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Tracking long-term shifts in non-native freshwater macroinvertebrates across three European countries

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Abstract

Non-native species introductions have been acknowledged as one of the main drivers of freshwater biodiversity decline worldwide, compromising provided ecosystem services and functioning. Despite growing introduction numbers of non-native species, their impacts in conjunction with anthropogenic stressors remain poorly documented. To fill this gap, we studied temporal changes in α (local scale) and γ (regional scale), as well as β (ratio between γ and α) diversity of non-native freshwater macroinvertebrate species in three European countries (the Netherlands, England and Hungary) using long-term time series data of up to 17 years (2003–2019). We further calculated four ecological and four biological trait metrics to identify changes in trait occurrences over time. We found that α and γ diversities of non-native species were increasing across all countries whereas β diversity remained stable. We did not identify any significant changes in any trait metric over time, while the predictors tested (land use, climatic predictors, site-specific factor) were similar across countries (e.g., site characteristics or climatic predictors on non-native species trends). Additionally, we projected trends of α , β , and γ diversity and trait metrics until 2040, which indicated that non-native species will decline across all countries to lower levels except in England for γ diversity and the Netherlands for α diversity where an increase was observed. Thus, our findings indicate shifts in non-native freshwater macroinvertebrate diversity at both local and regional scales in response to the various growing anthropogenic pressures. Our findings underscore the continuous dynamics of non-native species distribution, with the diversity of individual communities and overall landscapes witnessing changes. However, the differentiation in species composition between communities remains unaltered. This could have profound implications for conservation strategies and ecological management in the face of continuously changing biodiversity patterns.

Keywords: non-native species; long-term time series; diversities; taxonomic composition, functional ecology

Introduction

Since the creation of invasion science as an academic field (Elton, 1958), important methodological (Catford et al., 2009) and conceptual (Daly et al., 2023) advances have resulted in it dynamically evolving into an important multidisciplinary research area (Richardson & Pyšek, 2008; Vilà & Hulme, 2017). Invasion science refers to the study of (non-native) species that are intentionally (e.g., intentional release) or unintentionally (e.g., through ballast waters, contaminated material) translocated outside their natural range by human activities (Briski et al., 2012; Simberloff et al., 2013; Essl et al., 2018), the causes and consequences of their spread, and the subsequent ecological and socio-economic impacts (Vaz et al., 2017; Bacher et al., 2018; Turbelin et al., 2023). Scientific advances in this field are now needed more than ever, as increasing globalization, climate change, and human activities such as changes in land use and pollution are leading to an unprecedented rate of non-native species introductions (Chytrý et al., 2009; Domisch et al., 2013; Seebens et al., 2017), with numerous species spreading and impacting functional characteristics of ecosystems, the economy, or human health (Blackburn et al., 2011; Simberloff et al., 2013; Henry et al., 2023).

There is accumulating evidence that non-native species can have substantial impacts at all organizational scales (i.e., local to global; Blackburn et al., 2014; Haubrock et al., 2021a). At the local scale, non-native species can alter the ecological equilibrium of ecosystems, modifying the composition of communities (Moorhouse et al., 2014; Hejda et al., 2009; Soto et al., 2023a) while degrading – or even suppressing – provided functions and services (Gilioli et al., 2017; Charles & Dukes, 2007; Pejchar & Mooney, 2009). Non-native species can reshape regional and global biodiversity through a process called biotic homogenization (McKinney & Lockwood 1999; Didham et al., 2005) and thereby reducing the resilience of

ecosystems to natural and anthropogenic factors (Olden et al., 2004; Chaffin et al., 2016; Pilotto et al., 2022).

All types of habitats and ecosystems have been colonized by non-native species, including freshwaters (Strayer, 2010; Ricciardi et al., 2022), which provide numerous regulating and provisioning, but also cultural services (Dodds et al., 2013; Angeler et al., 2014). River networks offer convenient dispersal pathways to aquatic species (Beisel, 2001; Balzani et al., 2022; Soto et al., 2023a), partially explaining the commonly high richness of native species (Rahel & Olden, 2008). Yet, dendritic river networks also function as dispersal corridors for non-native species and therefore constitute a significant risk for accelerated biodiversity loss (Blackburn et al., 2019; Pyšek et al., 2020; Diagne et al., 2021). In addition, human disturbances (e.g., land use change, pollution, etc.) and climate change can alter natural communities, potentially creating novel conditions that might favor non-native species (e.g., in terms of habitat, climatic suitability, or reduced biotic resistance; Capinha et al., 2013; Haubrock et al., 2020).

Species diversity, which is defined as the species richness in a sample or a community *sensu* Whittaker (1972), with the fundamental unit of diversity being the number of species, individuals, or both (Iknayan et al., 2014), can be considered at three levels: locally (α diversity; the number of different species in a site), regionally (γ diversity; the number of different species in a region), and β diversity, as the degree of community differentiation calculated as the ratio between regional and local diversity (*sensu* Whittaker, 1972). In parallel, the study of organismal traits (i.e., characteristics of an organism that affects its performance but also its response to abiotic and biotic factors in the environment; Döge et al., 2015) occurring within respective ecosystems provides an opportunity to highlight biodiversity effect-mechanisms of different environmental changes (Pillar et al., 2013; Biggs

et al., 2020). Variations in the freshwater macroinvertebrate diversity can be attributed to differences in the chemical, physical, and environmental characteristics of freshwater ecosystems, which can exhibit considerable regional variation, in addition to the presence of non-native species (Haubrock et al., 2023a). In invasion contexts, non-native macroinvertebrate species can impact both compositional and functional dynamics by suppressing native species and their traits or by introducing novel traits (Renault et al. 2022; Le Hen et al., 2023). Understanding these interactions and consequences is critical, especially as ecosystems across the globe experience shifts due to ongoing anthropogenic pressures (Haubrock & Soto, 2023).

Here we investigated temporal changes in non-native freshwater macroinvertebrate diversity (α , β , and γ diversity) across three European countries: the Netherlands, England, and Hungary. We hypothesized (i) increasing trends in α , β , and γ diversity of non-native species accompanied by (ii) changes in trait and functional metrics and regional differences due to the arrival of new non-native species. We further hypothesized that (iii) trends in α and β will be influenced by varying site-specific factors such as land use, geographic and climatic predictors, and native community characteristics, as we expected non-native species being facilitated in certain conditions (e.g., habitat alteration and connectivity, favorable environmental conditions, simple native communities). Lastly, we hypothesized that (iv) future projections will indicate further increases in compositional diversity and traits metrics of non-native species.

