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Science of the Total Environment

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https://doi.org/10.1016/j.scitotenv.2023.161486

Science of the Total Environment 867 (2023) 161486

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Alien species and climate change drive shifts in a riverine fish community and trait compositions over 35 years

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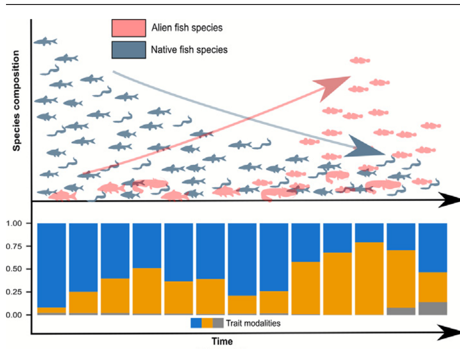
HIGHLIGHTS

- Alien fish in the Rhine river compensated for the loss of native species.
- Rising water temperatures likely allowed invasive fish species to become established.
- Trait metrics did not reflect changes in compositional metrics but indicated severe changes.
- Changes in trait composition were driven by the alien fish *Neogobius melanostomus*.
- Expressed changes in functional traits provide a high value for impact assessments.

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Sergi Sabater

Keywords:
Rhine river
Freshwater fish
Long-term study
Alien species
Functional ecology
Traits

ABSTRACT

Alien fish substantially impact aquatic communities. However, their effects on trait composition remain poorly understood, especially at large spatiotemporal scales. Here, we used long-term biomonitoring data (1984–2018) from 31 fish communities of the Rhine river in Germany to investigate compositional and functional changes over time. Average total community richness increased by 49 %: it was stable until 2004, then declined until 2010, before increasing until 2018. Average abundance decreased by 9 %. Starting from 198 individuals/m^2 in 1984 abundance largely declined to 23 individuals/m^2 in 2010 (−88 %), and then consequently increased by 678 % up to 180 individuals/m^2 until 2018. Increases in abundance and richness starting around 2010 were mainly driven by the establishment of alien species: while alien species represented 5 % of all species and 0.1 % of total individuals in 1993, it increased to 30 % (7 species) and 32 % of individuals in 2018. Concomitant to the increase in alien species, average native species richness and abundance declined by 26 % and 50 % respectively. We identified increases in temperature, precipitation, abundance and richness of alien fish driving compositional changes after 2010. To get more insights on the impacts of alien species on fish communities, we used 12 biological and 13 ecological traits to compute four trait

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http://dx.doi.org/10.1016/j.scitotenv.2023.161486
Received 26 October 2022; Received in revised form 16 December 2022; Accepted 5 January 2023
Available online 7 January 2023

metrics each. Ecological trait dispersion increased before 2010, probably due to diminishing ecologically similar native species. No changes in trait metrics were measured after 2010, albeit relative shares of expressed trait modalities significantly changing. The observed shift in trait modalities suggested the introduction of new species carrying similar and novel trait modalities. Our results revealed significant changes in taxonomic and trait compositions following alien fish introductions and climatic change. To conclude, our analyses show taxonomic and functional changes in the Rhine river over 35 years, likely indicative of future changes in ecosystem services.

1. Introduction

Extinction and speciation processes constitute the natural renewal of biodiversity (Johnson et al., 2017). At global scales, the growing extent of human impacts on ecosystems worldwide, including changes in climatic conditions and land-use, overexploitation of resources, or introduction of alien species (Sala et al., 2000; Cowx and Collares-Pereira, 2002), increases the frequency of occurrence of these processes. At regional scales, the man-made alterations of habitat quality greatly favour the increase of extinction rates, and cause a staggering decline in biodiversity (Dirzo et al., 2014; Johnson et al., 2017; IPBES, 2019).

Among the above-mentioned drivers of biodiversity decline, biological invasions play a central role, as growing numbers of alien species are introduced (deliberately or accidentally) beyond their native range (Blackburn et al., 2014; Turbelin et al., 2017; Seebens et al., 2018). Once successfully established, some alien species can proliferate locally before spreading geographically, and colonising new habitats, causing ecological and socio-economic impacts on recipient ecosystems (Arim et al., 2006). Invasive alien species can threaten biodiversity at all organisational scales, in all regions, ecosystems, or habitats (Bellard et al., 2016; Mollot et al., 2017; Blackburn et al., 2019; Pilotto et al., 2020; Pyšek et al., 2020). Biodiversity from freshwater ecosystems is no exception: in addition to being critically affected by anthropogenic activities (*e.g.* change in land use, climatic changes), environmental stressors can magnify the deleterious impacts of alien species, potentially leading to species extinction and to the loss of ecosystem functions (Sala et al., 2000; Gherardi and Acquistapace, 2007; Villéger et al., 2011; Haubrock et al., 2020).

Invasive alien fishes have been known to modify aquatic ecosystems (*e.g.* by altering community structure and the trophic web) and displace native species through competition and/or predation (Cambray, 2003; Gherardi et al., 2011; Haubrock et al., 2020, 2022). These impacts have been recently monetised, and economic losses incurred by alien fishes were reported as being mainly related to damages, resource losses, and impaired social welfare (Haubrock et al., 2022). Alien fish species can also negatively affect taxonomic diversity (Cambray, 2003; Gallardo et al., 2016), with potential consequences for the functional structure of the community. In these circumstances, the loss of native species can result in the concomitant losses of certain traits, whereas new species are prone to introduce “novel” traits or even replace those lost (Nock et al., 2016; Renault et al., 2022).

Information on ecological preferences and biological (*i.e.*, functional) traits (later on referred to as simply ecological and biological traits) are characteristic to each individual or species, determining its biology and functioning within a community, as well as shaping the ecological space it occupies. Traits are often considered plastic, in several cases slowly changing either by developmental acclimation or by on-time adjustments, allowing their constant optimisation or the maintenance of biological performance, even when environmental factors vary qualitatively or quantitatively (Hooper et al., 2005; Mason et al., 2005; Nock et al., 2016). In invaded habitats, the loss of individuals and species can be associated with the loss of traits, and this can have profound impacts on community structure and functioning when unique and/or specialised traits are lost (Clavel et al., 2011; Dias et al., 2021; Pilotto et al., 2022). In several instances, taxonomic and functional changes induced by alien species, and the consecutive loss of native species, have resulted in the homogenisation of freshwater communities. Indeed, ~40 % of European fish assemblages that experienced taxonomic differentiation were also functionally homogenised (Olden and Rooney, 2006; Villéger et al., 2011, 2014; Haubrock et al., 2020). Functional homogenisation of all local communities within a region (*e.g.* metacommunities) can increase vulnerability to large-scale environmental events by synchronising local biological responses across individual communities (Olden et al., 2004; Clavel et al., 2011; Villéger et al., 2014). Although some taxonomic and functional changes – commonly described with a series of trait metrics (see Baker et al., 2021) – induced by alien fish are known to occur in European lakes (Zhao et al., 2019), not much is known about riverine ecosystems. Furthermore, changing climatic or environmental conditions can induce shifts in the establishment rates and concomitantly abundance of alien fish (Strayer et al., 2017). This also induces functional changes—an aspect pertaining to the compositional and functional dimension of biological invasions that has not been studied in depth (but see Crozier and Hutchings, 2014).

