Two centuries for an almost complete community turnover from native to non-native species in a riverine ecosystem

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Abstract
Non-native species introductions affect freshwater communities by changing community compositions, functional roles, trait occurrences and ecological niche spaces. Reconstructing such changes over long periods is difficult due to limited data availability. We collected information spanning 215 years on fish and selected macroinvertebrate groups (Mollusca and Crustacea) in the inner-Florentine stretch of the Arno River (Italy) and associated water grid, to investigate temporal changes. We identified an almost complete turnover from native to non-native fish (1800: 92% native; 2015: 94% non-native species) and macroinvertebrate species (1800: 100% native; 2015: 70% non-native species). Non-native fish species were observed ~50 years earlier compared to macroinvertebrate species, indicating phased invasion processes. In contrast, α-diversity of both communities increased significantly following a linear pattern. Separate analyses of changes in α-diversities for native and non-native species of both fish and macroinvertebrates were nonlinear. Functional richness and divergence of fish and macroinvertebrate communities decreased non-significantly, as the loss of native species was compensated by non-native species. Introductions of non-native fish and macroinvertebrate species occurred outside the niche space of native species. Native and non-native fish species exhibited greater overlap in niche space over time (62%–68%) and non-native species eventually replaced native species. Native and non-native macroinvertebrate niches overlapped to a lesser extent (15%–30%), with non-natives occupying mostly unoccupied niche space. These temporal changes in niche spaces of both biotic groups are a direct response to the observed changes in α-diversity and species turnover. These changes are potentially driven by deteriorations in hydromorphology as indicated by alterations in trait modalities. Additionally, we identified that angling played a considerable role for fish introductions. Our results support previous findings that the community turnover from native to non-native species can be facilitated by, for example, deteriorating environmental conditions and that variations in communities are multifaceted requiring more indicators than single metrics.
INTRODUCTION

Global changes are increasing the spread of non-native species (Capinha, Brotons, et al., 2013; Capinha, Larson, et al., 2013; Mazza et al., 2014), often causing irreversible ecological damages (Essl et al., 2020; Gozlan, 2008; Gozlan & Newton, 2009). Freshwater systems have been identified to be particularly vulnerable to invasions (Gherardi, 2007; Ricciardi & Rasmussen, 1999; Sala et al., 2000; Strayer, 2010). Several freshwater species, particularly fish, molluscs and crustaceans, have been intentionally or unintentionally introduced into lakes and rivers by humans (e.g. Haubrock, Kubec, et al., 2019; Mrugala et al., 2015). For example, the introduction of edible non-native crustaceans (e.g. Procambarus clarkii) and molluscs (e.g. Corbicula spp.) has frequently been related to cultural introductions (e.g. religious releases or the introduction of species native in the original area of a certain culture to maintain traditions, see e.g. Bodon et al., in press; Britton & Morton, 1979; Cianfanelli et al., 2017; Counts, 1983; Liu et al., 2013), while the introduction of a broad spectrum of fish and other macroinvertebrate species is often related to stockings, ballast water of ships, aquaculture and recreational angling (Cambray, 2003; Savini et al., 2010).

According to the invasion meltdown theory (Crane et al., 2020; Simberloff, 2006; Simberloff & Von Holle, 1999), the successive introduction of non-native species can, above a certain threshold, facilitate the introduction of further non-native species, potentially increasing effects on native communities (Ellender & Weyl, 2014). Investigating effects of such frequent non-native species introductions in freshwater ecosystems, however, generally suffers from a lack of appropriate long-term data that are needed to reconstruct introduction events (Strayer et al., 2006) as well as the resulting changes in the (native) community (Haubrock, Azzini, et al., 2019; Haubrock, Balzani, et al., 2019). Historical notes on the occurrence of non-native species play an important role as they can allow to reconstruct a timeline of species introduction and to reliably approximate species population trends (Bried & Siepielski, 2018; Bucharova & van Kleunen, 2009; Carlton, 2009). Such temporal information retrieved from early natural history collections, scientific records, surveys or citizen science (Horns et al., 2018) often are based on presence/absence data, which can potentially be used to compare species occurrences over time (Pollock, 2006). Nevertheless, such information must be carefully evaluated due to the often unclear origin and the sampling method applied.

