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RESEARCH ARTICLE

Divergent temporal responses of native macroinvertebrate communities to biological invasions

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Abstract

Biological invasions pose a major threat to biodiversity, ecosystem functioning, and human well-being. Non-native species can have severe ecological impacts that are transformative, affecting ecosystems across both short-term and long-term time-scales. However, few studies have determined the temporal dynamics of impact between these scales, impeding future predictions as invasion rates continue to rise. Our study uses a meta-analytical approach to dissect the changing taxonomic and functional impacts of biological invasions on native macroinvertebrate populations and communities in freshwater ecosystems across Europe, using a recently collated European long-term time series spanning several decades. Our findings reveal a complex temporal pattern: while initial stages of invasions (i.e. five years after the first record of non-native species) often exhibited benign impacts on macroinvertebrate abundance, richness, or functional diversity, the long-term (i.e. the period following the early invasion) effects became predominantly negative. This pattern was consistent between taxonomic and functional metrics for impacts at both the population and species level, with taxonomic metrics initially positively affected by invasions and functional metrics being more stable before also declining. These results suggest that even initially benign or positively perceived impacts could be eventually superseded by negative consequences. Therefore, understanding the magnitude of invasion effects increasingly requires long-term studies spanning several years or decades to offer insights into effective conservation strategies prioritising immediate and future biodiversity protection efforts. These findings also highlight the importance of integrating multiple taxonomic, functional and temporal components to inform adaptive management approaches to mitigate the negative effects of current and future biological invasions.

KEYWORDS
ecosystem functionality, freshwater ecosystems, invasive species, non-native species , management strategies, temporal dynamics

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Ross N. Cuthbert and Phillip J. Haubrock should be considered joint senior author.

1 | INTRODUCTION

Biodiversity underpins ecosystem functioning, service provisioning, and human well-being, but is facing rapid erosion through accelerating anthropogenic global changes (Filstrup et al., 2019; Tilman et al., 2017). Globalisation, in combination with environmental changes, has amplified the rate and impacts of biological invasions, which are expected to increase in the future (Rahel & Olden, 2008; Seebens et al., 2017). Currently, it is estimated that invasions have been documented for only about ~1% of known global biodiversity (Briski et al., 2024). Despite this, biological invasions have become a pervasive anthropogenic phenomenon that comprises species populations that have been introduced—whether directly or indirectly—by human activities into regions where they lack an evolutionary history (Soto et al., 2024). More than 37,000 non-native species have been introduced and established so far. Of these, evidence of negative impacts has been documented for ~3500 species (IPBES, 2023), with their cumulative effects running into the US$ trillions (Diagne et al., 2021) and contributing to at least 60% of documented extinctions globally (Blackburn et al., 2019; IPBES, 2023).

While the broadscale impacts of biological invasions are well-documented, there remains a notable gap in our understanding of their temporal dynamics (Strayer, 2012; Strayer et al., 2011). The duration and magnitude of the impacts of biological invasions are not static but change over time. This is due to various ecological and evolutionary mechanisms that influence organism traits, biotic interactions or population dynamics (Catford et al., 2022; Strayer et al., 2006). Ultimately, there is no unified consensus on how the impacts of non-native species may change over time. Nevertheless, it has been proposed that non-native species' impacts are greatest during the early stage of an invasion and decrease over time (Strayer, 2012), but this is mediated by levels of ecological novelty. Additionally, impact dynamics have been described as following a sigmoidal curve (Soto, Ahmed, Balzani, et al., 2023), starting with an initial phase of acclimatisation (i.e. lag phase, Crooks, 2005), leading to exponential growth and ultimately reaching a steady state (Haubrock et al., 2022). Other perspectives of the dynamics of impact are based on factors such as absolute abundance (Sofaer et al., 2018) or specific changes in (i) the non-native species performance (e.g. behavioural changes), (ii) the recipient community or (iii) cumulative changes in the abiotic environment (Strayer et al., 2006). These factors can each lead to the same non-native species exhibiting varying impacts and magnitudes among invaded environments (Catford et al., 2022).

Freshwater ecosystems are particularly threatened by biological invasions due to their relatively high native—especially endemic—biodiversity (Beisel, 2001; Francis & Hardwick, 2012). However, non-native species can occasionally also exert positive effects on freshwater ecosystems, such as enhancing the growth, survival or reproduction of certain species through direct or indirect interactions (Albertson et al., 2021; but see Carneiro et al., 2024). The rapid rate of declines in native biodiversity in these ecosystems, faster than in terrestrial counterparts (Sala, 2000), emphasises their importance for conservation and sustainable management (Sinclair et al., 2024). Furthermore, the vulnerability of freshwater environments is exacerbated by a history of anthropogenic alterations and uses (Dodds et al., 2013), having amplified the risks and impacts associated with biological invasions (Ricciardi & MacIsaac, 2011). Freshwater biodiversity loss due to biological invasions can be further exacerbated by other symptoms of global change, such as increasing water temperatures, alteration of precipitation, runoff or nutrient flux regimes, as well as habitat degradations (e.g. canalisation of levees and construction of weirs, pollution), which often outpace the ability of native species to adapt (Ormerod et al., 2010; Woodward et al., 2010).