The Rhine river, one of the most heavily anthropogenically impacted freshwater rivers in Europe with a total length of 1250 km (Tittizer, 1997; Van der Velde et al., 2000; Uehlinger et al., 2009), provides numerous services such as transportation, power generation and drinking water (Cioc, 2002; Uehlinger et al., 2009). The opening of the Rhine-Main-Danube canal in 1992 links the Rhine catchment *via* the Main tributary with the Danube river, and serves as a major pathway facilitating the spread of alien species (Tittizer, 1997; Bij de Vaate et al., 2002; Balzani et al., 2022). However, while information on the taxonomic identity of alien species present in highly anthropogenically altered ecosystems like the Rhine river is available, not much is known about the changes in the community and trait composition that have occurred as a response to these introductions (Nehring and Klingenstein, 2008; Rabitsch et al., 2013), nor how environmental changes over time drove these.

In the current era of globalisation, ongoing climatic changes, and an increased interest in the protection of natural resources, long-term studies have become increasingly necessary to provide a better understanding of introduction processes, reconstruct introduction events, and community dynamics (Franklin, 1989; Hooper et al., 2005; Strayer et al., 2006). Yet, long-term data has rarely been used to disentangle the effects of alien species on the taxonomic and trait diversity of fish communities, nor to investigate effects of climatic or environmental changes (but see Guareschi et al., 2021). Using long-term biomonitoring data from the Rhine river in western Germany (1984–2018), we investigated changes in the taxonomic and trait composition in invaded fish communities over time. To this end, we specifically investigated if changes in the communities' taxonomic and trait composition were driven by disappearances of native fishes or by replacements by alien fishes as well as climatic changes over time and consequently, if identifiable changes were indicative of taxonomic and functional (*i.e.*, trait) homogenisation and subsequently, responding to environmental changes. We tested the following hypotheses: (i) the increase in alien fish abundance will be at the expense of native species, resulting in a decrease in the overall native communities' abundance, (ii) the arrival and establishment of alien fishes will introduce novel functional traits, reshaping the ecological space occupied by the community, (iii) changes in environmental parameters, and more particularly climatic factors, will drive compositional changes.

2. Methods

2.1. Data collection

To investigate the changes in composition of freshwater fish communities over spatiotemporal scales, we used a time series of fish abundance from the Rhine river in western Germany. Fish samplings were conducted in the Rhine river between 1984 and 2018, although not continuously (Table S1), over different seasons (*i.e.*, spring and summer) and from 31 sites. In total, the samplings covered ~170 km of the Rhine river from the border to the Netherlands upstream (6°12′55″N–7°11′55″N; 50°39′49″E–51°49′46″E; Fig. 1). Fish were collected at each site following a standardised protocol by bank fishing from the right river bank through continuous electrofishing. Over the study period, 403 samplings were conducted, capturing a total of 43,888 individuals identified at the species level. For each fish species, abundance (*i.e.*, the number of individuals per sampling) data were averaged across sites for each year.

2.2. Fish biological and ecological traits

The sampled fish species were characterised with traits extracted from three resources: *www.freshwaterecology.info* (Schmidt-Kloiber and Hering, 2015), *www.fishbase.org* (Froese and Pauly, 2010) and *scholar.google.com* (Google Scholar sources). When trait data were missing at the species level, information was retrieved from the genus. We retained a total of 25 traits split into: (i) 13 ecological traits, sub-divided into 43 'modalities' (*e.g.* if the considered ecological trait is 'habitat', the different modalities correspond to the diversity of habitats which the species can occupy; Table S2) describing the environmental tolerance of species, and (ii) 12 biological traits with 37 modalities reflecting characteristics of species (Table S2; Devin and Beisel, 2007).

2.3. Community metrics

To investigate changes in the composition of the fish community over the investigated period (1984–2018), five commonly used taxonomic metrics were computed for each site and year: (i) total abundance, (ii) species richness, (iii) Shannon diversity, (iv) Pielou evenness and (v) temporal species turnover (Table S3; Baranov et al., 2020). Taxonomic metrics were computed using the R package 'vegan' (Oksanen et al., 2020). The turnover of overall communities, native communities and alien communities were calculated using the *turnover* function implemented in the R package 'codyn' (Hallett et al., 2020). In addition, we calculated the beta-diversity (*i.e.*, as a measure of the ratio between regional and local species diversity) across all sites sampled within each year as a proxy for taxonomic homogenisation using *beta.div.comp* function implemented in the R package 'adespatial' (Dray et al., 2022).

2.4. Trait metrics

To investigate trait changes in fish communities over time, all trait modalities (*i.e.*, ecological and biological) were 'fuzzy coded' with the *prep.fuzzy.var.function* following Chevenet et al. (1994) using the R package 'ade4' (Dray and Dufour, 2007). The fuzzy coding procedure indicates to which extent a taxon exhibits each trait category by proportionally scaling them between 0 and 1 (Schmera et al., 2015). This is essential as it simplifies the synthesis of trait information and enables the synthesis of diverse kinds of biological information (Baker et al., 2021). Then, four trait metrics: trait richness (TRic), trait divergence (TDiv), trait dispersion (TDis) and trait evenness (TEve; Table S3; Baker et al., 2021; Renault et al., 2022) were calculated using the *alpha.fd.multidim* function from the R package 'mFD' (Magneville et al., 2022). Trait metrics were computed for ecological and biological traits separately.

2.5. Abiotic and biotic predictors

Site-specific characteristics were used to investigate the spatiotemporal changes in fish communities. To assess the effects of climatic variables, we extracted the average daily temperature and precipitation of the 12 months before the sampling event from a gridded European-scale observation-based dataset for each year and site (spatial resolution: 0.1 °C; www.ecad.eu/E-OBS/; Cornes et al., 2018). Lastly, we estimated the richness and abundance of alien species in each year of each time series as biotic predictors to investigate their effects on the community.

2.6. Statistical analyses

To investigate changes in taxonomic and trait composition of communities over time, canonical analysis of principal coordinates (CAPs) were performed based on the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). The CAPs were based on (i) species abundance and the community weighted means (CWM, *i.e.*, the mean value for each trait for the whole community weighted by the abundance of the species carrying the trait) of (ii) ecological and (iii) biological traits for each year. Further, permutational multivariate analysis of variance (PERMANOVA, permutations = 9999) based on the Bray-Curtis dissimilarity index were performed using *adonis2* function of the R package 'vegan' (Oksanen et al., 2020) on the species abundance matrix to identify the significance of abiotic (*i.e.*, latitude, temperature, precipitation) and biotic predictors (*i.e.*, alien species abundance and richness) and then the significance of ecological and biological trait modalities. Then, two PERMANOVAs (Bray-Curtis dissimilarity index, permutations = 9999) were separately performed on the matrices of the ecological and biological traits CWM to identify the significance of abiotic and biotic predictors.

Finally, taxonomic and trait metrics as well as climatic variables were modelled as the response variables over time. In addition, we identified periods in which community and trait-based metrics significantly changed over time by fitting an autoregressive AR (1) process (Nathan et al., 1999) for the residuals enabled the computation of derivatives of fitted splines using the method of finite differences to estimate the rate of change (slope) in the fitted smoother. This produced diagnostic plots of the time series with which periods of significant changes were identified and superimposed within the respective time series upon the respective trends over time (Simpson, 2018). Based on the results from the autoregressive models we identified significant changes to have occurred in ~2010. Accordingly, we splitted the study period into two (1984–2010: 25 years; 2010–2018: 8 years; Fig. S1) to identify the effects of alien fishes in the community. Taxonomic and trait metrics were modelled using the gam function from the R package 'mgcv' (Wood, 2021). All metrics were modelled using a negative binomial distribution except for species abundance and richness, modelled using a Poisson and Gaussian distribution respectively. Hence, each model was composed of the specific response variable (*i.e.*, taxonomic, biological and ecological trait metrics) and the explanatory variables: 'year', 'latitude', 'temperature' and 'precipitation'. Considering non-linear trends over time, our models included a cubic regression smooth spline for the predictor "year" (Wood, 2006) and a smoothed spline for abiotic predictors.