Temporal changes in community composition triggered by frequent introductions of non-native species not only affect the taxonomic composition and diversity of a community but also its trait compositions. Traits at the community level have been used to predict and explain species invasions and are argued to indicate competitive processes through the displacement of native by non-native species in trait-niche space (Blonder, 2018; Lamanna et al., 2014). Moreover, previous studies have shown that traits play an important role in outlining species-specific behaviours and local adaptations, such as adaptive feeding behaviour due to, for example, emergent multiple predator effects (e.g. Barrios-O’Neill et al., 2014; Lindqvist & Huner, 2017). Of particular interest is the introduction of new traits through new species, such as a higher fertility (e.g. Bishai et al., 1974; Marchetti et al., 2004; Usher, 1986) elevated abiotic tolerances (Copp et al., 2009; Gherardi, 2006), novel defences or predation techniques (Bosher et al., 2006; Fine et al., 1997; Kimbro et al., 2009). Moreover, non-native species can alter the trait compositions of native species with specific traits potentially disappearing due to increasing competition (Brown et al., 2002; Mangla et al., 2011) or resource partitioning (Haubrock, Azzini, et al., 2019; Jackson et al., 2014). Such studies indicated that the analysis of species traits can elucidate important biotic interactions between native and non-native species. However, the dynamics of trait composition through time have not gained sufficient scientific attention and remain mostly anecdotal (Fox et al., 2007; Lindqvist & Huner, 2017). This is particularly true in the context of multiple introduction events (Chapple et al., 2012) and in comparative analyses across different biotic groups.

One ecosystem where information on the temporal course of fish and macroinvertebrate species introductions does exist is the Arno River in Tuscany (Italy), which is known for its anthropogenic usage and economic importance for the development of the city of Florence (Masters, 1998; Rinaldi & Simon, 1998; Sznura, 2010). We compiled presence/absence data for fish and macroinvertebrate species (molluscs and crustaceans) from the Arno River between ~1800 and 2015, as well as their species-specific trait information and analysed temporal changes in species and trait composition for the two biotic groups. In particular, we calculated changes in (a) α-diversity and temporal turnover, (b) trait modalities as a prerequisite to (c) functional composition, functional metrics and resulting niche space to understand whether non-native species occupy an empty or occupied niche, which would inform on competition dynamics. Finally, we (d) inferred and discussed potential drivers of these changes. For the latter, we faced the common issue of lacking continuous information on environmental variables over such a long period of time. We thus compensated for this using changes in traits that reflect changes in certain environmental conditions as proxies, and by compiling information on environmental change using historical notes.

We hypothesized (i) a significant temporal turnover in species over the past 215 years driven by the successive introduction of non-native species. We further hypothesized that this turnover is concomitant with (ii) an identifiable turnover in trait modalities and changes in the niche space of the biotic assemblages. Moreover, we tested two (partially) competing hypotheses: (iii) non-native species introduced novel traits, hence occupying empty niche space, or (iv) non-native species did not introduce new traits, resulting in overlapping or partially overlapping niche space with native species.

**KEYWORDS**

Arno River, fish, functional redundancy, hydromorphology, invasion, macroinvertebrates, time series analysis, traits
2 | METHODS

2.1 | Study site

The Arno River is the second largest river in Central Italy with a length of 241 km and a watershed of approximately 8,200 km². Its cultural usage is tightly linked with the history and development of the city of Florence (Supplement 1). It has a mean annual discharge of about 110 m³/s (Nocita & Zerunian, 2007) and a typical Mediterranean hydrological regime with severe flow reductions during summer. In Florence, the Arno River (Figure 1) is sectioned by various weirs and exhibits a high density of aquatic vegetation during spring, but a sparse riparian vegetation along the riverbanks. With the use of floodgates, the water regime is controlled during winter periods to prevent floods and to regulate water levels during dry periods in summer. Mean summer and winter water temperatures of the Arno River in the city of Florence are 29.6°C and 11.1°C, respectively (Supplement 1).