Impacts of biological invasions on freshwater communities have been consistently reported in terms of species loss (taxonomic metric), but a component of the ecosystem often overlooked by invasion scientists is the change in community composition and functioning due to non-native species introductions (Strayer, 2012; Shuai et al., 2018, Toussaint et al., 2018, but see Renault et al., 2022). Some species may severely impact ecosystems through structural mechanisms, such as those labelled as ecosystem engineers, which can drastically alter functioning (e.g. *Dreissena polymorpha* or *Cyprinus carpio*) (Crooks, 2002; Ward & Ricciardi, 2007). These species affect various aspects of the invaded ecosystem, including its resource availability and the physicochemical environment, thereby altering the habitat and the conditions for other species present (Fanson et al., 2024). Functional losses can also occur before a native population is extirpated, particularly when low-density species become 'functionally extinct'. Thus, as a result of declining native biodiversity, there may not only be a taxonomic homogenisation but also a rising functional similarity among communities (Olden & Poff, 2004). Considering both the taxonomic and functional dimensions of non-native species' impacts on native communities can enhance our understanding of the changes associated with biological invasions (Renault et al., 2022). Nevertheless, large-scale data-driven appraisals of the direction of effects of biological invasions over time remain scarce.

The recent compilation of freshwater long-term time series data provides an unprecedented opportunity to examine the effects and dynamics of biological invasions at large scales (Haubrock et al., 2022; Haubrock & Soto, 2023; Haubrock, Soto, Ahmed, et al., 2024; Haubrock, Soto, Kourantidou, et al., 2024). Here we used a recently collated European long-term time series database of benthic macroinvertebrate populations (Haase et al., 2023) to understand how native communities respond to biological invasions through a meta-analytical approach. Our general hypothesis is that the impact on native communities will increase over time, more specifically characterised by: (i) an overall negative effect on native communities; (ii) increasing species losses and severe functional disruptions to native communities as invasions progress over time; and (iii) impacts on the individual species' level being more pronounced than at the community level.

2 | METHODS

2.1 | Data compilation

To identify how macroinvertebrate communities respond to biological invasions in terms of taxonomical and functional composition, we used a recently collated European macroinvertebrate time series database comprising 1,816 time series from rivers and streams across 22 European countries between 1968 and 2020 (Haase et al., 2023). Each time series (hereafter 'site') was surveyed at the same geographic position throughout the sampling period. The whole freshwater macroinvertebrate community was surveyed (i.e. not restricted to specific taxonomic groups) and contained the abundance of each species. Each site spanned at least eight sampling years, which were not necessarily consecutive. Sampling had a consistent sampling effort and was done during the same season or over three successive months. While the sampling method and taxonomic resolution varied among sites, they remained consistent within each site over time (see Table S1).

2.2 | Nativeness and non-nativeness

The native or non-native status of each taxon was assessed at the country level by consulting four sources: (i) *Global Alien Species First Record Database* (Seebens et al., 2017), (ii) *Global Invasive Species Database* (GISD, iucngisd.org/gisd/, Pagad et al., 2015), (iii) the *Global Biodiversity Information Facility* (GBIF; gbif.org) and (iv) *Invasive Species Compendium* (CABI, cabi.org). In case of a mismatch in the assessment of the status of species among countries, we followed the *Global Alien Species First Record Database* (Seebens et al., 2017) classification as the most reliable and updated database. This ensures a consistent and accurate species classification across our study sites for analysing the dynamics of biological invasions.

2.3 | Data processing

We first identified the initial year when a non-native species was reported at each site. We then split the database into two subsets: pre-invasion (the temporal period before the first record of a non-native species) and post-invasion (the temporal period after the first record of a non-native species). Subsequently, the post-invasion dataset was further segmented into two periods: (i) the early-invasion period, encompassing the first 5 years after the initial record of the respective non-native species and (ii) the late-invasion period, covering the period following the early-invasion phase. While we acknowledge that dynamics of biological invasions can be highly context-dependent (Haubrock, Soto, Ahmed, et al., 2024; Soto, Ahmed, Balzani, et al., 2023)—for example, by specific taxonomic traits and the characteristics of the invaded ecosystems—we chose a five-year threshold to differentiate between early and late invasion due to the nature of our data; i.e. longer periods would have substantially reduced our sample size. Each period included a minimum of two sampling years to facilitate our analyses. Following these steps, we retained 224 time series from 12 countries featuring non-native species proportions ranging from 0.87% to 8.69%, with a mean proportion of 2.26%. Among these, 113 time series (50.44%) contained more than one co-occurring non-native species (see Figure 1 and Figure S1).