All analyses were conducted in the R environment, version 4.1.1 (R Core Team, 2021). The level of significance was set at $\alpha < 0.05$.

3. Results

Over the 35 years of this study, 43 fish species (32 native and 11 alien species) were caught in the lower part of the Rhine river (Table S4). The Cyprinidae was the most diverse family in terms of species (20 out of the 43 sampled species), followed by Salmonidae (4 species), Gobiidae (4 species) and Percidae (3 species). The 12 remaining families were represented by a single species (Table S4; Fig. S2). Over the studied period, the average annual temperature and precipitation increased by ~0.94 °C (~ 0.03 °C year^{-1}) and ~ 0.26 mm (~0.008 mm year^{-1}), respectively. While temperature fluctuated throughout the period, peaking in 2006, precipitation steeply inclined after 2010 (Fig. S3).

3.1. Compositional changes in communities over time

Between 1984 and 2018, total community richness increased by 49 %, albeit declining between 2004 and 2010 before increasing again until 2018 (Fig. 2a). Starting from 198 individuals/m^2 in 1984, the overall community

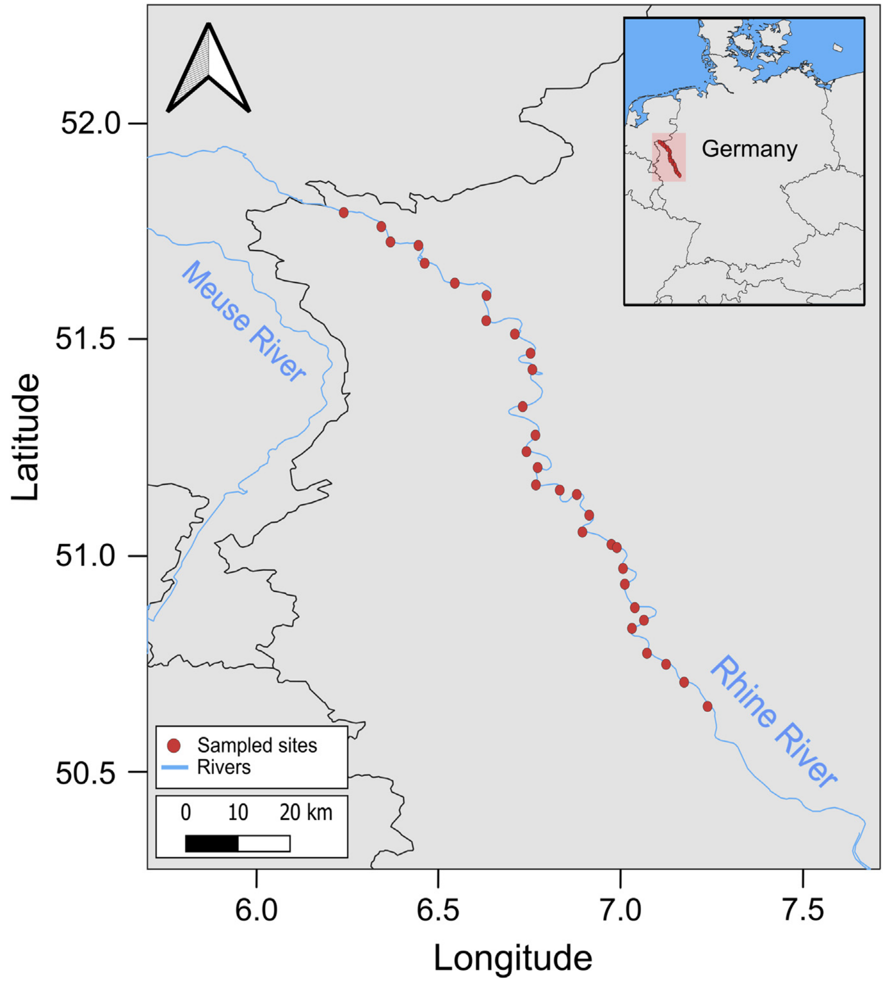

Fig. 1. Representation of 31 fish sampling sites along the Rhine river (Germany).

abundance largely declined to 23 individuals/m^2 in 2010 (−88 %), and then consequently increased by 678 % up to 180 individuals/m^2 until 2018 (Fig. 2b). Despite the slow increase at the beginning of the studied period, the richness and abundance of alien species considerably increased after 2010 (Fig. 2) and peaked in 2013 with a maximum of 8 alien species and again in 2018 with 7 alien species. The common carp *Cyprinus carpio* (first recorded in 1993), the rainbow trout *Oncorhynchus mykiss* (first recorded in 1998) and the European catfish *Silurus glanis* (first recorded in 2004) were the first alien species that were detected and successfully established in the studied stretch of the Rhine river (Table S4). While *C. carpio*, *O. mykiss*, and *S. glanis* represented 5.0–8.3 % of the total species richness before 2006 (Fig. 3a), their abundance remained negligible (0.1–0.4 %; Fig. 3b). In 2010, the abundance of five identified alien fish species increased to 14.9 %. In the period 2010–2013, six novel alien fish species established in the river: the pumpkinseed *Lepomis gibbosus*, the monkey goby *Neogobius fluviatilis*, the bighead goby *Ponticola kessleri*, the round goby *N. melanostomus*, the topmouth gudgeon *Pseudorasbora parva*, and the European bitterling *Rhodeus amarus* (Table S4), constituting a total of 29.6 % of the total species richness and 52.1 % of the total communities abundance in 2013 (Fig. 3).

The establishment of the six novel species increased alien species richness, which peaked in 2018 (30.4 %; Fig. 3a), alongside with their abundance, totalling 69.9 % in 2015 (Fig. 3b). Considering solely the alien community, species from the genus *Neogobius sp.* were first detected in 2010. In this genus, *N. melanostomus* dominated the alien fish community in 2018 (98.25 % of the total alien communities abundance, Fig. 4b). For the native fish communities, the roach *Rutilus rutilus* was the most abundant species at the beginning of the study period (75.14 %, Fig. 4a) and declined sharply in 2010 (2.30 %). The bleak *Alburnus alburnus*, which represented 1.76 % of the total native community abundance in 1984, and the ide *Leuciscus idus*, 1.52 % in 1993, became more abundant in 2018, respectively occupying 24.47 % and 22.00 % (Fig. 4a).

The communities' beta-diversity increased until 2010 before decreasing toward 2018 (Fig. S4). The total community turnover remained constant over time (Fig. 5a), with the turnover of the native fish communities slightly increasing in recent years from 0.48 to 0.60, albeit being non-significant ($R^2 = 0.135$; $p = 0.238$; Fig. 5b). The turnover of the alien fish community decreased significantly after 2006, from 0.89 to 0.34 ($R^2 = 0.210$; $p \leq 0.01$; Fig. 5c).