2.2 | Collection of species presence data and trait information

We collected historic and contemporary literature, as well as museum records, on the presence and absence of fish and macroinvertebrates within the inner Florentine stretch of the Arno River (Figure 1). Moreover, we consulted local historians, naturalists and experts (Elena Tricarico, Nicola Fortini, Annamaria Nocita) to identify suitable literature to complete the datasets (Supplement 2). The collected records and the samples of the historical collections kept at the Natural History Museum of Florence included information on native species as well as the time of introduction in the Arno River and the directly associated water grid (stream and spring tributaries). The information on aquatic insects was insufficient (Ruffo & Stoch, 2005). Therefore, among macroinvertebrates, we restricted our analyses to crustaceans and molluscs (hereafter, 'macroinvertebrates'). The available data covered the years prior to ~1800, years within the periods of 1850–1900, 1900–1950, 1950–2000 and lastly the year 2015. Hence, for our analysis, we chose these time slices as they corresponded adequately with the available information.

Presence/absence data can be used as an indicative proxy to detect shifts over time. This is, because changes in abundance are often seen as 'early' signs of community change as abundance data can track smaller and initial stages of change (Bried & Siepielski, 2018; Horns et al., 2018). However, if changes are visible with presence/absence data, these are indicators of more profound differences within a community (Bried & Siepielski, 2018). We thus compiled presence/absence data on 38 fish species (12 native, 26 non-native), 15 molluscs (9 native, 6 non-native) and 8 crustaceans (6 native, 2 non-native) species (Table 1).

To analyse changes in trait composition during the transition from native to non-native communities in the Arno River, we downloaded the species- and genera-specific traits for the studied fish and macroinvertebrates species from www.freshwaterecology.info (Schmidt-Kloiber & Hering, 2015; Supplement 3). Specifically, we compiled different traits on habitat and region preference for fish species. Single fish traits were checked or completed using www.fishbase.org (Froese & Pauly, 2010) and Kottelat & Freyhof (2007). For macroinvertebrates, we compiled trait information covering habitat, region and saprobic preference parameters and life-history parameters. Missing values at the species level were supplemented using information from the genus level averaging the available species information. To every trait modality, an integer is assigned describing the affinity of each taxon to the specific trait modality. If the affinity of a species to a trait modality was not identified and there was no information available for the evaluation, a score of 0 was given for the respective modalities. In total, we analysed 19 traits with 65 modalities for fish and 25 traits with 146 modalities for macroinvertebrates (Supplement 4).
| Group       | Subgroup | Species                          | Common name          | Distribution status | Range       |
|-------------|----------|----------------------------------|----------------------|---------------------|-------------|
| Fish        |          | *Acipenser sturio*               | European sea sturgeon| Native              | 1800–1950   |
|             |          | *Alosa fallax*                   | Twall shad           | Native              | 1800–1950   |
|             |          | *Anguilla anguilla*              | European eel         | Native              | 1800–2000   |
|             |          | *Barbus tyberinus*               | Horse barbell        | Native              | 1800–1950   |
|             |          | *Cottus gobio*                   | European bullhead    | Native              | 1800–1950   |
|             |          | *Esox lucius*                    | European pike        | Native              | 1800–2000   |
|             |          | *Padogobius nigricans*           | Arno goby            | Native              | 1800–2000   |
|             |          | *Rutilus rubilio*                | South European roach | Native              | 1800–1900   |
|             |          | *Scardinius erythrophthalmus*    | Common rudd          | Native              | 1800–1900   |
|             |          | *Squalius squalus*               | Italian chub         | Native              | 1800–2000   |
|             |          | *Telestes muticellus*            | Vairone              | Native              | 1800        |
|             |          | *Tinca tinca*                    | Tench                | Native              | 1800–2015   |
|             |          | *Abramis brama*                  | Common bream         | Non-native          | 2015        |
|             |          | *Alburnus alburnus*              | Bleak                | Non-native          | 2015        |
|             |          | *Ameiurus nebulosus*             | Brown bullhead       | Non-native          | 1950–2000   |
|             |          | *Barbus barbus*                  | Common barbell       | Non-native          | 2000–2015   |
|             |          | *Barbus plebejus*                | Italian barbell      | Non-native          | 1950–2000   |
|             |          | *Blicca bijerkena*               | white bream          | Non-native          | 2000        |
|             |          | *Carassius auratus*              | Goldfish             | Non-native          | 1950–2000   |
|             |          | *Carassius carassius*            | Crucian carp         | Non-native          | 2015        |
|             |          | *Chondrostoma soetia*            | Italian nase         | Non-native          | 1950        |
|             |          | *Cobitis taenia*                 | spined loach         | Non-native          | 1800–2000   |
|             |          | *Ctenopharyngodon idella*        | Grass carp           | Non-native          | 1950–2000   |
|             |          | *Cyprinus carpio*                | Common carp          | Non-native          | 1800–2015   |
|             |          | *Gambusia holbrooki*             | Eastern mosquitofish  | Non-native          | 1950–2015   |
|             |          | *Gobio gobio*                    | Gudgeon              | Non-native          | 2000        |
|             |          | *Ictalurus punctatus*            | Channel catfish      | Non-native          | 2015        |
|             |          | *Lepomis gibbosus*               | Pumpkinseed          | Non-native          | 1950–2015   |
|             |          | *Micropterus salmoides*          | Black bass           | Non-native          | 2000        |
|             |          | *Padogobius bonelli*             | Padanian goby        | Non-native          | 2015        |
|             |          | *Perca fluviatilis*              | European perch       | Non-native          | 2000        |
|             |          | *Pseudorasbora parva*            | Topmouth gudgeon     | Non-native          | 2015        |
|             |          | *Rutilus pigus*                  | Pigo                 | Non-native          | 1950–2000   |
|             |          | *Rutilus rutilus*                | Roach                | Non-native          | 2015        |
|             |          | *Sander lucioperca*              | Zander               | Non-native          | 2000–2015   |
|             |          | *Scardinius hesperidicus*         | Rudd                 | Non-native          | 1950–2000   |
|             |          | *Silurus glanis*                 | European catfish     | Non-native          | 2000–2015   |
|             |          | *Squalius cephalus*              | European chub        | Non-native          | 2015        |