2.4 | Community composition

To identify how native macroinvertebrate communities respond to biological invasions in terms of taxonomic and functional composition, we calculated two taxonomic (species abundance and species richness) and two functional metrics (functional dispersion [F_{Dis}] and functional evenness [F_{Eve}]), after excluding the non-native species from the community. Abundance was calculated at the population

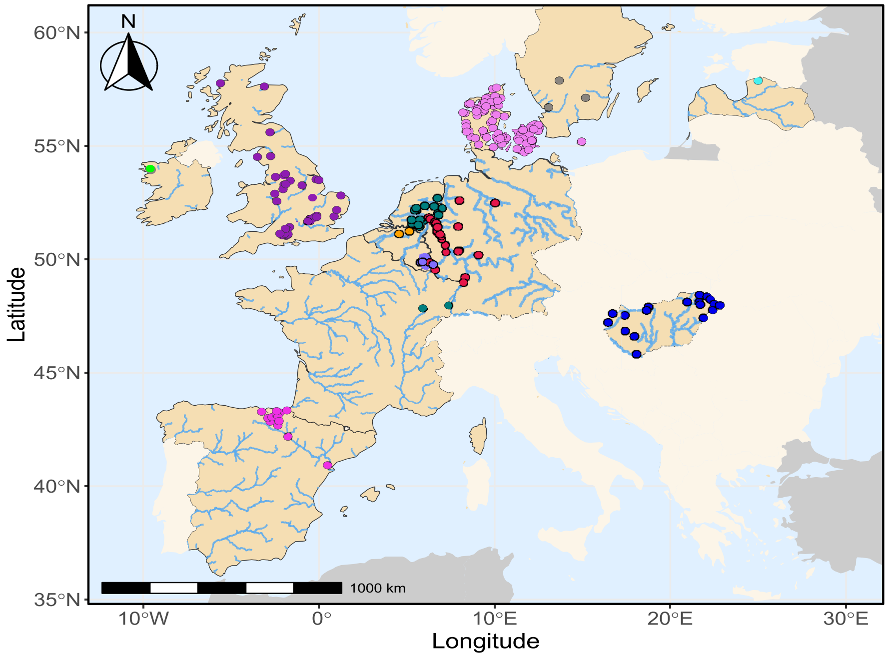

FIGURE 1 The geographical locations of the evaluated sites. Each dot represents a time series, color-coded to indicate different countries. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

level (i.e. abundance of each species within a community in a given year at each site), while the other metrics were calculated at the community level (i.e. for each year of each site) for each period (i.e. pre, early, and late invasion).

For functional metrics, firstly, we extracted the functional traits of all native species from three sources: (*i*) *AQEM* trait database (AQEM consortium, 2004), (*ii*) freshwaterecology.info (Tachet et al., 2010; Schmidt-Kloiber & Hering, 2015) and (*iii*) the *DISPERSE* database (Sarremejane et al., 2020). All species' functional traits were split into 12 ecological and 18 biological traits (see Table S2). Ecological preferences refer to the potential tolerance of species to environmental and niche change (Devin & Beisel, 2007). Biological traits refer to the ecological functions of species in an ecosystem (Devin & Beisel, 2007). Subsequently, we calculated two functional metrics: (*i*) F_{Eve}, describing how evenly the functional trait space is filled by species and (*ii*) F_{Dis}, referring to the mean distance of individual species to the centroid of all species in the trait space, both using *dbFD* function of in the FD R package (Laliberté et al., 2014).

These metrics are important for detecting shifts in community composition, that is a decline in species richness or a shift in the dominant species that may result from non-native species outcompeting or displacing native species. By integrating functional metrics, including F_{Dis} and F_{Eve}, we extended our analysis beyond community structure to examine changes in the roles species play within ecosystems gaining insights into how invasions may alter not just the composition but the functional integrity of macroinvertebrate communities, potentially leading to ecosystem-level consequences.

2.5 | Calculation of effect sizes

We calculated the effect size of the response of native macroinvertebrate communities to invasion using Hedges' *g*, based on the formulas provided by Borenstein et al., 2009. To do this, first, we calculated Cohen's *D* and the associated variance (V_d) as the difference of the mean in the pre-and post-invasion (both early and late invasion in turn) databases for each metric calculated (i.e. abundance, richness, F_{Dis} and F_{Eve}) divided by the standard deviation of the differences as follows:

$$\text{Cohen's } D = \frac{\overline{x}_{\text{after}} - \overline{x}_{\text{before}}}{S_{\text{within}}}; \qquad V_d = \frac{1}{n} + \frac{d^2}{2 \times n} \times 2 \times (1 - r), \quad (1)$$

where $\overline{x}_{\text{after}}$ refers to the average of the metric for the temporal period after the invasion, $\overline{x}_{\text{before}}$ the average of the metric for the temporal period before the invasion, and S_{within} is the within-groups standard deviation, pooled across groups. *d* refers to the calculated Cohen's *D*, *n* is the sampling size, and *r* is the correlation between before and after groups. We used a conservative estimate of *r*, taking a value of 0.5 as an intermediate and standardised dependency for all sites.

