laini et al. 2019).

Statistical analysis

To determine the effect of ACI, RCI, and their interaction with community taxonomic and functional measures, a linear mixed models’ framework was used (LMM; functions lmer and anova from the package lmerTest; Kuznetsova et al. 2017). LMMs are powerful and robust tools for analyzing complex data sets with repeated or clustered observations (Schielzeth et al. 2020). LMMs were developed using both biocontamination metrics as fixed factors and sampling site and year as random factors at both the national and basin scale (River Trent and Thames basins represent more than 90% of the data set). Models were assessed by checking the graphical distribution of residuals for normality and homoscedasticity according to Zuur et al. (2009) and square-root transformed where necessary (for functional richness and also taxonomic metrics within the Trent basin). Further mixed effect models, considering the total number of alien taxa as fixed factors (within an ANCOVA approach), were developed to determine potential differences based on the number of invader taxa in samples at the national level using the same random factors as outline above. In this case, natural log transformations were applied (except for FRed). Piecewise regression was applied to identify potential inflection points if a metric displayed significant associations with biocontamination indices (Appendix 1: Table S4). Statistical analyses were performed using R software v. 4.0.2 (R Core Team 2020).

Results

Combinations of one to eight co-occurrent invader taxa were recorded in our samples, with *Potamopyrgus antipodarum* and *Crangonyx pseudogracilis/floridanus* sens. lat. being the most common alien species within communities when just a single invader was present. Subsequent colonists, especially in cases of two or more invaders, were typically *Pacifastacus leniusculus*, *Dugesia tigrina*, *Dikerogammarus haemobaphes*, and *Chelicorophium curvispinum* (Appendix S1: Table S2). Statistical analysis indicated that RCI (richness of alien taxa) rather than ACI (invader abundance) was the most significant factor for multiple biological invaders, affecting three out of four indices tested: WHPT TOTAL, N_TAXA-WHPT, and functional richness at the national scale (Table 1 and Fig. 1). The effect on functional redundancy was less clear and no significant trend was observed at the national scale. Along the gradient of relative richness of invaders (RCI), the response varied depending on the number of invader taxa present for all metrics (significant interactions particularly evident in the first three cases: WHPT TOTAL $F_{4,\ 1136.2} = 325.6$, $P < 0.001$; N_TAXA-WHPT $F_{4,\ 1190} = 546.7$, $P < 0.001$; FRich $F_{4,\ 1193.6} = 454.1$, $P < 0.001$; FRed $F_{4,\ 1213.1} = 9.5$, $P < 0.001$). When the relative richness of invaders increased within the community (RCI value along the x-axis in Fig. 2) the effects were most marked in rivers with less invaders to start with (*n*. invaders = 1–2), especially for taxonomic indices and functional richness (Fig. 2). Results at the river basin level indicated similar significant patterns and negative effects for invader richness (RCI) for the three metrics presented above (Appendix S1: Table S3). However, both richness and abundance of invaders were significant for taxonomic metrics in the River Trent data set. In contrast, FRed only displayed a negative response to invader abundance (ACI) within the Trent basin (Appendix S1: Table S3).

Discussion

Although multiple co-occurring alien invaders are becoming increasingly common, little quantitative

Table 1. Results of linear mixed model (LMM) and responses of the four biological indices analysed at the national scale (England, n = 1,249 samples).

Biological indices	DenDF	F	P
WHPT TOTAL			
RCI	1221.4	103.87	$<2 \times 10^{-16}$***
ACI	1159.3	2.65	0.104
RCI × ACI	1143.1	3.32	0.069
N_TAXA-WHPT			
RCI	1241.7	107.02	$<2 \times 10^{-16}$***
ACI	1222	0.59	0.444
RCI × ACI	1198.7	1.40	0.237
Functional richness			
RCI	1231.5	89.03	$<2 \times 10^{-16}$***
ACI	1232.1	0.04	0.849
RCI × ACI	1211	1.01	0.316
Functional redundancy			
RCI	1202.4	0.19	0.667
ACI	1244.8	0.66	0.416
RCI × ACI	1237.7	0.07	0.794

Notes: WHPT-TOTAL, the Whalley, Hawkes, Paisley, and Trigg score; N–TAXA-WHPT, the number of taxa used to calculate WHPT-TOTAL; ACI, abundance contamination index; RCI, richness contamination index; DenDF, denominator degrees of freedom. numDF = 1.