The applied ordination suggested a clear segregation in the community's taxonomic composition, with years after 2010 characterised by a significant increase in alien species richness and abundance, as well as changes in temperature and precipitation, as confirmed by the applied PERMANOVA (Fig. 6a; Table S5). Moreover, the applied PERMANOVA identified all community weighted means CWM (both ecological and biological) to significantly vary over time (Table S6), as within each trait, modalities of both ecological (Fig. S5) and biological traits (Fig. S6) changed in their relative prevalence, showing notable differences in their respective proportion before and after 2010. After 2010, the community was dominated by species characterised by smaller adult fishes and larvae, shorter life span, moderate relative fecundity, bigger eggs, and provision of parental care (Fig. S6; Table S6). Regarding ecological traits, the post-2010 community was characterised by fishes preferring rheophilic conditions in a demersal habitat, and feeding in benthic habitats (Fig. S5; Table S6). A comparable pattern was identified for the CWMs of ecological and biological trait compositions (Fig. 6b,c), as confirmed by the PERMANOVA

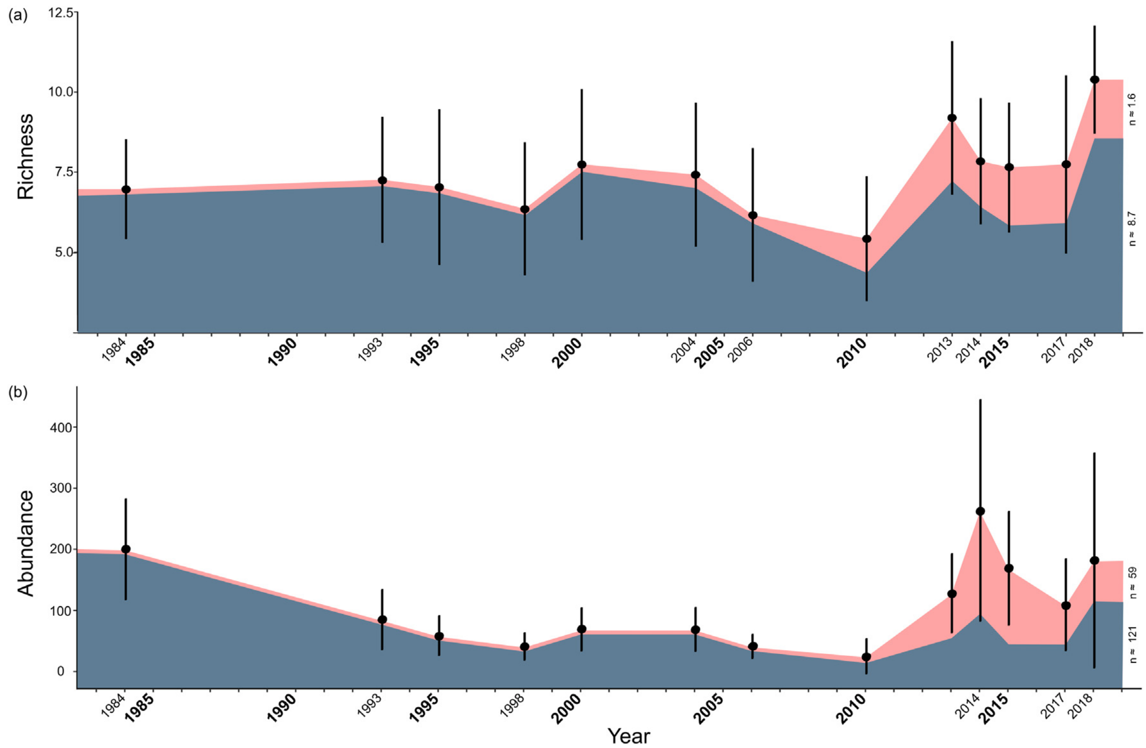

Fig. 2. (a) Total species richness and (b) total community abundance of the Rhine river fish community from 1984 to 2018 indicating the average values ± the respective standard deviation for each sampled year and the respective share of native (blue) and alien species (red). Numbers on the right indicate the (a) total species richness and the (b) total community abundance of native and alien fish in 2018.

(Table S7). Changes after 2010 were significantly related to an increase in alien species' richness and abundance as well as increases in temperature and precipitation (Fig. S3).

3.2. Temporal patterns in the community taxonomic and trait metrics

Without separating the time series into two distinct periods, we identified a fluctuation in richness (*i.e.*, a low around the year 2010 encompassed by two periods of high species richness), a decline in abundance, and an incline in Shannon diversity as well as inclines in both ecological and biological trait dispersion ($p < 0.05$; Fig. S7). Between 1984 and 2010, species richness did not change significantly (Fig. 7a; Table S8), whereas species abundance significantly decreased from on average 198 (± 82) to 23 (± 28) individuals/m^2 ($R^2 = 0.624$; $p \leq 0.01$; Fig. 7b). Species richness and abundance were significantly positively affected by latitude, temperature and precipitation (Table S8). No significant changes in Shannon diversity and Pielou's evenness were detected (Fig. 7c,d). With regard to trait metrics, only an increase in trait dispersion (TDis) of ecological traits was detected ($R^2 = 0.292$; $p = 0.01$; Fig. 7g).

After 2010, species richness and abundance increased significantly from approximately six to ten species, and from on average 23 (± 28) to 180 (± 176) individuals/m^2 (richness: $R^2 = 0.425$; $p \leq 0.01$; abundance: $R^2 = 0.731$; $p \leq 0.01$; Fig. 7a,b). No further significant change was detected (Fig. 7; Table S8). While species richness after 2010 was positively related with latitude, the identified increase in abundance was primarily driven by the increasing richness (and abundance) of alien species as well as an increase in temperature, precipitation, and latitude. Changes in Shannon diversity and Pielou's evenness were only significantly negatively related to the abundance of alien species (Table S8).

4. Discussion

The direct and indirect impacts of alien fishes and meteorological conditions are major drivers of biodiversity loss in freshwater ecosystems worldwide (Villéger et al., 2014; Gallardo et al., 2016; Bellard et al., 2018; Haubrock et al., 2020), often leading to taxonomic homogenisation (Olden et al., 2004; Pilotto et al., 2020; Haubrock et al., 2022). Our data, collected with a standardised protocol over the period 1984–2018, revealed significant changes in taxonomic and trait composition following the introduction of alien fishes after 2010 and concomitant changes in climatic conditions. We further identified changes in community composition following declines in the richness and to some extent also the abundance of native communities until 2010, before indicating taxonomic homogenisation, while in the case of the abundance—after alien fish species were detected to dominate in 2015— reached levels comparable to those measured in the first year, while richness reached a considerably higher level. While climatic changes (*i.e.*, in temperature and precipitation) likely benefited some alien species reflecting characteristic traits, these however did not determine the transition to a community dominated by aliens as both variables expressed no period of significant change during the study period (Fig. S1m, n).