**Macroinvertebrates**

| Species       | Distribution status | Range   |
|---------------|---------------------|---------|
| *Belgrandia thermalis* | Native             | 1800–2000 |
| *Physa fontinalis*        | Native             | 1800–1900 |
| *Planorbarius corneus*    | Native             | 1800–1900 |
| *Planorbus carinatus*     | Native             | 1800–1900 |
| *Stagnicola fuscus*       | Native             | 1800    |

(Continues)
Changes in taxonomic composition and alpha diversity

In this study, we computed two common community metrics to investigate the changes within the fish and macroinvertebrate communities over the investigated period. These were the species richness (α-diversity), which is expressed as the total number of species per period and the temporal species turnover (estimated as the proportion of species gained, i.e. 'appearances', or lost i.e. 'disappearances', between two observations, using the R package 'codyn'; Hallett et al., 2014), which characterizes temporal shifts in the identities of occurring species and thus, community composition over time. Furthermore, we tested if the percentage of non-native fish and macroinvertebrates increased significantly over time using a correlation analysis (Spearman correlation). Spearman was preferred as it is a nonparametric test, which does not require data normality assumptions.

Changes in trait modality compositions

Considering the identified turnover in species composition due to the introduction of non-native species and the decrease or extirpation of native species, we investigated the changes in the proportion of individual fish and macroinvertebrate trait modalities during the study period. For this purpose, we tested for significant correlations (Spearman correlation) between the increase in the number of non-native species and the changing proportions of trait modalities for fish and macroinvertebrate species.

Changes in functional composition, metrics and resulting niche space

We used changes in functional metrics to describe changes in the Hutchinsonian niche space (n-dimensional hypervolume, with n being equal to the axes corresponding to species-specific requirements; Blonder, 2018), that is, niche differentiation (Blonder et al., 2018; D’Andrea & Ostling, 2016). In this context, different trait spaces reflect different community niches, and are hereafter referred to as niche space. The display of trait-based niche space can hence indicate an ecological differentiation among species, attributable to processes such as competition (Blonder, 2018).