Methods

Data acquisition

To investigate temporal trends in non-native macroinvertebrate diversity, we used a recently collated European database of freshwater macroinvertebrate species abundances from lotic

systems (i.e., streams and rivers; Haase et al., 2023; Haubrock et al., 2022; Soto et al., 2023b). All macroinvertebrate species reported in this dataset were identified to the species level and sampled using different sampling methods and protocols across time series, but were kept consistent within each time series. Only time series with a minimum of eight years – not necessarily consecutive – were considered, obtaining a database containing 1,826 European time series. We first sorted the time series data by country and then used visual analysis to pinpoint countries with clustered data by plotting all the corresponding sites. We retained only those time series grouped by country that could be matched over the same time period, which allowed us to obtain more robust data on communities that exhibit similar temporal patterns and responses to environmental variables. This filtering resulted in three European countries which fulfilled the previous minimum requirements: Hungary, England, and the Netherlands. To additionally ensure the comparability among time series – given the heterogeneity of the database (i.e., different starting and ending years for each time series) – we selected the period with the maximum number of time series within each country (Figure 1; Table S1).

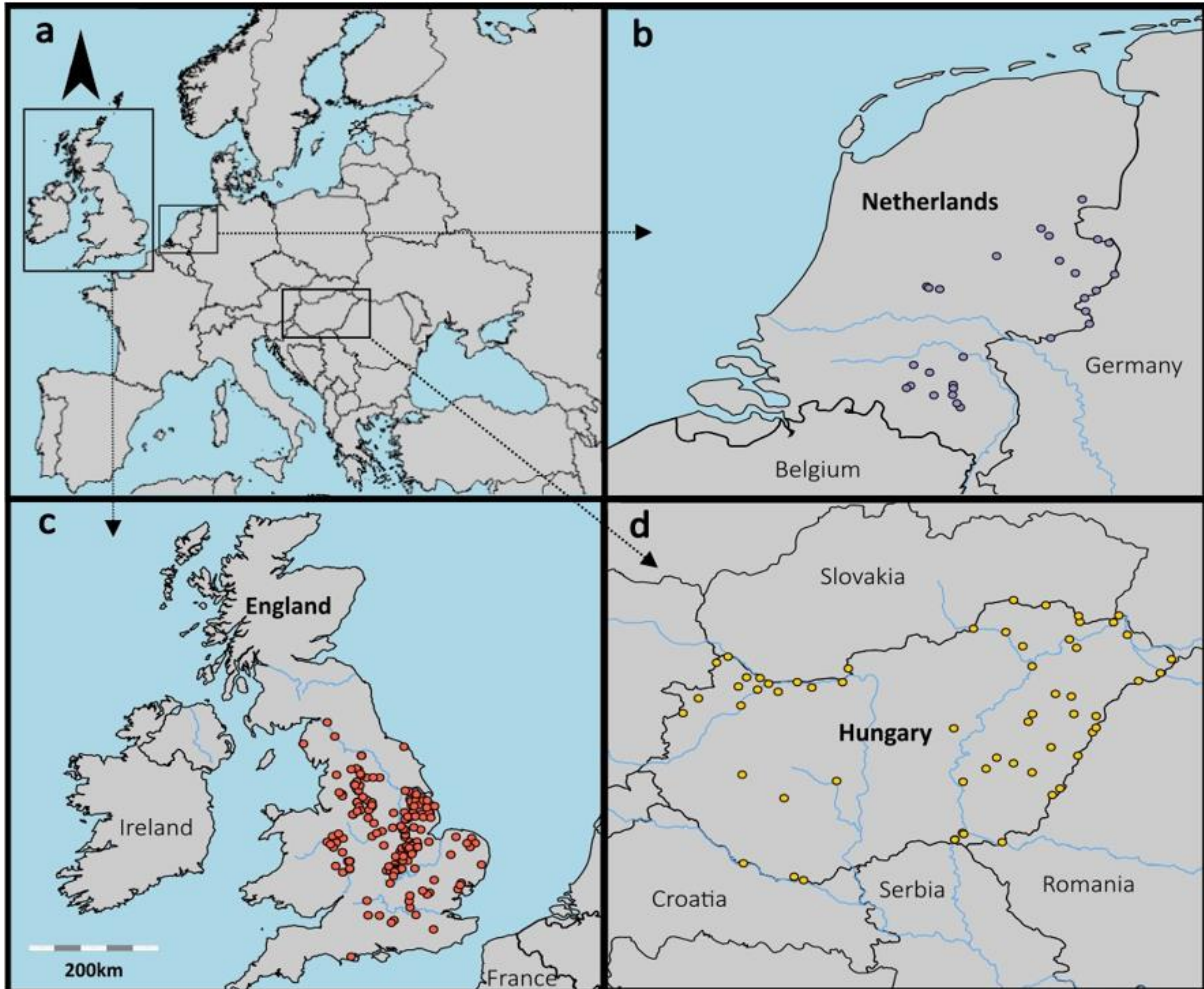


Figure 1: European location (a) of time series for each country the Netherlands (b), England (c) and Hungary (d). The points correspond to the sites where sampling was performed (i.e., to the origin of the time series).

Fill missing values

To account for missing years (i.e., years that were not sampled), we used the *mice* function of the *mice* R package (Buuren & Groothuis-Oudshoorn, 2011) using multivariate imputation by chained equations for each country independently to fill the species' presence and their respective abundance in each time serie. For this, we used the predictive mean matching (PMM) method, which calculates the predicted value of each target variable and creates multiple imputations (i.e., replacement values) for multivariate missing data, and set the

multiple imputations to five and established the maximum number of iterations to fifty. This approach enables the comparison of time series data, while avoiding the potential effect of missing years on long-term trends and permitting to obtain the same number of data points in each year making them directly comparable.

Identifying non-native species

To identify non-native macroinvertebrate species in each country, we used three sources to verify the native range of species: the *Global Alien Species First Record Database* (Seebens et al., 2017), the *Global Biodiversity Information Facility* (GBIF; <https://www.gbif.org/>) and the *European Network on Invasive Alien Species* (NOBANIS; <https://www.nobanis.org/>). When different sources presented conflicting results regarding the non-native status, we followed the information from the *Alien Species First Record Database* (Seebens et al., 2017), as it is considered the most comprehensive and reliable database on non-native species worldwide. The list of species considered non-native can be found in the supplemental data (Table S2).