4.1. Patterns in community composition before 2010

Trends in the abundance and richness of alien species can shift following external changes (Rahel and Olden, 2008; Früh et al., 2012), and have destabilising effects on invaded communities (Cardoso and Free, 2008; Strayer et al., 2011). The three alien fish species already present before 2010 in the Rhine river (*C. carpio*, *O. mykiss*, and *S. glanis*) are well-known for their substantial impacts on ecosystems and native species (*e.g.* through habitat degradation, competition, predation and the spread of diseases; Cambray, 2003; Copp et al., 2009; Gherardi et al., 2011; Guillerault et al., 2015). Yet, their abundances remained at relatively low levels (<0.5 % of the overall community abundance), whereas these species can reach considerably high biomasses with detectable impacts (Driver, 2005). The overall and significant decline in native species abundances by −90 % is however unlikely to have occurred due to their presence (Copp et al., 2009). Consistent with this assumption, several studies have reported that

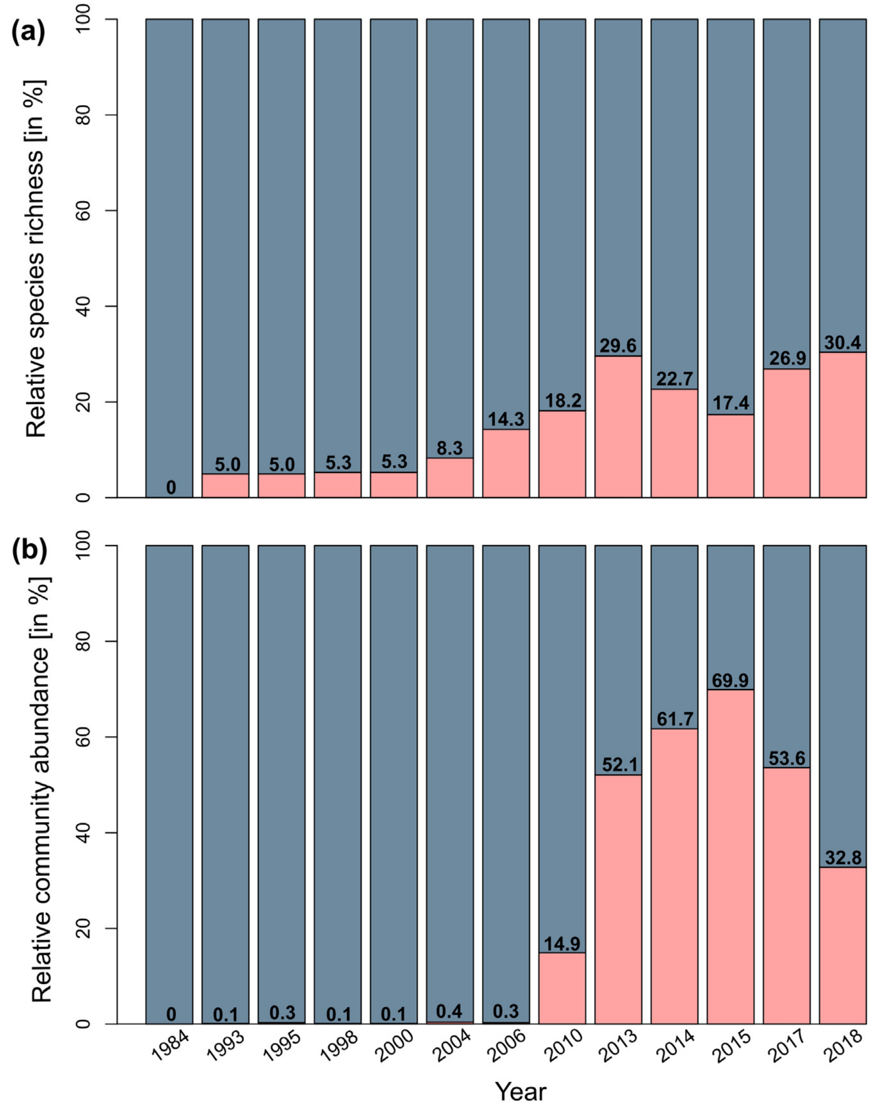

Fig. 3. (a) Relative species richness and (b) relative community abundance of native (in blue) and alien (in red) fish species of the Rhine river from 1984 to 2018.

the impacts of poorly abundant alien species on communities are often undetectable or absent (Parker et al., 1999; Ricciardi, 2003; Thiele et al., 2010). Rather, there could be additional stressors not encompassed by our data, *e.g.* anthropogenic alterations in the water quality of the Rhine river (Tittizer, 1997; Van der Velde et al., 2000), leading to a decline in native species and increasing diversity across sites. Changes in climatic conditions or the nutrient load of the Rhine following improvements in the sewage treatment plants in the early 1990s (Malle, 1996) have limited the availability of prey (*e.g.* zoo- and phytoplankton), and this may partially explain the community composition pattern found (pers. comm. Nikola Theissen). The opening of the Rhine-Main-Danube canal in 1992 likely contributed further to the observed decline in native fish communities, as their composition and numbers considerably changed from 1993 onwards. While the direct presence of Ponto-Caspian species is unlikely, increased shipping and perturbation have likely contributed to the identified declines.

4.2. Patterns in community composition after 2010

In the Rhine river, the arrival of new alien species was likely linked to the opening of the Rhine-Main-Danube canal in 1992 (Tittizer, 1997; Bij de Vaate et al., 2002). Indeed, three out of the six alien fish species (*N. fluviatilis*, *P. kessleri* and *N. melanostomus*) are native to the Ponto-Caspian region, and it took 18 years before they arrived and established (Kottelat and Freyhof, 2007; Froese and Pauly, 2010). The introduction of other alien fishes (*L. gibbosus*, *P. parva* and *R. amarus*) is most likely linked to intensified aquaculture and angling (Kottelat, 2006; Kottelat and Freyhof, 2007; Froese and Pauly, 2010). It is, therefore, not surprising that our results suggest compositional changes (driven by the spatiotemporal spread of highly abundant Ponto-Caspian fish species) to have progressed along a latitudinal gradient. This finding however highlights the effectiveness of riverine ecosystems to facilitate the spread of alien species through the increase of propagule pressure (Lockwood et al., 2005; Cassey et al., 2018). Furthermore, the introduction of these alien species after 2010 led to profound changes in the taxonomic composition and homogenisation of invaded communities. While this is in line with previous studies (Van der Veer and Nentwig, 2015; Olden and Rooney, 2006), the overall communities' turnover remained stable due to a slight increase in the native species' turnover, and a decrease in alien species' turnover after 2010, depicting the process of alien species reshaping invaded communities.

After 2010, the richness of alien fish increased to ~30 % of the overall community richness, constituting up to 70 % of the overall abundance (an increase in the overall communities abundance from 2010 by +1031 % in 2014 or + 678 % in 2018) before declining by ~33 % and possibly