***P < 0.001.

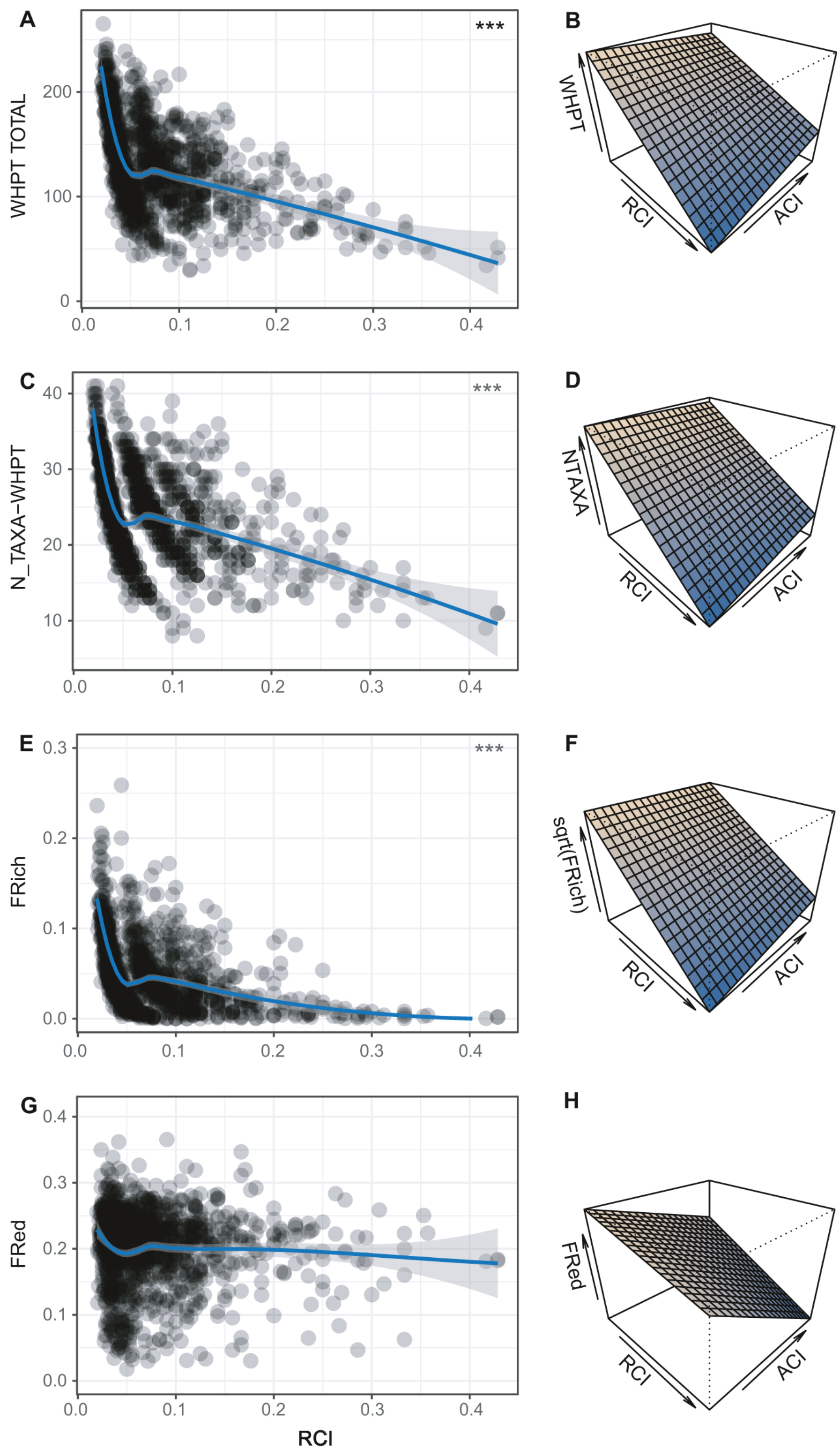

FIG. 1. (A, C, E, G) Relationship between the four biological indices (WHPT-TOTAL, the Whalley, Hawkes, Paisley, and Trigg score; N–TAXA-WHPT, the number of taxa used to calculate WHPT-TOTAL; functional richness; functional redundancy) and RCI (richness contamination index). (B, D, F, H) Three-dimensional plots showing predicted mixed model results for each index as a function of RCI and ACI at the national scale. Curves for each metric (left column) were fitted with loess regression lines. Standard errors (dark gray) are also displayed. Functional richness is square-root transformed in panel F. $^{***}P < 0.001$.