Non-native species metrics

To identify temporal trends in the presence of non-native species across the three countries (the Netherlands, England and Hungary), we calculated several diversity and compositional metrics: Firstly, we determined the total abundance and richness of both native and non-native species for each site and year to calculate their proportion within the respective community. Furthermore, we calculated three diversity metrics (α , β , and γ) specifically for non-native species to assess their individual temporal trends within the respective time series and in the case of γ diversity within countries. The α diversity was calculated as non-native species richness in each year within each individual time series. The γ diversity was calculated as the total number of non-native species per year within each country. Lastly, β diversity was

calculated as the ratio between γ and α diversity for each year and site (i.e., $\beta = \gamma / \alpha$, *sensu* Whittaker, 1972).

Specific site predictors

We compiled data on site-specific characteristics which may modulate the temporal changes in diversity and community metrics of both native and non-native species. First, we extracted the geographic coordinates of each site reflecting a time series (World Geodetic System 1984, WGS). Then we obtained two climatic predictors, namely the average annual temperature and precipitation, which were extracted from the *E-OBS* gridded European-scale from Copernicus Climate Change Service observation-based dataset for each year and site (spatial resolution: 0.1°; www.ecad.eu/E-OBS/; Cornes et al., 2018). The obtained daily measurements were then averaged across the 12 months preceding each sampling event.

For each site, the distance to the nearest upstream barrier (such as dams or weirs) was obtained from the *Global Reservoir and Dam Database v1.3*. Elevation data was calculated with the *MERIT Hydro digital elevation model* (Yamazaki et al., 2019) using the *Hydrography90m* dataset that delineates stream channels at 90 m spatial resolution and includes a high density of headwater streams (Amatulli et al., 2022). Three spatial variables were calculated using GRASS GIS functions (Jasiewicz & Metz, 2011; GRASS Development Team, 2017): stream slope and Strahler order (i.e., a hierarchical classification of stream networks based on the number of their tributaries and orders) were extracted using the *r.stream.slope* function (Jasiewicz & Metz, 2011), and distance from the outlet was calculated using the *r.stream.distance* function (Jasiewicz & Metz, 2011). In addition, we calculated the percent coverage of urban areas (% urban area) and of water bodies that include: streams, rivers, ponds and lakes (%-water bodies) at each location and for every sampling year as

indicators of upstream catchment land use, using the *r.univar* function (Neteler et al., 2012). Finally, the α diversity of native species and their abundance were calculated for each site and year incorporating them as additional predictors. A table summarizing all predictors and their range for each country can be found in the supplemental data (Table S3).

Traits and trait and functional metrics

To examine changes in trait occurrences over time, we used the *www.freshwaterecology.info* database to collect and summarize the biological and ecological traits of all macroinvertebrates in our time series (Schmidt-Kloiber & Hering, 2015; Tachet et al., 2010). We retained 11 biological and 8 ecological traits, encompassing 67 and 45 modalities, respectively (Table S4, S5). When no trait information was available for a species, we removed it from the dataset. In cases where a specific trait information was missing for a species, we supplemented the available information by referring to the respective genus level (except for *Molanna angustata* and *Katamysis warpachowskyi*, where information was completed at the order level). Then, all ecological and biological trait modalities were ‘fuzzy coded’ with the function *prep.fuzzy.var* using the R package *ade4* (Chevenet et al. 1994; Bougeard & Dray, 2018). The fuzzy coding procedure indicates to which extent a taxon exhibits each trait’s modality by proportionally scaling them between 0 and 1 (Schmera et al., 2015). This approach simplifies the synthesis of trait information and enables the integration of diverse biological data (Baker et al., 2021). Then, four trait metrics were computed separately for both biological and ecological traits using the *alpha.fd.multidim* function from the R package *mFD* (Magneville et al., 2022): trait richness (T_{Ric}) and functional richness (F_{Ric}) as descriptors of the amount of niche space occupied by all species within a given community; trait divergence (T_{Div}) and functional divergence (F_{Div}) as measures of how widespread or clumped species are within the respective niche space, weighted by their relative abundance;

trait dispersion (T_{Dis}) and functional dispersion (F_{Dis}) as the average distances of individual species to the group centroids of all species; and trait evenness (T_{Eve}) and finally functional evenness (F_{Eve}) describing the distribution of abundances across the niche space (i.e., in each trait; Baker et al., 2021; Renault et al., 2022). Note that we used ‘trait metrics’ for metrics computed using biological traits and ‘functional metrics’ for metrics computed using ecological traits, to distinguish the nuanced differentiation between individual organism traits and traits reflecting the broader ecological processes and functions (Baker et al., 2021; Le Hen et al., 2021). These metrics were calculated at the regional level by averaging data from all the sites sampled over time.

Trends of community diversity and trait metrics

To identify the most important variables predicting changes in diversity metrics (α , β , and γ) and trait and functional metrics, we employed random forests (RF) to assess the importance of predictor variables in accounting for variance in calculated metrics. This was done using the function *rfsrc* from the R package *randomForestSRC* (Ishwaran et al., 2023). We set the number of trees to 2,000 and the number of variables randomly selected as candidates for splitting a node to 7. In our final models, we retained only the variables that explained the most variation in variance (see Figure S1, S2, S3 and S4). Then, we checked the collinearity of the finally selected variables using the *vifstep* function in the *usdm* R package (Naimi et al., 2014) for each model. A conservative variance inflation factor (VIF) threshold of 5 was applied (Table S6), and variables with elevated VIF values were evaluated according to their ecological relevance and by expert opinion (Zuur et al., 2009; Dorman et al., 2013).

Then, to investigate the temporal trends of diversity and trait and functional metrics within each country, we employed Generalized Additive Models (GAMs) using the *gam* function of the R package *mgcv* (Wood, 2017). First, we visually inspected the residual

distribution of each model using histograms and observed overdispersion in the data, leading us to select quasi-poisson distributions for count data. Then, α or β diversity were analyzed as a response of the most-explanatory variables (see Figure S1). For α and β diversity models, we specified each time series as a random effect to account for geographical variability (Table S7 and S8). Conversely, γ diversity and trait and functional metrics were solely analyzed as a function of time (i.e., sampling year; Table S9, S10 and S11).

Extrapolation over time

To investigate the future trends of non-native species α , β , and γ diversity, as well as the trait metrics until 2040 for each country, we used quadratic robust regression models implemented in the *lmrob* function of the R package *robustbase* (Maechler et al., 2022). The predictions were only made as a function of time; i.e., we did not select other predictors since such an approach would require it to extrapolate their values as well, thereby adding more uncertainty. The quadratic term was added to the model to account for potential non-linear trends in the data. We determined the maximum number of iterations using the *find_scale* function with a C level of 1,000 and calculated the estimate of the covariance matrix using the *vcov.avar1* argument. Then we used the *predict* function of the R package *stats* (R Core Team, 2022) to project future trends of the trait metrics until 2040. The confidence interval was also calculated, giving an indication of potential future trends. As such, these projections can only indicate a future trend, not estimate precise values reached by a certain year. All analyses were performed in R version 4.2.2 (R Core Team, 2022).