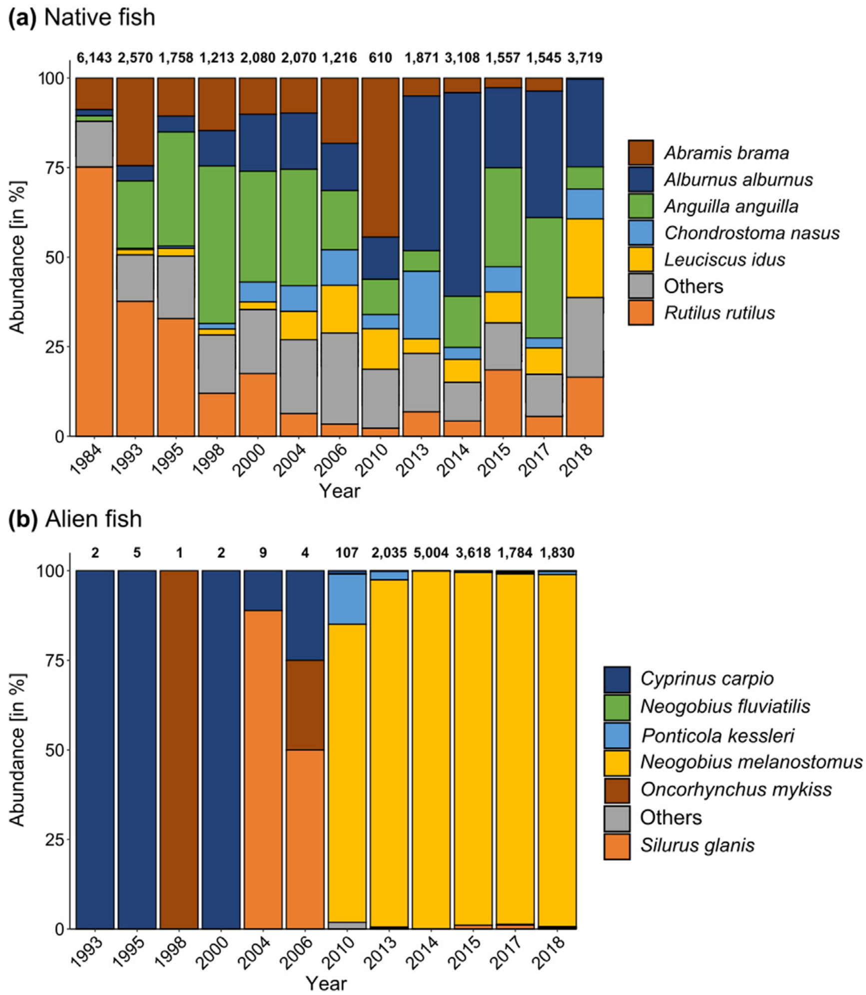

Fig. 4. Relative abundance of the six most abundant (a) native and (b) alien fishes during the study period. Number on top of each bar indicates the total abundance of all (a) native and (b) alien species collected in that respective year.

stabilising at lower abundance levels in 2018, resembling typical invader boom-bust dynamics (Strayer et al., 2017; Soto et al., 2023). Compositional changes have often been observed in the invasion of freshwater ecosystems (Clavero and García-Berthou, 2006; Gallardo et al., 2016; Haubrock et al., 2020). In our study, the observed changes can be ascribed to the establishment of six additional alien species between 2010 and 2013, with L. *gibbosus*, *N. fluviatilis*, *P. kessleri*, *N. melanostomus*, *P. parva*, and *R. amarus* contributing 69.9 % of the total community abundance in 2015. Although all of these are comparably small species (≤ 20 cm), they can reach high densities and thus, biomass, accompanied by notable impacts to invaded ecosystems (see *e.g.* Britton et al., 2010; Števove and Kováč, 2016). These alien species probably benefited from previous declines of native species and environmental changes (Marvier et al., 2004; Früh et al., 2012; Heringer et al., 2020), while their added abundance has resulted in the overall community reaching comparable abundances to those measured in 1984 – underlining the turnover from native to alien species communities (Haubrock et al., 2020) – suggesting that total community abundances are somewhat limited due to the productivity of the ecosystem (Storch et al., 2018). Indeed, as ectothermic animals, fish species are sensitive to environmental changes (Magnuson et al., 1979). Several studies have highlighted the negative impacts of temperature increases and precipitation shifts on native fish communities (Magnuson et al., 1979; Marchetti and Moyle, 2001; Lamouroux and Cattanéo, 2006) but also on aquatic communities in general (Durance and Ormerod, 2007; Chessman, 2009; Heino et al., 2009). Yet, their effects remain difficult to predict (Haase et al., 2019; Baranov et al., 2020). Concomitantly, we found temperature and precipitation to incline over the studied period, consequently driving compositional changes in the investigated community. Although observed increases in temperature (~ 0.94 °C) and precipitation (~ 0.26 mm) seem low, even minor changes – as well as fluctuations – can lead to substantial (*i.e.*, seasonal) changes in native communities (Magnuson et al., 1979; Lamouroux and Cattanéo, 2006) and benefit alien species (Rahel and Olden, 2008; Radinger and García-Berthou, 2020). As such, the increase in water temperature has likely permitted invasive fish species to cross physiological thresholds that were formerly limiting or slowing down their biology.

The introduction of alien species after 2010 induced further changes in the community's traits composition. These were mainly driven by the alien species *N. melanostomus*, which dominated the communities' abundance since the first year it was observed by contributing up to ~98 % of the total abundance of alien fish in 2018. The dominance of *N. melanostomus* which can severely impact invaded ecosystems (Kipp and Ricciardi, 2012), may be linked with the demonstrated presence of Asian clam *Corbicula fluminea* in Rhine river (Merschel and Bau, 2015), used as its main food resource (Nagelkerke et al., 2018; Coughlan et al., 2022). Other alien fish species not belonging to the *Neogobius* genus were observed with < 100 individuals throughout the entire period. This dominance of *N. melanostomus* suggests that comparably less abundant species occupied a less dominant role (Grabowska et al., 2019). However, it is possible that the sampling method applied here (*i.e.*, electrofishing) was not adequate to capture the total abundance, *e.g. C. carpio* or *S. glanis*, which tend to occupy deep benthic zones. For this reason, it is possible that the abundances of these species

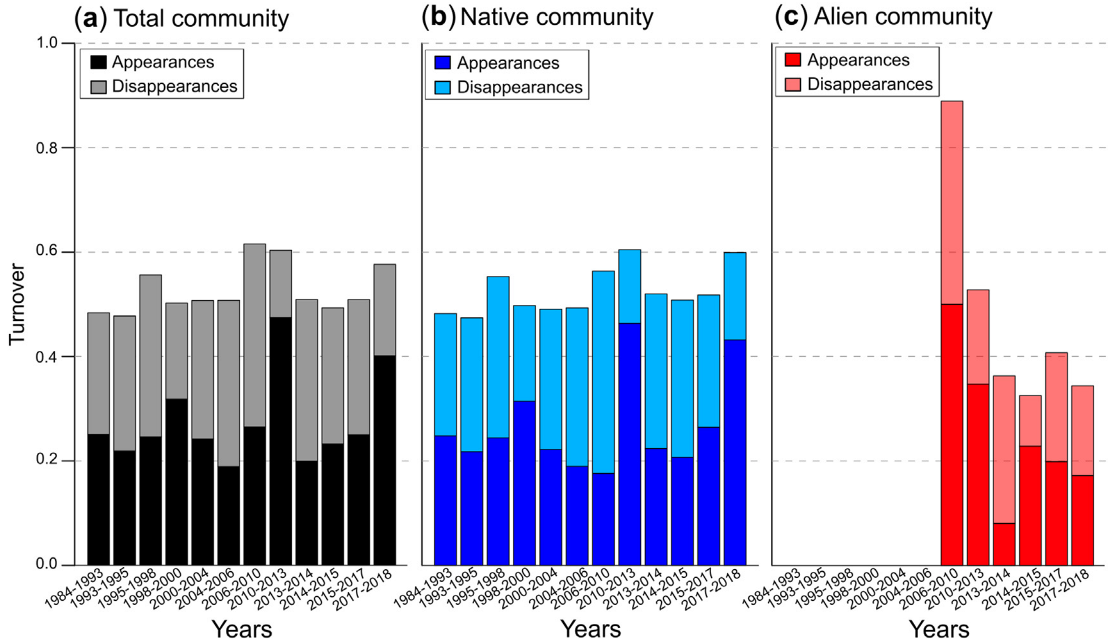

Fig. 5. Temporal turnover rate displaying appearances and disappearances of fish species in the Rhine river from 1984 to 2018. (a) Overall turnover in the whole community. (b) Turnover for native fishes. (c) Turnover for alien fishes. Please note that there was no detectable turnover in the alien community before 2006 despite the presence of several, continuously present alien fish species.

were underestimated (compared to the abundances observed by Singh et al., 2010 or Šmejkal et al., 2015).