Because Cohen's *D* has a bias for small samples, as it tends to overestimate them, we transformed it into the meta-analysis statistic Hedges' *g*, which corrects this bias through a factor *J*. This factor will always be less than 1, such that Hedges' *g* will be less than Cohen's *D* in absolute value (Hedges, 1981; Borenstein et al., 2009). Additionally, we also extracted the variance of Hedges' *g* (V_g) as follows:

$$J = 1 - \frac{3}{4(n-1)-1}; \qquad \text{Hedges' } G = J \times d; V_g = J^2 \times V_d, \quad (2)$$

In the case of species abundance, the effect size was extracted for those individual species present in both the pre- and post-invasion stages (i.e. at the population level). Thus, each species had an individual effect size. For the other metrics, each effect size corresponded to the community level.

2.6 | Statistical analyses

To quantify the response of the native macroinvertebrate communities after the arrival of non-native species, we applied a mixed-effects meta-analysis based on the standardised mean difference (SMD) using the *rma.mv* function from the metafor R package (Viechtbauer, 2010). The use of these models allows for the incorporation of both fixed and random effects and takes into account the heterogeneity of variances due to differences in sampling, but primarily due to the inherent variation among sites. The variation from each site was used to calculate the weighting importance that each site will have in calculating the effect size, which is the inverse of the variance of the effect size of each study case, whereby more weight is given to more precise studies. We performed our meta-analytical model using the effect size and respective variance as response variables with a combination of different predictors to test our specific hypothesis. Firstly, we established an 'intercept-only' model (i.e. without predictors) to understand the response of native macroinvertebrate communities to biological invasions and check if there is substantial heterogeneity in our effect sizes that could be explained by predictors. Subsequently, (i) we included the invasion stage (early vs. late invasion) to understand how the impacts of non-native species change over time; (ii) taxonomic (species abundance and richness) and functional community metrics (F_{Dis} and F_{Eve}) as well as invasion stage to understand how the native community metrics change over time—individual metrics were also modelled to understand the specific changes of the metrics; and (iii) ecosystem level (population vs. community) and invasion stage, where population level refers to the effect size extracted from the abundance of individual species and community level to the remaining community metrics. In each model, we specified the country, river and site as nested random effects to capture the variability among study sites. We decided to run our models without an intercept assuming no initial effect in the community, allowing the comparison with zero. In our meta-analyses, we chose not to apply any type II error correction methods based on the understanding that such correction methods (e.g. Bonferroni) are often considered overly conservative for meta-analyses and are not recommended (Koricheva et al., 2013).

2.7 | Publication bias

To assess the influence of error that publication bias might introduce in our meta-analysis, we ran a sensitivity analysis. To do this, we used a funnel plot, which is a graphical method that indicates the effect sizes that are missing to homogenise the accumulated effect size. In case of the absence of publication bias, plotting the effect size against a measure of uncertainty (standard error) should reflect a symmetrical shape around the overall effect (Nakagawa et al., 2022). To statistically measure the asymmetry of the funnel plot, we used Eggers's linear regression method by regressing the effect size estimates against the standard error to check if the intercept deviates from zero (Egger et al., 1997; Nakagawa et al., 2022).

3 | RESULTS

3.1 | Overview

Our meta-analysis included 5953 effect sizes from 224 sites (i.e. time series that contain both native and non-native species) to investigate the response of native macroinvertebrate communities to biological invasions. The average effect size across these sites was 0.030 with 95% of the confidence intervals (CI) crossing zero (CI: −0.0121 to 0.0722), thus indicating no significant effect (Table S3). Notably, there was substantial heterogeneity across study cases ($I^2=76.10\%$), indicating that there may be underlying differences in monitoring designs, populations, and environments that contribute to the observed differences in effect sizes that can be explained through moderators. We detected a marginal degree of asymmetry based on funnel asymmetry by Egger's regression test ($p=.045$, $df=5951$) (Figure S2). However, funnel asymmetry can arise from heterogeneity of the effect size or merely by chance, thus not invalidating our results (Nakagawa & Santos, 2012). Additionally, we found a positive response of the native macroinvertebrate community during the early stage of invasions (effect size: 0.08, CI 0.035–0.126; Figure 2). As invasions advanced, effect sizes, however, turned negative, reversing the response of the community to the non-native species (effect size: −0.052, CI: −0.099 to −0.005) (Figure 2).

3.2 | Change of impacts over time

For taxonomic composition, we observed a significant positive effect size of 0.096 (CI: 0.050–0.142), while no significant effect was observed at the functional level (effect size: 0.025, CI: −0.024–0.075). When taxonomic and functional metrics were partitioned into early and late stages, both taxonomic and functional metrics became significantly negative (effect size$_{\text{taxonomic}}$: −0.106, CI: −0.132 to −0.079; effect size$_{\text{functional}}$: −0.191, CI: −0.231 to −0.151) in the late stage of the invasion. Regarding the community metrics, abundance, richness and functional dispersion for both ecological and biological traits exhibited an initial