Therefore, we quantified changes in community niche space within the individual biotic groups, using four metrics: functional trait divergence (FDiv; measure of variance of the species function, whereby clustering extent indicates niche differentiation; Mason et al., 2005), functional dispersion (FDIs; overall convex hull volume occupied by all occurring traits in multidimensional space), functional richness (FRic; descriptor of how much niche space is occupied by present species, measured as the number of unique trait value combinations in each period; see Supplement 4), and functional evenness (FEve; measure of nearest neighbour distance among species, indicating the regular distribution of species in occupied niche space; Schleuter et al., 2010; Villéger et al., 2008). Together, these metrics can depict shifting trends in a communities’ occupied niche space when displayed over time. Each metric was computed for a community’s respective time slice using the ‘dbFD.function()’ of the R-package ‘FD’ (Lailliberté et al., 2014) after ‘fuzzy coding’ standardization (Chevenet et al., 1994).
of the traits using the ‘prep.fuzzy.var.function()’ of the same package. We repeated this procedure for native and non-native species independently. To test for significant changes in these metrics, we applied a correlation (Spearman correlation) of the individual functional metrics over time. To display changes in native and non-native species’ niche space over time, we used a canonical analysis of principal coordinates (CAP; R-package ‘vegan’; Oksanen, 2007; Oksanen et al., 2019), which was run on ‘Gower’ dissimilarity (Gower, 1971) for native and non-native species’ traits and ‘Jaccard’ distance for information regarding the occurrence of species as it is adequate for presence/absence data (Anderson & Willis, 2003).

2.6 Identification of potential drivers

Changes in specific trait modalities over time can reflect a response to external stressors. Therefore, we conducted another CAP with the same specifications as before, but pooling native and non-native species. Upon this ordination, we fitted trait modalities that had nonlinear relationships with the principal coordinates to identify those modalities that correlated significantly with the ordination axes. Trait modalities included into this analysis were selected using backward selection until the minimal Akaike’s information criterion (AIC) was obtained. All analyses were initiated with a model containing all traits and second-degree interactions and conducted using the R-package ‘vegan’ (Oksanen et al., 2019).

Environmental data (i.e. on changes in hydromorphology, climate, land use and pollution) were not available for the entire period; monitoring of climate data sparsely covered the time since the mid-1940s (www.regione.toscana.it/documents/10180/23101/Cambiamenti-climatici-in-Toscana-1990-2015/). However, we were able to compile data on the growth of the city area of Florence (1800: 54 km²; 1900: 61.8 km²; 2015: 102.3 km²; www.istat.it), human population growth (1900: 205.589; 1950: 374.625; 1970: 460.912; 2000: 356.172; 2015: 377.207; www.istat.it) and historical changes in the use of the Arno River as an additional resource (Supplement 1). We matched and discussed available historical notes on changes in the river's hydromorphology and angling use in relation to the results obtained from the CAP.

3 RESULTS

3.1 Changes in taxonomic composition and alpha diversity

Over time, the α-diversity of fish increased (Figure 2a). The first non-native fish species, the common carp Cyprinus carpio, was already present in ~1800 (Fortini, 2018) and it has often been considered as naturalized or even native (Vilizzi et al., 2015). Many other non-native fish species occurred in 1900–1950 and their proportion in the community increased further throughout the studied period (Figure 2a; Table 1). The observed nonlinear change in non-native α-diversity (overall increasing towards 2000, followed by a slight decrease in 2015, Supplement 5) was identified as significant (Spearman correlation $r_{Sp} > .7; p < .05$). In contrast, native species decreased continuously with only the common tench Tinca tinca remaining until 2015. The overall temporal turnover (0.71) in all fish species indicated a directional change in community composition towards non-native species ($r_{Sp} > .7; p < .05$; Figure 2a). This change was reflected by more gains than losses in non-native species (Figure 2b).