Results

We retained a total of 259 time series ($n = 60$ in Hungary, $n = 171$ in England, $n = 28$ in the Netherlands; Table S1). Across all time series, we found 726 unique macroinvertebrate

species (697 native and 29 non-native species). Hungary had, with 21 species (7.6% of all species), the highest number of non-native species, followed by the Netherlands with 17 species (5.6%) and England with 10 species (3.3%).

Community change over time

Non-native species abundances (e.g., individual counts of all taxa) followed a similar temporal pattern across the studied countries, and remained stable over time (Figure 2a, c and e). Raw non-native species richness increased across all three countries, reaching a peak in 2016 in the Netherlands and England, and 2013 in Hungary (Figure 2b, d and f).

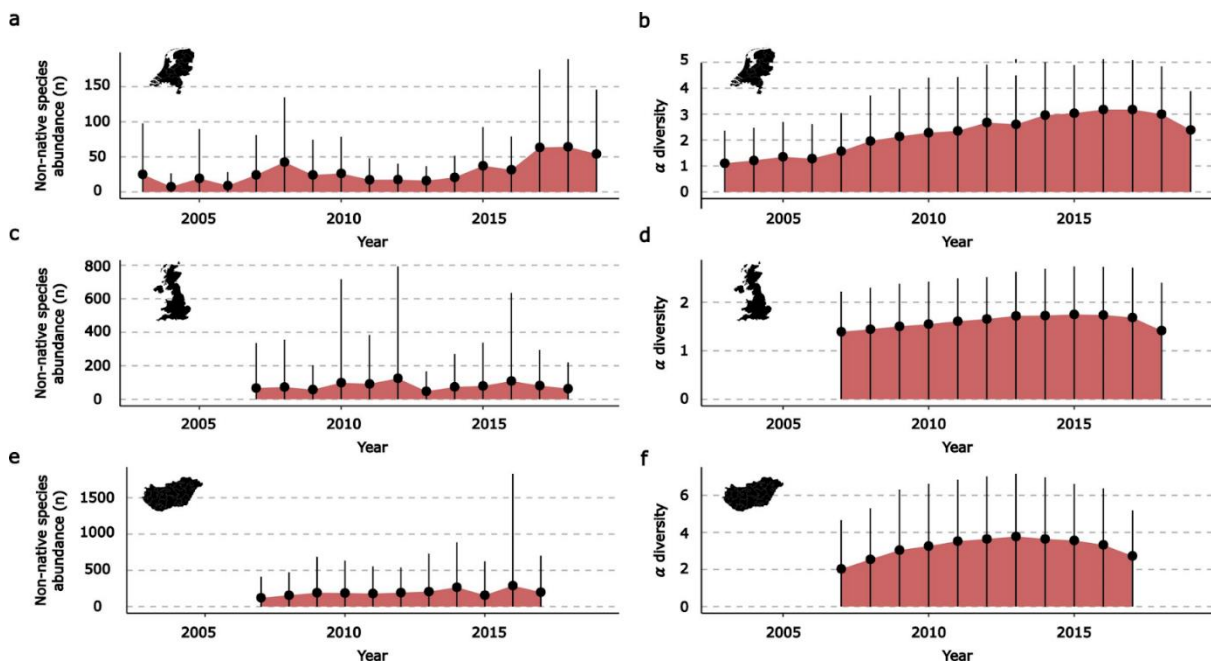


Figure 2: Temporal trends of total non-native species abundance (left column) and α diversity (right column) in the Netherlands (a-b), England (c-d) and Hungary (e-f). The plots display the average values \pm their standard deviation (SD).

When modeled using GAMs, the α diversity of non-native species increased over time in Hungary and the Netherlands and remained stable in England (Figure 3a). The β diversity of non-native species slightly decreased in Hungary, remained stable in the Netherlands, and increased in England (Figure 3b). Non-native species γ diversity increased in all three countries (Figure 3c).

In terms of the importance of predictors for changes in α and β diversity in each country, notable regional differences in their significance were observed. In England, α diversity of non-native communities decreased with increasing elevation and distance to the next upstream barrier. Similarly, β diversity of non-native species in England increased with increasing distance to the next upstream barrier but decreased with increasing %-waterbodies in the site's proximity. In the Netherlands, non-native α diversity increased with increasing native α diversity and Strahler order. Conversely, the year of sampling had a negative impact on non-native β diversity, while the distance to the outlet had positive effects. Lastly, in Hungary, α diversity of non-native communities increased with decreasing distance to the next upstream barrier and increasing Strahler order. In Hungary, non-native β diversity increased with decreasing %-waterbodies in the site's proximity and increasing distance to the next upstream barrier.

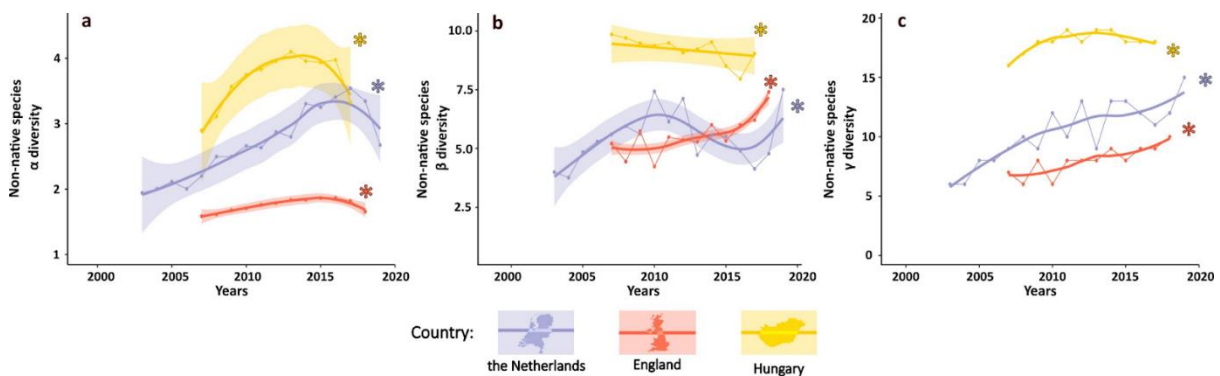


Figure 3: Temporal change of non-native species α (a), β (b) and γ diversity (c) over time for the Netherlands (purple), England (red), and Hungary (yellow).