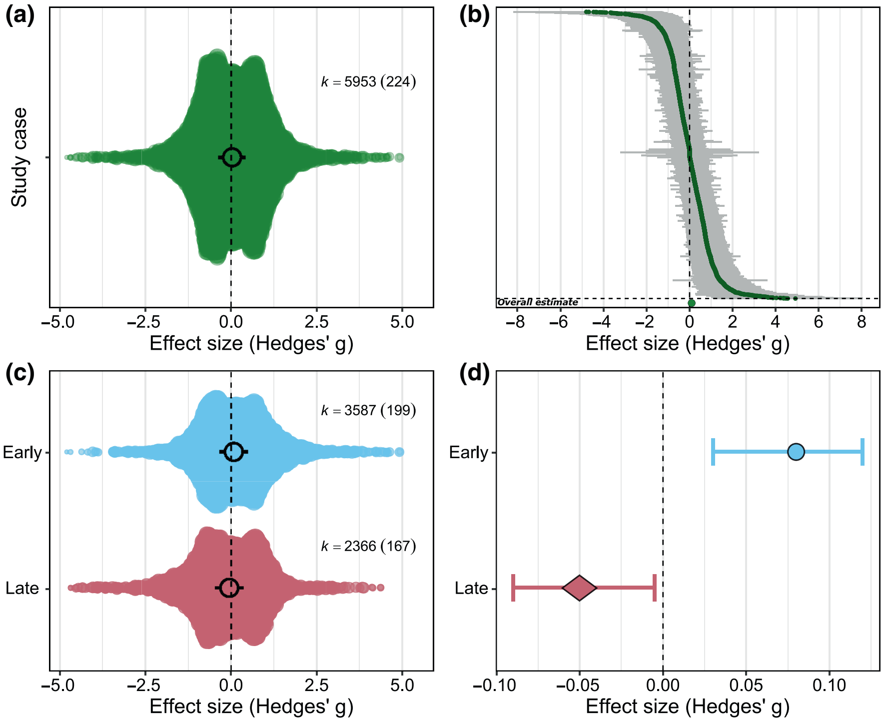

FIGURE 2 Overall effects of biological invasions on riverine macroinvertebrate communities. (a) Distribution of the effect size and the precision (1/standard error[SE]) of each effect size and the average effect size (hollow dot) with a confidence interval (CI), where *k* indicates the number of effect sizes and the number within parentheses the number of sites. (b) Effect size across study cases (green dots) and the associated variance (grey bars) with an overall effect size at the bottom and diamonds refer to the late stage. (c) Distribution of the effect size for each stage of invasion (i.e. early and late) as well as the mean effect size (hollow dot) and (d) Forest plot with the results of the meta-analytical model with the mean effect size and 95% confidence interval (CI) represented by the bar and diamonds refer to the late stage.

positive response (all $p < .01$), while functional evenness exhibited a negative response (all $p < .01$, Table S4). Interestingly, all the metrics studied became negative in the late stage of invasion (Figure 3b,c) (Table S4).

3.3 | Populations versus communities responses

The temporal response was consistent at both the species and community levels. During the early stage of invasion, both levels exhibited a positive response in the macroinvertebrate community (effect size$_{\text{species}}$: 0.065, CI: 0.018–0.111; effect size$_{\text{community}}$: 0.110, CI: 0.061–0.159). However, a significant negative effect was observed for population-specific responses during the late stages of invasion (effect size = −0.105, CI: −0.132 to −0.078), reflecting a similar pattern at the community level where the interaction term between community response and the late stage of invasion was notably negative (effect size = −0.186, CI: −0.222 to −0.150) (Figure 4, Table S4).