The α-diversity of macroinvertebrates decreased nonlinearly with an initial drop in 1900–1950, followed by an increase in 1950–2000 and another decrease in 2015 (Figure 2). These underlying changes in the macroinvertebrate community occurred in a two-step process: In 1800, the macroinvertebrate community consisted exclusively of native species. By 1900–1950, various native species had already disappeared (loss of 17%; Figure 2a) while the majority of non-native macroinvertebrates appeared after 1900–1950 (1950–2000: 43%). Similar to the non-native fish species, the percentage of non-native macroinvertebrates increased significantly ($r_{Sp} > .7; p < .05$, Supplement 5). Both temporal turnover and gains of non-native macroinvertebrate species increased significantly over time ($r_{Sp} > .7; p < .05$), indicating a directional change in community composition (turnover = 0.77; Figure 2a).

For both, native fish and macroinvertebrate species, only losses but no gains were observed. For non-native fish and macroinvertebrate species, both gains and losses occurred, although gains dominated in the fish community (39 gains and 33 losses over the entire period) and losses dominated in the macroinvertebrate community (16 gains and 27 losses over the entire period; Figure 2b). As a consequence, the continuous increase in non-native species over time, fostered by introductions of non-native macroinvertebrate and fish species and paralleled by the decrease or extirpation of native species, led to an almost entire turnover in the investigated communities (Figure 2; Table 1).

3.2 Changes in trait modality compositions

We recorded a change in the proportion of several trait modalities through time (fish: 19; macroinvertebrates: 24). The majority of trait modalities correlated significantly with the increase in non-native fish and macroinvertebrate species (Supplements 6 and 7). Accordingly, 13 fish and 12 macroinvertebrate traits changed significantly due to changing trait modalities over time. For the fish community, these, for instance, indicated an increase in eurytopic rheophily but also significant changes in the utilized reproductive habitat, feeding habitat and diet, body length, fecundity (relative and female), parental care, shape and swimming factor (Figure 3). The macroinvertebrate community expressed comparatively more diverse trait modalities compared to the fish community. These
showed variations in ecological preferences (hydrological habitat, current and substrate preferences), saprobity, species maximum size, reproductive cycles per year, feeding habit and resistance form (Figure 4). Additionally, reproductive behaviour changed, indicating the loss of polyvoltine species and an increase in univoltine species.

3.3 Changes in functional composition, metrics and resulting niche space

Changes in functional metrics were identified (Table 2). While the overall functional richness of the entire fish community did not
change significantly over time \( (r_{Sp} > .7; p > .05) \), the functional richness of native fish species decreased significantly \( (r_{Sp} = -.924; p = .0025) \). Simultaneously, functional richness and functional evenness of non-native fish species increased significantly \( (r_{Sp} > .7; p < .05) \). The functional metrics estimated for the macroinvertebrate community varied similarly, with no overall significant changes over time \( (r_{Sp} = .62; p > .05) \). However, while the functional richness of native macroinvertebrates decreased significantly \( (r_{Sp} = .977; p = .004) \), no other metric changed significantly for non-native macroinvertebrates \( (r_{Sp} = .43; p > .05) \).

The niche space of the only non-native fish species (C. carpio; Linnaeus, 1758) present in the Arno River before \(~1800\) and \(1850–1900\) was outside the niche space occupied by native species (Figure 5). In the period \(1900–1950\), already \(61.7\%\) of the overall niche space (occupied by native or non-native species) overlapped between natives and non-natives. By \(1950–2000\), this overlap increased to \(67.9\%\). From 2015, the only native species present (T. tinca; Linnaeus, 1758) was outside the non-native species’ niche space. This pattern thus reflects a complete reversal of the state in \(~1800\) (Figure 5). As with fish, the niche space of the two non-native macroinvertebrate species that were first recorded in \(1900–1950\) were outside the niche space of the native macroinvertebrate species. By \(1950–2000\), \(29.8\%\) of the overall niche space (occupied by native or non-native species) overlapped between natives and non-natives. In 2015, this overlap decreased to \(15.3\%\) (Figure 5).