Trait and functional metrics change over time

Trait and functional metrics exhibited similar trends over time across the three countries, with the exception of F_{Ric} in the Netherlands, which showed a decrease over time (Figure 4f). Regarding biological traits, we observed significant temporal changes in T_{Div} in the Netherlands and T_{Eve} in both England and Hungary (Table S10). For ecological traits, F_{Ric} showed significant changes over time (Table S11). The random forest analyses indicated that ‘time series length’, ‘non-native species abundance’, and ‘non-native species α diversity’ were the most important predictors (Supplement 1). The duration of time series had no effect on the computed metrics, whereas the abundance or number of non-native species had positive or negative effects .

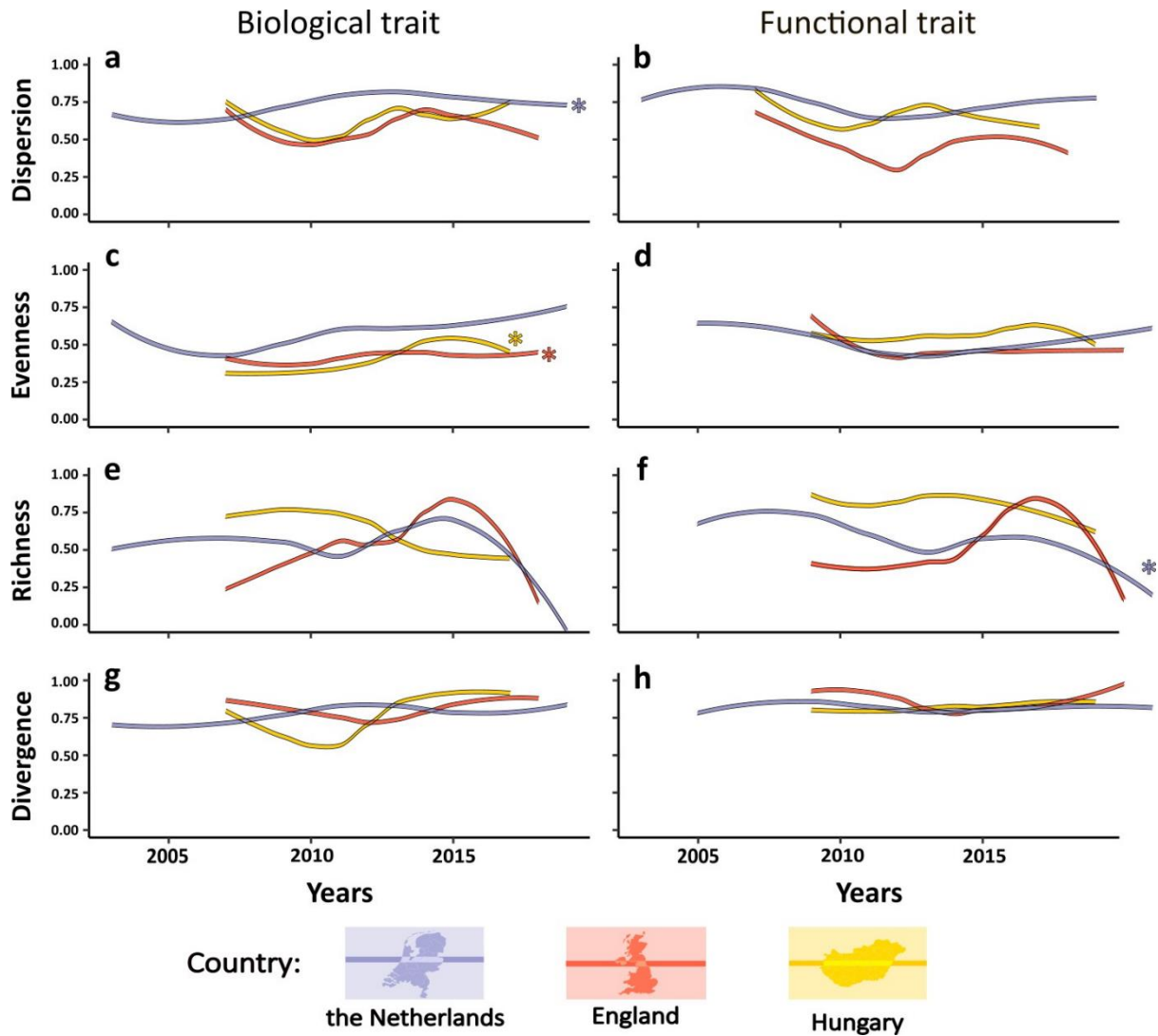


Figure 4: Biological trait metrics (a, c, e and g) and ecological functional metrics (b, d, f and h) for the non-native species over time. The ‘*’ indicates that the metrics change over time was found significant by the generalized additive model.

Extrapolation

Until 2040, a general decline in non-native species α diversity was predicted across all countries (Figure 5). However, this decrease was more pronounced in England and Hungary compared to the Netherlands, underlined by considerable uncertainties and large confidence intervals. Non-native species β diversity was projected to increase in England, while it decreased in Hungary and the Netherlands. Additionally, the γ diversity of non-native

communities was predicted to decrease in Hungary and the Netherlands, while remaining relatively constant in England (Figure 5).