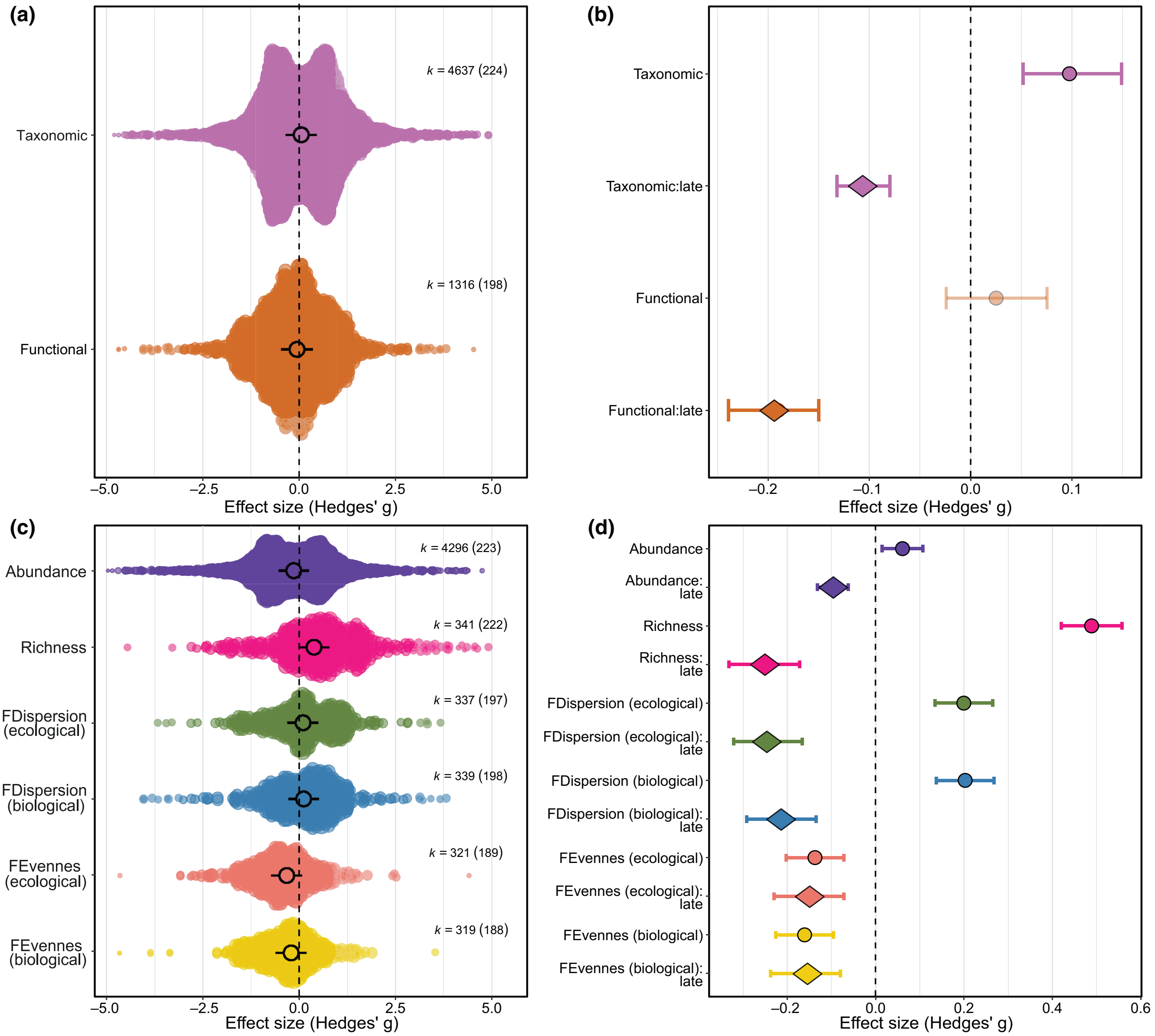

FIGURE 3 Distribution of the effect sizes for (a) taxonomic and functional levels with mean effect size, (b) forest plot with the results of the meta-analytical model with the mean effect size and 95% confidence interval (CI) represented by the bar, diamonds refer to the late stage. (c) Distribution of the effect sizes for community metrics: Abundance, richness, functional dispersion (ecological and biological) and functional evenness (ecological and biological) with the mean effect size with 95% confidence interval (CI) and (d) forest plot with the results of the meta-analytical model with the mean effect size and 95% confidence interval (CI) represented by the bar diamonds refer to the late stage. *k* indicates the number of effect sizes and the number within parentheses the number of sites. The model provides relative effects ('late' differs from 'early') by directly estimating the effect of each condition without subtracting a common baseline.

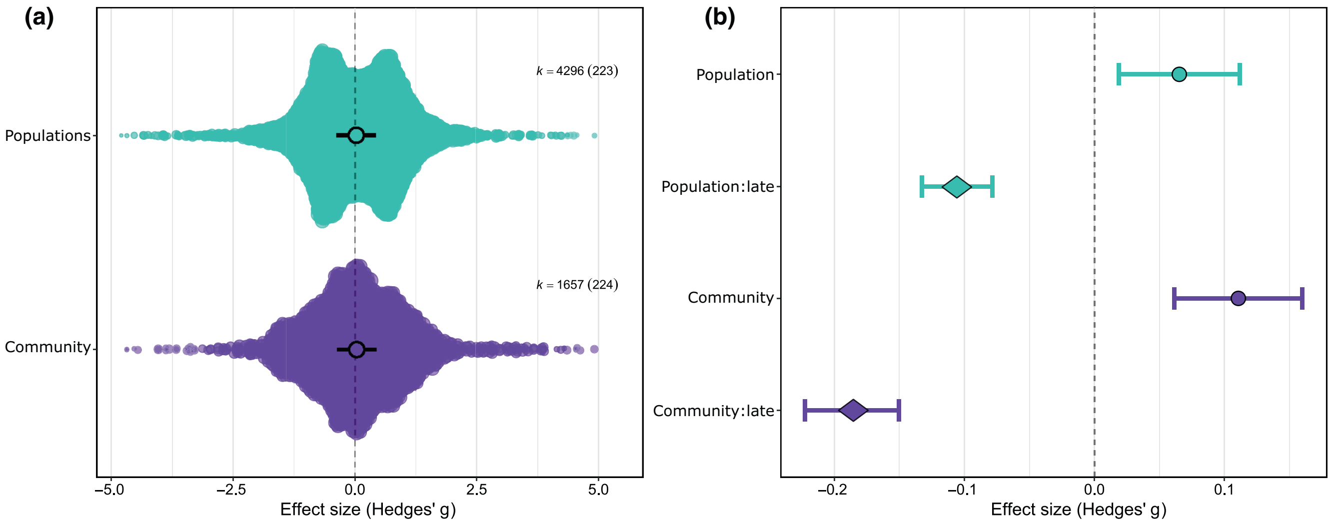

FIGURE 4 Distribution of the effect sizes for (a) species and community level with mean effect size (hollow dot) and (b) forest plot with the mean effect sizes and 95% confidence intervals for the model terms. *k* indicates the number of effect sizes and the number within parentheses the number of sites and diamonds refer to the late stage. The model provides relative effects ('late' differs from 'early') by directly estimating the effect of each condition without subtracting out a common baseline.