There are two main differences in changes in niche space patterns observed in fish and macroinvertebrates: First, non-native macroinvertebrate species occurred about \(50–100\) years later than in fish and the replacement process from natives to non-natives lagged accordingly. Second, the replacement process itself differed. As for fish, a much higher overlap in niche space among native and non-native species was observed than in macroinvertebrates. In macroinvertebrates, this overlap was much lower, as native and non-native macroinvertebrate species occupied different niche spaces.

### 3.4 Identification of potential drivers

The canonical analysis of principal coordinates (CAP) identified five trait modalities for fish as ordination defining (females maturity; protection with nester or egg hiders; spawning in winter time; reproduction habitat of rock and gravel spawners with benthic larvae; and reproduction habitat of non-obligatory plant spawner; Figure 6). Littoral species that spawn on gravel during winter were characteristic for the native communities before \(1900–1950\) and decreased after \(1950\). These were replaced by non-obligatory plant spawners. Coinciding with a decrease in winter spawning species, later maturation and nest guarding were traits introduced by, and characteristic for, non-native species communities after \(1900–1950\).

For macroinvertebrates, we identified seven modalities as being characteristic for changes among community compositions of
TABLE 2

| Group      | Time slice | Non-native | Native | All |
|------------|------------|------------|--------|-----|
| Macroinvertebrates | 1800–1900 | 3.81e-15  | 2.21e-03 | na  | 0.9291  | 0.923  | 0.9820  | 0.984  | 0.256  | 0.256 |
|            | 1900–1950 | 6.39e-13  | 0.9365  | 0.763  | 0.9311  | 0.9291  | 0.9270  | 0.992  | 0.165  | 0.161 |
|            | 2015      | 2.42e-12  | 0.8400  | 0.731  | 0.8400  | 0.8400  | 0.763   | 0.763  | 0.132  | 0.132 |

4 | DISCUSSION

4.1 | Changes in alpha diversity and temporal turnover

Studies investigating biodiversity change at several locations around the globe have found no consistent local decrease in $\alpha$-diversity across locations, despite local changes in community composition (Dornelas et al., 2014; Pilotto et al., 2020). The introduction of non-native species, which is among the leading causes of native biodiversity decline (Pyšek et al., 2020), might affect $\alpha$-diversity at local scales by keeping it either constant or even increasing it as invaders replace native species (Hermoso et al., 2011). In the case of the Arno River, we confirmed our hypothesis (i) that a temporal turnover occurred in the past 215 years. This turnover from native to non-native species was, however, accompanied by opposite temporal trends in $\alpha$-diversity for the two biotic groups. For fish, we found that the successive introduction of non-native fish species compensated the loss of native species richness. In contrast, the loss of native macroinvertebrates outweighed the gains from non-native species, and therefore $\alpha$-diversity decreased. Our results, therefore, confirm previous considerations that variations in species composition are more informative indicators of changes in biotic communities than $\alpha$-diversity metrics (Pilotto et al., 2020).

Considering that past monitoring methods were likely less efficient than modern approaches, it also is possible that several native species present in the early time periods may have been overlooked. This would result in a greater initial number of native species, and thus an even higher temporal turnover rate. Nevertheless, introductions for both groups started mostly after 1900 and the introduction history is known for several species that were introduced for specific purposes (see C. carpio: Balon, 1995; Silurus glanis: Economidis et al., 2000; P. clarkii: Kouba et al., 2014). Therefore, we are confident that our reconstruction of the freshwater communities of the Arno River for the studied periods is reliable.

Nonetheless, past and current species introductions are not sufficient to explain the ongoing biotic homogenization (i.e. spatially distributed communities becoming increasingly similar over time) of aquatic ecosystems. For instance, downstream sections of rivers are
more affected by non-native species than upstream sections. This is because many successful non-native species are more tolerant towards wider ranges of environmental conditions than native species (Früh et al., 2012a, 2012b) and disturbances are occurring more frequently in larger rivers than in upper river sections. This further indicates interactive effects between biotic invasions and other anthropogenic pressures in shaping freshwater communities.