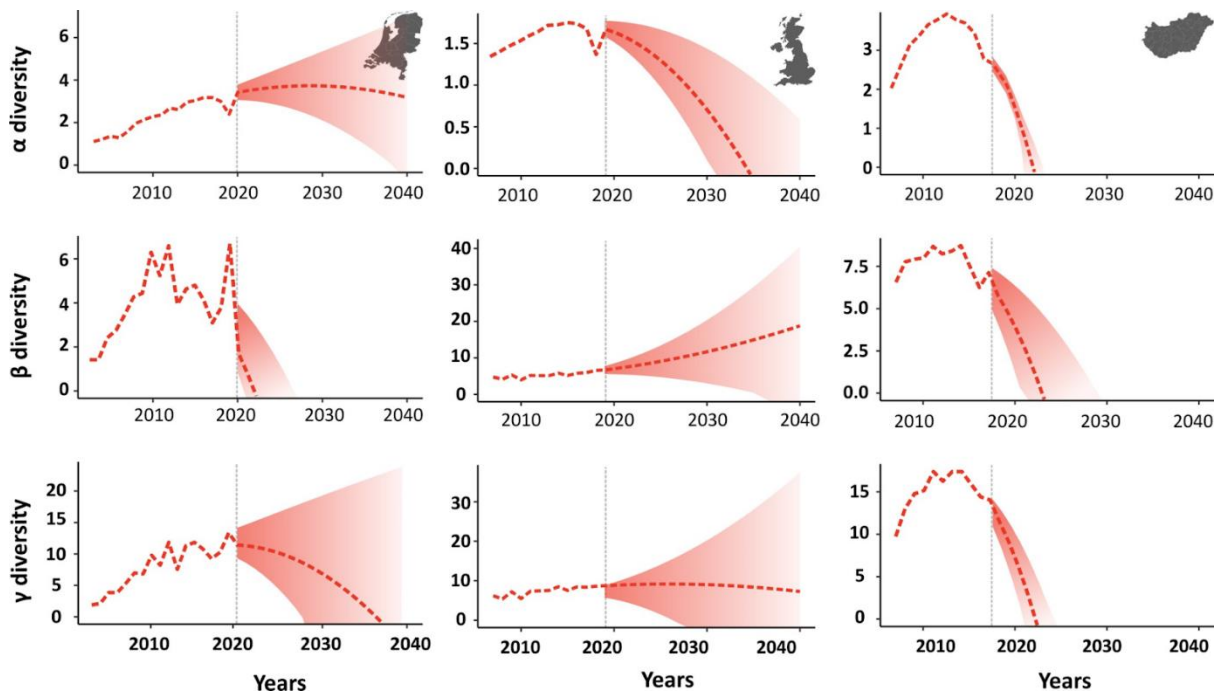


Figure 5: Trends of α , β and γ non-native species diversity were extrapolated using robust regressions for the Netherlands (a, d, and g), England (b, e, and h), and Hungary (c, f, and i). The vertical dashed line represents the beginning of the extrapolation, and the red gradient corresponds to the 95% confidence interval.

Extrapolation of the trait and functional metrics revealed several significant trends despite large confidence intervals. T_{Ric} and F_{Ric} was projected to decline rapidly for all countries (Figure 6g-i). In contrast, F_{Div} and T_{Div} were predicted to increase for England and Hungary, while remaining stable for the Netherlands (Figure 6j-l). Both F_{Eve} and T_{Eve} were predicted to increase in all countries, except for T_{Eve} in England and F_{Eve} in Hungary (Figure 6d-f). Finally, both F_{Dis} and T_{Dis} were projected to increase in all countries, except for T_{Dis} in the Netherlands and F_{Dis} in Hungary (Figure 6a-c).

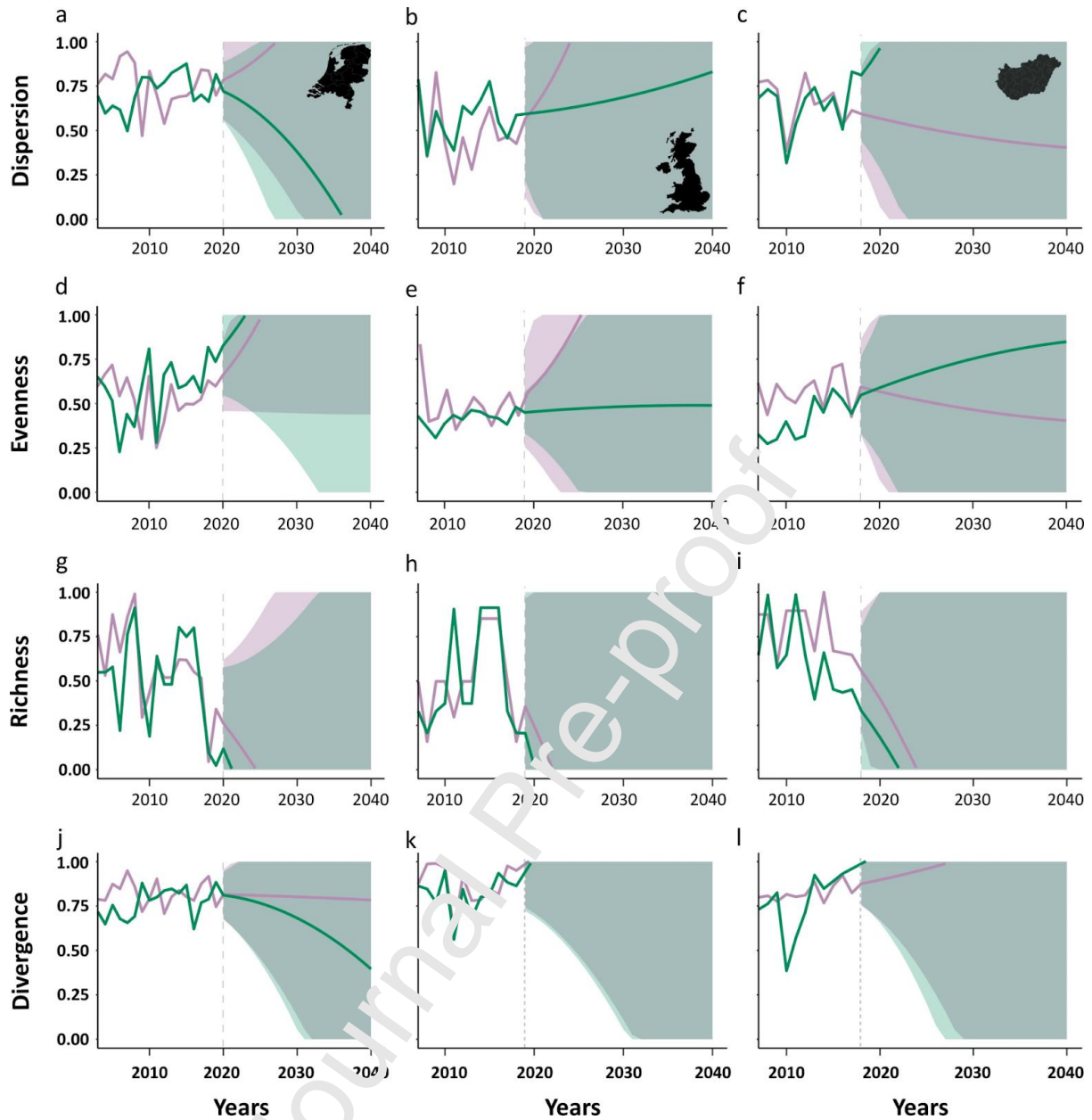


Figure 6: Extrapolated trends of trait and functional metrics analyzed using a robust regression model for the Netherlands (a, d, g and j), England (b, e, h and k) and Hungary (c, f, i and l). Functional metrics are represented by the purple line, while the trait metrics are represented by the green line. The vertical dashed line indicates the beginning of the extrapolation. The purple gradient represents the 95% confidence interval of the functional metrics, and the green gradient represents the 95% confidence interval of trait metrics. The gray part represents the overlap between the two confidence intervals.