4 | DISCUSSION

Macroinvertebrates are vital bioindicators of aquatic ecosystem health because they are highly susceptible to environmental changes (Hauer & Resh, 2017). The dynamics of benthic macroinvertebrate communities are highly complex (Haubrock, Soto, Kourantidou, et al., 2024; Wallner, 1987) and can be altered by a myriad of factors such as biological invasions, climatic shifts, land-use changes and pollution (Guareschi et al., 2021; Hauer & Resh, 2017; Let et al., 2021). Among global environmental changes, biological invasions remain poorly understood in relation to temporal impact dynamics. Our meta-analysis showed varying responses of native macroinvertebrate communities to the different facets of non-native macroinvertebrate introductions over time. Initially, our results suggested that invasions may be perceived as having a beneficial impact on macroinvertebrates in the first 5 years, while as invasions progress, the alterations become negative. A similar pattern was also found for taxonomic and functional composition, with an initial positive or benign response of macroinvertebrate communities, while both taxonomic and functional metrics became negative during the late stage of invasions. Therefore, disregarding temporal dimensions may mask ecological impacts, which become increasingly adverse over time.

4.1 | Community metrics and stages of the invasion

One of the main challenges in invasion science is understanding how the impacts of non-native species change over time (Strayer, 2012). We observed that during the initial 5 years of the invasion following the first record of non-native species, native macroinvertebrate communities in European riverine ecosystems showed a slightly positive response (i.e. 'invasion honeymoon', Phillips et al., 2010). This early positive response may be attributed to temporary increases in resource availability or habitat complexity, which typically accompany the initial stages of invasions (Rodriguez, 2006). However, as invasions advance, the response of native macroinvertebrate communities becomes negative as the multi-faceted impacts of non-native species are more pronounced (Volery et al., 2020). These impacts of non-native species may be, in turn, modulated by their respective abundance (Sofaer et al., 2018). While some non-native populations grow exponentially in the early phases of invasion, others may exhibit a lag phase (i.e. a delay in the detection of their impacts) (Crooks et al., 1999). Thus, non-native species may not have reached a sufficiently high abundance in the initial period to negatively affect native biodiversity or functioning, thereby avoiding noticeable negative impacts (Crooks, 2005; Ricciardi, 2012). Furthermore, the extent of the impact is also influenced by ecosystem characteristics and particularly, ecological novelty, whereby non-native species within 'novel weapons' could more rapidly affect native populations that are unadapted (Callaway & Ridenour, 2004). Our results conversely suggest that impacts were generally delayed in European riverine macroinvertebrates, but became widely negative in the longer-term.

The response of native macroinvertebrate communities differed among metrics and the affected facet (i.e. taxonomic vs. functional). The initial taxonomic response was significantly positive, likely due to a greater increase in native richness than the decline in abundance. This positive response could be attributed mostly to the early stages of invasion, where the introduction of non-native species may temporarily generate the perception of a positive impact and a delay in detecting the negative impacts (Rodriguez, 2006; Phillips et al., 2010). In the early years following introduction, non-native species may be more likely to coexist with native species, occupying niches not fully exploited by these species, leading to an increase in ecosystem complexity and potentially a higher number of species (Schlaepfer et al., 2011). Moreover, the sporadic appearance of native species in sampling years may boost the richness in the early-invasion stage. However, such increases may mask underlying negative impacts on ecosystem structure and function, which tend to be more notable as the invasion progresses. A negative response of native communities was conversely observed in the functional evenness for ecological and biological traits, suggesting a greater imbalance in the distribution of functions among native species. For instance, the food web might become simplified if only a few species carry out most functions, potentially making the web more susceptible to collapse (David et al., 2017). Additionally, non-native species can replace or even dominate the roles associated with crucial functions such as nutrient cycling, which can have cascading effects on water quality and primary production (Covich et al., 1999). On the other hand, positive responses of native macroinvertebrate communities were observed in abundance, richness, and functional dispersion components (ecological and biological traits). A positive effect can also emerge when non-native species serve as an additional food resource, potentially bolstering native populations (Rodriguez, 2006). The creation of new habitats by engineer species such as *Dreissena polymorpha* might also make it easier to colonise these new habitats by native species (Ward & Ricciardi, 2007). Interestingly, the response of all community metrics studied was negative in the later stages of invasion, suggesting an initial phase of adaptation to the new environment and a potential lag in detecting their impacts, known as 'invasion debt' (Essl et al., 2011). One of the most significant impacts of non-native species on native communities, which can reverse the initial positive response, is the ability of non-native species to outcompete native macroinvertebrates. They not only exert strong competitive pressures on essential resources such as food and habitat, but also induce disruptive effects on the ecosystem, leading to a reduction in native populations (Cameron et al., 2016; Hansen et al., 2013; Reynolds & Aldridge, 2021). However, while competition is pervasive, numerous other impact mechanisms can take effect (IUCN, 2020). Further research is needed to uncover the dominant mechanisms corresponding to the macroinvertebrate impacts, which we detected in European rivers.