4.3. Patterns in trait composition

Taxonomic changes in communities over time are often accompanied by trait changes (Baker et al., 2021; Haubrock et al., 2020; Liu et al., 2022). Here, we found trait changes to follow a similar pattern to the shift in taxonomic composition, with the communities' trait structuring driven by alien species richness and abundance, as well as changes in temperature and precipitation. On the other hand, no significant changes in trait metrics were observed in parallel to compositional changes. This result is peculiar, as it contrasts with other studies showing alien species simultaneously leading to both taxonomic changes and functional homogenisation (Pool and Olden, 2012; Villéger et al., 2014; Pilotto et al., 2022). However, functional homogenisation may be hard to detect in the early stages of an invasion, in particular during the establishment and possible lag phase, which may explain the discrepancy of our results with the available literature. This additionally stresses the importance of computing different diversity indices to properly prove impacts of alien invasions on recipient communities.

In the present work, the only trait metric changing over time was trait dispersion (TDis) of ecological traits before 2010. Often, TDis is expected to increase at the onset of the invasion process, in particular when alien species introduce novel traits which extend trait space (Renault et al., 2022). Yet, this metric rose before alien species started to invade the investigated communities, and rather accompanied the increase in beta-diversity. Beta-diversity is widely known to increase when the studied habitats become more heterogeneous, augmenting dissimilarity, and likely increasing the dispersion of species traits that cope with a large diversity of environmental conditions. The demise (at least in abundance, also evidenced by the temporal species turnover analysis) of ecologically similar species in the native community is consistent with this assumption. This has increased trait divergence (TDiv) among species from the different habitats, in addition to removing the less adapted individuals (species). After 2010, TDis remained stable, even if beta-diversity declined, and confirmed the maintenance of species' TDiv among habitats.

Other ecological and biological trait metrics were stable over time, providing unexpected, yet interesting insights. The non-significant changes in trait richness indicate that the demise of species carrying a certain set of traits is accompanied by acquiring new (alien) species carrying new sets of trait modalities not expressed by the native community (McGeoch and Jetz, 2019). Furthermore, it should be considered that due to its zoogeographic history, the natural fish communities of western Europe are relatively species-poor (Kottelat and Freyhof, 2007). As such, it is possible that introductions of alien species, which are often functionally and especially morphologically different (*e.g.* the asp *Leuciscus aspius*) as compared with other fish species, lead to an initial increase in trait diversity and richness. This does not mean that the demised species were functionally replaced, but rather that the losses in traits were counterbalanced by the invader carrying the same or similar traits, as well as bringing new traits into the community, resulting in a similarly occupied trait space. In other words, invaders may have a high degree of functional identity as compared with native species, suggesting, here again, that environmental filtering may have been strong and contributed to the selection of particular traits.

The shifts in ecological and biological traits observed after 2010 were mainly driven by one abundant alien species, namely *N. melanostomus*. This can explain trait metrics not indicating significant changes, albeit the high abundance (and thus also biomass and density) of this species likely impacting the studied sites. This lack of an identifiable trait change, however, could also be caused by a high redundancy between the traits of native and alien species (Loreau, 2004; Baiser and Lockwood, 2011; Villéger et al., 2011) or by alien species compensating for declining alien species by invading empty niches (Herbold and Moyle, 1986; Liew et al., 2016; Nagelkerke et al., 2018). High functional redundancy has been shown to increase both community resilience and ecological stability (Pillar et al., 2013; Biggs et al., 2020), and likely arises when environmental conditions are restricting (reduced phenotypic variation in trait expression and characteristics). The possibility of a high functional redundancy between alien and native species in the Rhine river could indicate that ecosystem functions (Vilà et al., 2010, 2011) were maintained despite the detected taxonomic turnover and alterations in the ratio of several expressed biological and ecological traits. This further suggests that alien species can, while simultaneously altering invaded habitats and recipient biodiversity when

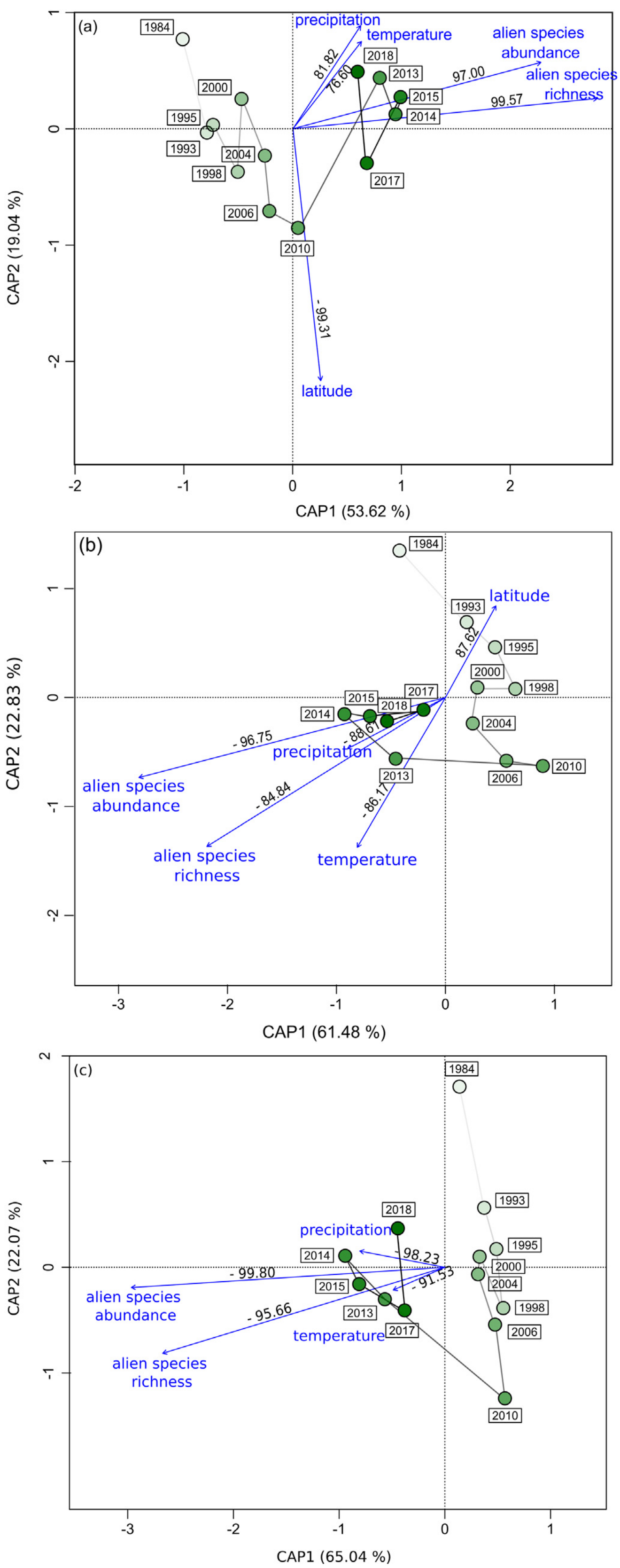

Fig. 6. Canonical analysis of principal coordinates (CAP) on (a) the taxonomic community composition (based on species abundances), the community weighted means (CWMs) of (b) ecological and (c) biological traits across years. Blue arrows indicate significant abiotic and biotic predictors. Values along the arrows indicate the correlation with the dominant axis.

becoming abundant, maintain functional roles or fill previously arisen voids. By contributing to stabilise community resilience in perturbed habitats, alien species may seemingly help to preserve an ecosystem's functioning in the short-term, although the long-term effects remain unknown raising the controversy of the effects of alien species (Schlaepfer et al., 2011; Russell and Blackburn, 2017). Finally, our study advocates the need for the inclusion of additional or new traits introduced with the establishment of alien fish species which are not considered in *www.freshwaterecology.info* (Schmidt-Kloiber and Hering, 2015), further increasing the resolution of functional changes (D'Andrea and Ostling, 2016).