Discussion

The rate of biological invasions shows no signs of saturation and is not expected to plateau in the foreseeable future (Seebens et al., 2017). Consequently, the impacts of biological invasions could escalate and potentially reshaping ecosystems at all scales (local, regional and global) and levels (taxonomical, functional; Ricciardi & MacIsaac, 2011; Simberloff et al., 2013). In line with our first hypothesis, we observed an increase in α and γ diversity of non-native species across all countries. However, these increases were not accompanied by significant changes in trait and functional metrics, although they exhibited different patterns across countries. According to our second hypothesis, the drivers of diversity trends varied across countries, highlighting the importance of site-specific assessments. Contrary to our third hypothesis, however, our imputation of current trends indicated a future decline in non-native species diversity in all countries, coupled with a decline in non-native species trait and functional metrics.

Changes in α , β , γ diversity

Non-native species have the potential to disrupt communities by e.g., reducing the abundances or richness of native species (α diversity; Mainka & Howard, 2010; Soto et al., 2023b). Yet, not much is known about different diversities of non-native species. In our study, we observed that the total abundance and α diversity of non-native communities exhibited similar temporal patterns across all countries (Haubrock et al., 2023b, c). Specifically, in Hungary, the introduction of non-native species from the Ponto-Caspian region was likely facilitated by the opening of the Rhine-Main-Danube canal in 1992 (Bij de Vaate et al., 2002; Soto et al., 2023c). Additionally, increased international trade has contributed to the establishment of non-native species in the Netherlands and England (Gallardo & Aldridge, 2015). Consistent with findings from previous research (Moorhouse et al., 2014; Ruokonen et al., 2014; Mollot

et al, 2017), we observed a general increase in the α diversity of non-native macroinvertebrate species except for England. It has been shown, that the increase in non-native species had a negative impact on α diversity (i.e., number of native and non-native species), thereby highlighting the role of non-native species as a significant driver of species extinctions (Clavero & García-Berthou, 2005; Bellard et al., 2016b).

The presence and dominance of non-native species can have a myriad of ecological implications for ecosystems, ranging from individual species-level (e.g., decreased abundance) to community-level impacts (e.g., taxonomical restructuring of natural communities), potentially affecting ecosystem functioning (Ricciardi et al., 2013; Moorhouse et al., 2014; Bezerra et al., 2018). Nevertheless, the effects of non-native species introductions on biodiversity add to the effects of other drivers of biodiversity loss such as climate change or natural hazards (Turbelin et al., 2023), therefore posing a major challenge to biodiversity conservation (Bellard et al., 2016a; Pyšek et al., 2017). Especially when non-native species become dominant in invaded ecosystems as observed in Hungary where they accounted for 33.8–53.5% of the total community abundance, they can become disruptive (Bradley et al., 2019; Le Hen et al., 2023). However, it is worth noting that non-native species can also generate a perceived positive impact at local scales due to an increase in ‘*pseudorichness*’ (Külköylüoğlu, 2013) as in the case of England and the Netherlands.

Modification of γ diversity in freshwater ecosystems can have significant ecological and evolutionary impacts, influencing various aspects such as ecosystem functioning, food web dynamics, and the resilience of aquatic communities to environmental stressors (Sax & Gaines, 2003; Worm et al., 2006). The impacts of non-native species on α diversity can be context-dependent, appearing ‘positive’ at local scales, but often becoming diluted when considering larger spatial scales (Goodenough, 2010). In our study, we observed an increase

in non-native species γ diversity across all countries over time. The increase in Hungary however occurred early on and plateaued in recent years. Changes in environmental conditions can trigger a sudden—possibly exponential—increase in the abundance of these species (Haubrock et al., 2022; Soto et al., 2023d), which can have significant consequences for native biodiversity (Spear et al., 2021). While such ‘boom’ phases are often followed by stable abundances at lower levels (i.e., ‘busts’; Strayer et al., 2017), it is also possible that these species remain at low abundance for long periods (the so called ‘sleeping populations’; Spear et al., 2021), potentially never experiencing a ‘boom’ phase (Haubrock et al., 2022; Soto et al., 2023b). The intensification of climate change may make previously unsuitable areas, such as high-elevation areas, suitable for (often thermophile) non-native species (Haubrock et al., 2023c), while native species may be forced to migrate upstream in search of more suitable climatic conditions (Haubrock et al., 2023c). Under the influence of various stressors, α and γ diversity may converge, leading to a homogenization of non-native species at the regional scale (McKinney & Lockwood 1999), resulting in the same species at the local and regional level but it is important to note that our results can be significantly influenced by the choice of scale during the study.

Changes in non-native species β diversity in freshwater organisms can provide insights into the distribution of biodiversity and potential species turnover across different habitats, potentially impacting community composition and ecosystem processes (Gutiérrez-Cánovas et al., 2013; Mori et al., 2018). Contrary to our first hypothesis, we observed regional differences in β diversity across the countries studied. β diversity increased in all countries except Hungary, where it decreased. A decline in β diversity indicates a greater similarity among communities, a phenomenon known as ‘biotic homogenization’ (McKinney & Lockwood 1999), which can have consequences for ecosystems and the services they provided (McKinney & Lockwood 1999; Olden & Rooney, 2006; Petsch, 2016). The

differences in the distribution of non-native species can originate from differences in the pathways through which they are introduced (e.g., ballast waters, live food trade, aquarium release, aquaculture) and the vectors responsible for their spread (e.g., pet trade, contaminant equipment, human transport), but also indicate that the species are yet to spread. The increase in non-native species β diversity observed in England indicates more heterogeneous species across time, suggesting that the same non-native species are increasingly present across the studied region. The increasing even distribution of many non-native species, as indicated by the rising non-native species β diversity, can pose challenges for conservation efforts aimed at restoring degraded ecosystems to their pristine state (Haubrock et al., 2019). It underscores the importance of limiting the spread of non-native species and implementing early interventions (Hobbs et al., 2009).

Changes in trait metrics

Despite the increase in non-native species α and γ diversity in the three countries, we observed a decrease in F_{Ric} and T_{Ric} . This implies that the non-native species present in the last years exhibit similar traits, indicating a prevalence of ‘generalist’ species, able to consume different prey and adapt to a wider range of habitats; Richmond et al., 2005; Marvier et al., 2004). The trait and functional dispersion (T_{Dis} and F_{Dis}) also remained stable at the regional level. In England, the variation in trait and functional metrics was primarily influenced by %-waterbodies, while in Hungary, non-native species richness played a significant role. The drivers of trait and functional metrics in the Netherlands varied (Supplement 1). The widespread distribution of Ponto-Caspian species in Europe can be attributed to their unique traits, such as high fecundity and wide environmental tolerance (Gallardo & Aldridge, 2015; Soto et al., 2023a). Our results indicate that there has not been a drastic change in available traits, as evidenced by the absence of a significant influx of new species or the disappearance of abundant species. However, it should be remembered that these analyses were conducted

only on non-native species and may not fully reflect the dynamics and overall functioning of ecosystems (Baker et al., 2021).