4.2 | Populations versus communities

Non-native species not only alter the fate of individual native populations but also reshape entire biological communities (Vilà et al., 2011). Overall, the response of native species populations and communities were positively affected after the arrival of a non-native species. For instance, in ecosystems already under stress from human activity or ecological degradation, non-native species can act as unexpected facilitators of ecosystem function (MacDougall & Turkington, 2005; Ramus et al., 2017) but also as a detrimental ecological burden (Copp et al., 2009; Didham et al., 2005). However, in the later stages of invasions, both shifted to a negative response, highlighting the importance of temporal information when unravelling the complex dynamics of non-native species (Soto, Ahmed, Balzani, et al., 2023, Soto, Cuthbert, Ricciardi, et al., 2023, Soto, Ahmed, Beidas, et al., 2023). Contrary to what we expected, the response of the community's native species was more negative than that of the population. This may be because species considered as ecosystem engineers (such as *D. polymorpha*), dominate our time series (Haubrock, Soto, Kourantidou, et al., 2024; Soto, Cuthbert, Ricciardi, et al., 2023). Community-level effects may become more obvious and cumulative across species as the invasion progresses. Their ability to influence several aspects of the communities, such as trophic levels, underscores their complex and often indirect effects on trophic webs (Emery-Butcher et al., 2020). The negative population-level response could be attributed to, for example, direct competition with non-native species or other ecological pressures introduced by the invaders. Overall, these findings point to the critical need for early detection and management of non-native species to protect native biodiversity and maintain ecosystem integrity. Understanding the complex dynamics of invasions, including their delayed potential negative impacts, is essential for developing effective conservation strategies.

4.3 | Caveats

Although our findings contribute valuable insights into the temporal dynamics of the impacts of biological invasions over time, it is not without limitations. Firstly, despite a homogenised sampling effort in our time series, the detectability of non-native species can vary across different sites and time periods (e.g. starting year of time series) based on the specific socio-economic and historical context of each country as well as different sampling methods. The sampling techniques used may also not have captured the complete diversity of macroinvertebrate communities (e.g. crayfishes, Haubrock, Soto, Kourantidou, et al., 2024), leading to possible inaccuracies in assessing the impacts of invasions (but see Soto, Ahmed, Beidas, et al., 2023). The presence of other non-native species, such as predatory fish, was not accounted for in our analysis. These species can have additional, immediate and complex impacts on both native and non-native macroinvertebrate communities, especially through predation, modulating the response of the native community (Bernery et al., 2022). We also captured the impacts of biological invasions over a specific period, which may not fully encompass the longer-term dynamics of these invasions as they are modulated by successive invasions or other factors over time. As such, more pronounced or different trends could emerge over extended timescales beyond the scope of our current analysis with available data. Other factors not explicitly considered in our study, such as recovery programs, actions to manage non-native populations, pollution and broader environmental shifts like climate change, can also significantly influence the response of native species. Moreover, it should be acknowledged that biological invasions are a population-level, context-specific phenomenon that cannot be generalised at the species-level (Haubrock, Soto, Ahmed, et al., 2024). This realisation suggests that on a case-by-case basis, the impacts of non-native species on native biodiversity may vary in direction and magnitude. However, our results indicate that over time, the negative consequences of biological invasions outweigh any benign or positively perceived impacts.

4.4 | Conclusions

Our study builds an understanding of the intricate temporal dynamics of biological invasion effects on native macroinvertebrate communities in freshwater ecosystems. Initially, our findings confirm the lag phase where invasions may offer transient benefits or negligible impacts on macroinvertebrate populations taxonomically and functionally. However, as invasions advance through time, the evidence indicates a predominantly negative response at all levels (species, community levels). Adding this new dimension of time to taxonomic and functional communities underscores the importance of continuous and long-term monitoring of invaded ecosystems, especially for well-established invaders which are the main target of management approaches.

AUTHOR CONTRIBUTIONS

Ismael Soto: Conceptualization; formal analysis; methodology; visualization; writing – original draft. **Rafael L. Macêdo:** Methodology; writing – original draft; writing – review and editing. **Lais Carneiro:** Methodology; writing – original draft; writing – review and editing. **Elizabeta Briski:** Supervision; writing – original draft; writing – review and editing. **Antonín Kouba:** Supervision; writing – original draft; writing – review and editing. **Ross N. Cuthbert:** Supervision; visualization; writing – original draft; writing – review and editing. **Phillip J. Haubrock:** Supervision; visualization; writing – original draft; writing – review and editing.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and code that support this study can be found at GitHub (https://github.com/IsmaSA/Pre-vs-Post-invasion-stage) and at Zenodo (DOI: https://doi.org/10.5281/zenodo.13738299).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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