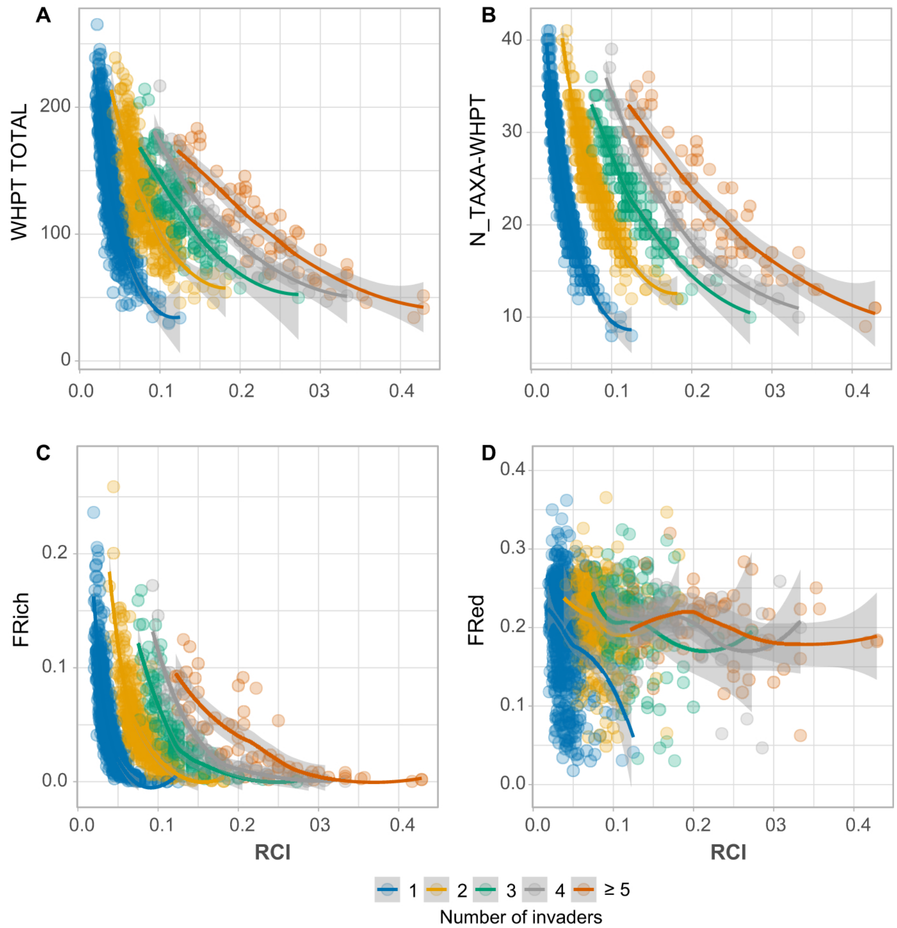

FIG. 2. Response of the four biological indices (A, WHPT TOTAL; B, N_TAXA-WHPT; C, functional richness; D, functional redundancy) based on the number of alien invaders in the community and the richness contamination index (RCI). Curves for each metric were fitted with loess regressions lines. Standard errors (dark gray) are also displayed.