Extrapolation of future trends

Understanding future biodiversity patterns at various spatial scales is of utmost importance for effective monitoring and conservation efforts (Guisan et al., 2013; Uribe- Rivera et al., 2017). When extrapolating future trends in non-native diversity it is however important to recognize that species introductions are still rising (Seebens et al., 2017; Haubrock et al., 2023d). It is therefore important to understand that the presented projections that show declines in non-native species α , β and γ diversity as well as trait and functional richness are imputations of the available but limited data. While these trends are subject to large uncertainty (indicated by large confidence intervals) as they are affected by limited time series and data, they are however indicative of a direction, indicating a decline in non-native species across these sites in the respective countries. Having used a cubic (instead of a linear) relationship in our model, the initially rising but then declining trends are indicative of declines being more likely, as increases would have been displayed as exponential increases. However, despite these shortcomings and them not taking into account the propagule pressure from new non-native species, they form a basis for future monitoring. This is crucial going forward, because if non-native species had previously replaced native species, these changes could — albeit affecting ecological processes (Chapin et al., 1998; Sagouis et al., 2015) — enable the amelioration of native biodiversity. It is important to note that while these taxonomic and trait changes are imputed, they may be counterbalanced by presence, recovery, and contributions of native species within the community. Despite ongoing species introductions, our results suggest that non-native species often remain at low abundance or revert to low abundance with limited impacts (Sofaer et al., 2018) after initial boom-bust dynamics (Soto et al., 2023a). This

highlights the complex dynamics of non-native species and the potential for native species to mitigate their effects.

Indeed, our projections indicate a potential reduction in β diversity, except in England, which would suggest a homogenisation of non-native species across local and regional scales (Pilotto et al., 2022). However, it is important to acknowledge that regional differences can complicate generalizations at larger scales. Factors such as extreme events, natural hazards, or the implementation of new management strategies to control non-native populations can significantly influence the projected diversity patterns. While our extrapolations provide insights into potential changes in non-native species diversity, it is important to recognize the substantial uncertainties associated with these predictions. Future outcomes can be influenced by various factors, including the implementation of new management policies and the occurrence of unforeseen events.

Conclusion

In conclusion, our study reveals that the taxonomic diversity of non-native species communities is shaped by a range of factors and exhibits regional differences, while functional and trait metrics remained relatively stable over time despite differences in non-native species occurrences. We also observe an increase in α and γ diversity of non-native species across all countries, driven by various anthropogenic impacts and environmental conditions. Thus, our predictions can provide a working basis indicating the direction of non-native species diversity trends in the coming years based on available data. In this case, continuous monitoring of the ecosystems is needed to adjust the management strategies in response to the multiple threats and to anticipate and adapt to potential unforeseen events (Radinger et al., 2019). We also highlight that long-term and continuous ecological monitoring can be utilized to detect and understand changes in community composition and

functional characteristics (Lindenmayer et al., 2012; Haubrock & Soto, 2023; Haubrock et al., 2023b) to (i) identify fluctuations of populations in invasive species (Daufresne et al., 2004), (ii) identify drivers of these fluctuations and invasion success (Bellard et al., 2016a), (iii) detect early warning signals of invasion such as the arrival of new non-native species (Scheffer et al., 2009), (iv) directly observe impacts of invasive species on diversity (Pyšek et al., 2020), and (v) predict future invasion trends under different scenarios (Briscoe et al., 2019).

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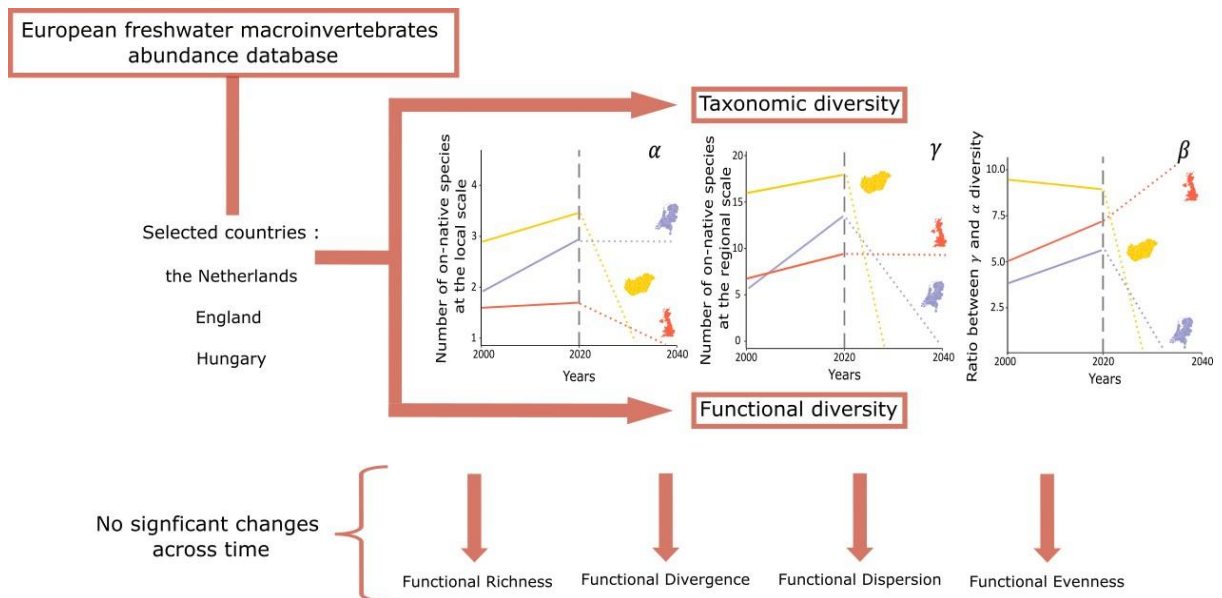
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Declaration of interest

The authors have no financial/personal interest or belief that could affect their objectivity to declare.

Graphical abstract :



Highlights

- Local and regional increase in non-native species in three European countries from 2003 to 2019
- No temporal changes in trait or functional metrics of non-native species
- Predicted a decline of non-native species' α , β and γ diversity until 2040
- Long term monitoring of non-native species is highlighted as important