5. Conclusion

Our results underline the importance of analysing long-term trends in invasion dynamics and facilitating drivers, which has often been limited by a lack of adequate long-term data or the non-continuity of annual sampling over time (Daufresne et al., 2004; Durance and Ormerod, 2007; Comte and Grenouillet, 2013; Jourdan et al., 2018; Haubrock et al., 2020, 2022). This has concomitantly limited insights into changing community functioning or ecological changes due to changes in alien species' trait composition. This was also the case in this work, as highlighted by the lack of information on the fish community between 1984 and 1993. Yet, having identified a disconnect between visible responses in taxonomic composition, and no detectable changes in functional metrics due to the invasion of alien species, suggests that both aspects pertaining to fish invasions must be considered in conjunction and separated at the same time. More specifically, taxonomic changes directly reflect biodiversity alterations, often at the expense of native species, which possibly cause changes in the occurrence of trait modalities and hence, potentially also functional changes, which can, but may not necessarily impact ecosystem functioning.

Our results further lead to the question, why native species declined pre-2010 and communities became more diverse, before alien species became abundant and increased taxonomic homogenisation. This finding highlights the importance of considering further variables to investigate the temporal effects of species introductions. These variables could reflect habitat fragmentation (Cowx and Collares-Pereira, 2002), the regulation of water flow (Poff et al., 1997; Albert et al., 2021), changes in the land use (Albert et al., 2021), pollution (Matthews et al., 1992; Taylor et al., 1993; Lappalainen and Soininen, 2006), the pressure of fishing (Cowx and Collares-Pereira, 2002; Butchart et al., 2010) – predictors which were not adequately available over the entire period to be considered in our models.

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.161486.

CRediT authorship contribution statement

Gwendaline Le Hen: Methodology, Formal analysis, Data curation, Writing – original draft, Writing – review & editing. **Paride Balzani:** Conceptualization, Supervision, Formal analysis, Writing – original draft, Writing – review & editing. **Peter Haase:** Resources, Writing – review & editing. **Antonín Kouba:** Resources, Writing – review & editing. **Chunlong Liu:** Resources, Writing – review & editing. **Leopold A.J. Nagelkerke:** Resources, Writing – review & editing. **Nikola Theissen:** Resources, Writing – review & editing. **David Renault:** Resources, Writing – review & editing. **Ismael Soto:** Conceptualization, Supervision, Formal analysis, Writing – original draft, Writing – review & editing. **Phillip J. Haubrock:** Conceptualization, Supervision, Formal analysis, Writing – original draft, Writing – review & editing.

Data availability

Data will be made available on request.

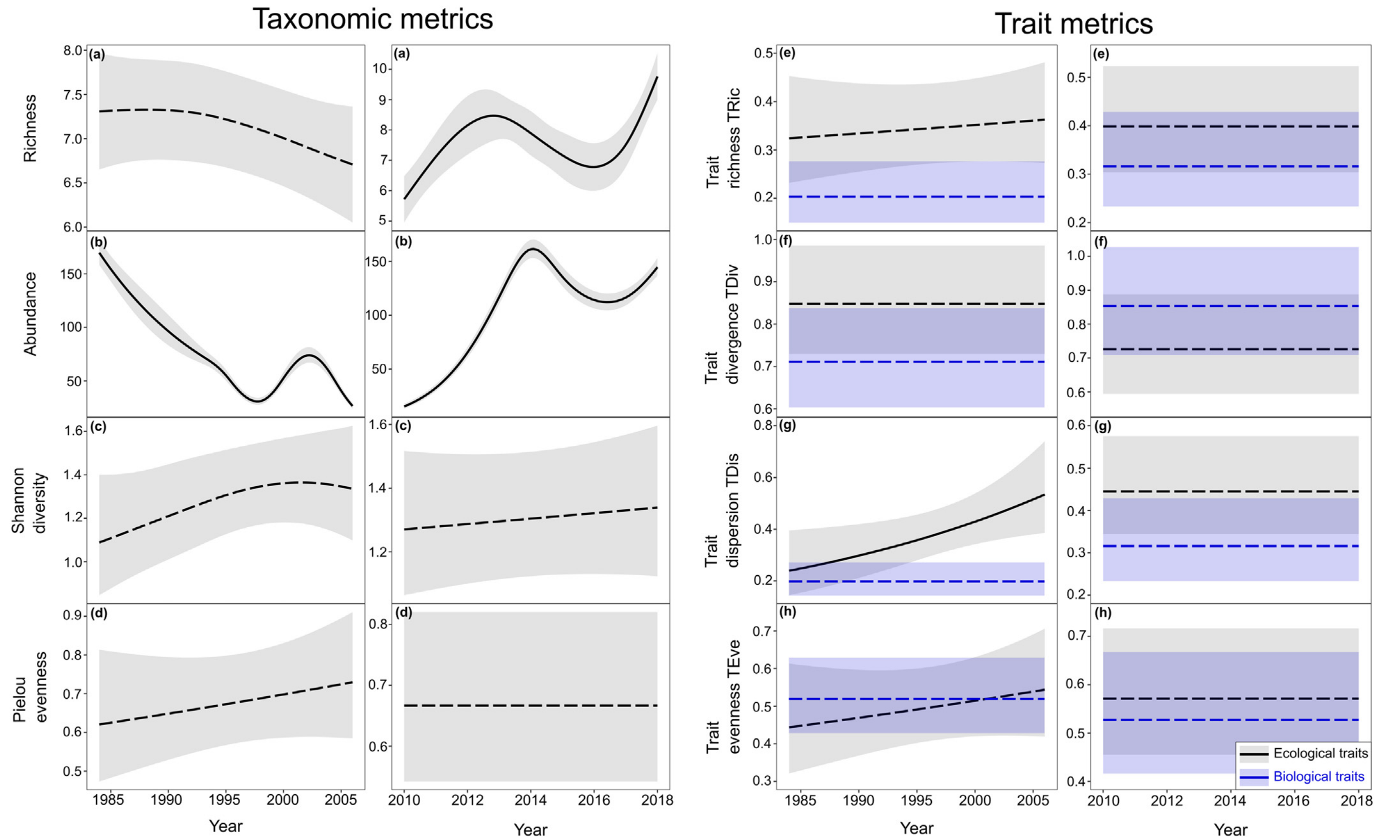

Fig. 7. Generalised additive models (GAMs) exploring the relationship between (a-d) taxonomic and (e-h) trait metrics of the studied communities. Trait metrics are divided into ecological (black lines) and biological (blue lines) traits. Solid lines indicate significant change over time, whereas dashed lines represent non-significant trends. See Table S8 for other significant predictors.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors express their sincere thanks to Michele Mugnai for helpful comments on a previous version of this manuscript and the "Commission Bourses de Mobilité à l'Étranger de l'Université de Rennes 1" and the ERASMUS + program for their financial support. The authors further acknowledge the help of Dr. Lep Omis. PH and PJH received funding from the EU Horizon 2020 project eLTER PLUS (Grant Agreement No 871128). IS is supported by the Grant Agency of the University of South Bohemia, project number 065/2022/Z.

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