evidence of the most common combinations and the effects on community taxonomic and functional measures over large spatial and temporal scales for rivers exists. In our extensive data set from UK temperate rivers, the well-established invaders *Potamopyrgus antipodarum* and *Crangonyx pseudogracilis/floridanus* sens. lat. were the most common invaders that occurred individually or together demonstrating their ubiquity and colonization potential (e.g., Loo et al. 2007). Both taxa are shredders primarily feeding on vegetation detritus, highly fecund with wide environmental tolerances (Tachet et al. 2010) and therefore should be on the "watch list" of all non-invaded and pristine sites as potential first invaders. However, given the dynamism of biological invasion events and the predictions of future accumulation of alien species in both mainland Europe (Seebens et al. 2021) and in the study area (Gallardo and Aldridge 2013), ongoing analysis and periodic evaluation of long-term monitoring data are advised to assess the most recent information available. This will help inform future conservation strategies (e.g., biosecurity and early warning planning) and predictions of potential geographical range changes. Overall, strong negative responses associated with the richness of alien invader taxa ("invasive biodiversity") rather than their abundance were apparent on several components of lotic biodiversity at both spatial scales examined. This may reflect the presence of multiple co-occurring alien invaders acting simultaneously and exerting heterogeneous pressures on the recipient community (e.g., from direct predation to resource competition and habitat modifications). These results may also help advance theoretical ecological understanding given that most existing conceptual models considering invasive species and their impacts primarily focus on the relationship between individual species abundance and its impact(s) (e.g., abundance–impact curves; Bradley et al. 2019). In contrast, for co-occurring alien invaders, the richness facet, and its role (here highlighted by marked effects on biological metrics) has scarcely been acknowledged or explored at the community or ecosystem level. Some spatial variability in the response of metrics values were detected especially for FRed. Functional redundancy was not significantly influenced by the level of biocontamination at the national scale, although at the local scale a significant negative association was observed with the relative abundance of alien invaders (ACI values) in the River Trent basin. Samples sites from the Trent basin displayed higher values of FRed compared to samples from the River Thames basin (F value$_{1,\ 167.7}$ = 10.17, $P < 0.01$); and at the same time higher mean and maximum ACI values, although the latter were not statistically different between basins. Given that FRed reflects the relative resilience and resistance of an ecosystem to pressures, these results suggest negative effects of highly abundant alien taxa on ecosystem vulnerability at the basin scale (e.g., Trent). Similarly, Loreau (2004) stressed the importance of spatial and temporal resolutions when assessing functional redundancy. Such spatial differences support the need to adopt a flexible approach (i.e. using a range of complementary community metrics) that considers the potential influence of scale when assessing multiple invaders, to understand their wider effects on recipient ecosystems. Differences in the sensitivity of functional richness and functional redundancy have been detected for macroinvertebrate communities along regulated rivers from France and Italy (Bruno et al. 2019, Laini et al. 2019). Likewise, Schmera et al. (2012) reported that invertebrate community functional richness was more sensitive to anthropogenic impacts than functional redundancy, but neither were sensitive to the presence of alien taxa (considered as a dummy variable: presence/absence) in Hungarian streams. Assessing and predicting whether alien invader taxa effectively replace and make up for loss in functional diversity due to extinction is a hot topic of debate in contemporary ecology (Toussaint et al. 2018). Based on the current results, the negative association between biocontamination and community functional measures (particularly richness) across spatial scales, appears indicative of an overall reduction in community functionality. It should be noted that rivers with different numbers of invaders respond differently when their relative richness increases, illustrating the importance of context specificity and starting point conditions. This was particularly evident during the initial phase of invasion events, when a small increase in the relative richness of invaders had the strongest effect (x-axis in Fig. 2) on most metrics considered. In contrast, rivers with a greater number of invaders displayed less of a response and would require a greater increase in the proportion of invader taxa to reach the same outcome. This suggests that introduced species could interact with other recently introduced species as stressed by the "plant–frugivore meta-network" (Fricke and Svenning 2020). Therefore, identifying an increase in the number and proportion of invaders is crucial for monitoring their wider effects on lotic biodiversity, and should be considered when interpreting results of routine monitoring data and identifying conservation priorities. Even small values of RCI (e.g., <5%, see Appendix 1: Table S4) appear to have negative implications for the wider aquatic community (especially for less invaded sites) and should be prevented. Overall, this also suggests that even a minor reduction of the relative richness of invaders (e.g., through specific management programs) may yield benefits for ecosystems, especially if other pressures are absent. The examination of both biocontamination facets in this study highlights the importance of preventing the arrival and establishment of new invaders, and especially limiting and controlling invader relative richness (i.e., RCI values) within a community. This research should enable more effective integration of biological invasion research into conservation programs and allow environmental managers to prioritize activities and anticipate potential pressures. However, the results also indicated that biological invasions may affect different facets of aquatic biodiversity and consequences cannot always be detected when using single component or metric approaches. Such a discrepancy cautions against the use of any single community facet of biological invasion as a surrogate for others. This study did not differentiate among the 12 invader taxa included, and future research focusing on disentangling, ranking and quantify the effect of each taxa, or each combination of taxa, should be a global scientific priority. Considering that multiple invasions are increasingly common internationally in both terrestrial and aquatic ecosystems (and in both plant and animal communities) similar approaches and analyses of long-term data set are recommended to provide a better science basis for the management and understanding of biological invasion.

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Supporting Information

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2385/full

Open Research

All site details and biological data can be obtained freely from the Environment Agency Department for Environment Food and Rural Affairs Ecology and Fish Data Explorer at https://environment.data.gov.uk/ecology-fish/ by selecting Invertebrates; to obtain the community data specify the period required (2006–2019), the geographic area on the map, and input site codes (SITE_ID) found in the first column of Appendix S1: Table S1. Biomonitoring metrics, site codes, and water body names used in this research (Guareschi et al. 2021*b*) are available from the Loughborough University Research Repository at https://doi.org/10.17028/rd.lboro.14632629. Scripts used to calculate functional indices (Laini et al. 2021) are available on Zenodo: https://doi.org/10.5281/zenodo.4807008.