4.2 | Changes in trait modality compositions

The information provided by the trait composition of communities is increasingly valued (Pyšek et al., 2009; Thuiller et al., 2006). For instance, Dencker et al. (2017) similar to Beukhof et al. (2019) used a limited selection of traits to investigate temporal and spatial incongruences to infer the effect of environmental drivers on the North Sea fish community. Despite the increasing appreciation and consideration of such trait information for temporal processes, traits have not been used to investigate the effect of species introductions on native communities over the entire invasion process (Theoharides & Dukes, 2007). In fact, the response of native species to non-native species introductions has rather being neglected (Buckwalter, 2016). The investigation of single snapshots in time (García-Berthou, 2007) results in an overall lack of information on other phases during the introduction or establishment of introduced species (Buckwalter, 2016; Theoharides & Dukes, 2007). Furthermore, several biological traits, particularly those indicating ‘euryoeciousness’ (i.e. the ability to live under variable conditions), were proclaimed to concur with the success of non-native species, despite not being tested using temporal datasets (Cuthbert et al., 2020; Devin & Beisel, 2007; Kolar & Lodge, 2001; Ricciardi & Rasmussen, 1998). In this study, we tackle this obvious gap for the first time, investigating changing trait modality occurrences and interactions in niche space. Following our hypothesis (ii), we concur that changes in trait modalities were identified as a direct response to the observed significant temporal species turnover.

The concurred temporal changes in fish traits indicate an increase in previously proclaimed euryoecious species. Euryoecious non-native fish species can adapt to various environmental conditions (Lenz et al., 2011; Marchetti et al., 2004), which often gives
them a competitive advantage over native species. Recently, Su et al. (2006, 2019), showed that established non-native fish species in various biogeographic regions were characterized by ‘extreme morphological traits’ and thereby differed from native but also non-established non-native species. In this regard, we also identified that a higher fecundity was expressed in successfully established non-native species (especially observed in fish species; Howeth et al., 2016). Exemplary species that represent these modalities are, for instance, *Pseudorasbora parva* (Temminck & Schlegel, 1846) or *S. glanis* (Copp et al., 2009; Gozlan, Andreou, et al., 2010). These results therefore confirm findings from Viola-Gispert et al. (2005), who stated that successful non-native fish species especially differ from native species in the expression of life-history and ecological traits.

Similar to fish, changes in macroinvertebrate traits also reflect a shift towards more euryoecious species (e.g. without preference for current velocities). Typical representatives are, for instance, *Gyraulus chinensis* (Dunker, 1848) or *Sinanodonta woodiana* (I. Lea, 1834) (Ohta et al., 2011; Spyra et al., 2012), which are generally less specialized with a tendency towards eutrophic rivers. In past studies, the effect of pesticides (Chiu et al., 2016) and increased fine sedimentation (Mathers et al., 2017) on macroinvertebrate traits were investigated. Both concluded that the complex expression in macroinvertebrate traits was adequate to mirror changes in communities or signal external stressors. Furthermore, we identified significant changes in all trait groups (region-related parameters, habitat preferences, saprobic preferences and life parameters), underlining the versatility of macroinvertebrate trait information.

4.3 | Changes in functional composition, metrics and resulting niche space

Changes in niche space have been used to infer competitive arising from species introductions at the community scale (Blonder, 2018; Lamanna et al., 2014), suggesting that in the presented study competitive processes between native and non-native fish and macroinvertebrates species led to a displacement of native species. However, recent advances in trait-based ecology indicate that, in some cases, differences among species traits can make competition stronger and increase the difficulty of coexistence (Blonder, 2018; Mayfield & Levine, 2010). Our analysis cannot discriminate between competing or coexisting species but the use of abundance data might help in future studies. This is because in presence/absence data only major changes over time, that is, the loss of a species with its species-specific traits, result in visible changes. With our presence/absence data, we could thus show an almost complete turnover in community composition of both biotic groups, paralleled by an almost complete turnover in niche space. The niche space of native and non-native fish species overlapped substantially, suggesting a potential increase in competition, eventually having resulted (among other possible factors) in the demise of native species and retreat of their niche space. Unlike fish, macroinvertebrates showed less overlap in niche space. This suggests the possibility of (a) direct competition that resulted in the retreat of native species, or (b) that changes in the environment created vacant niches, which were then occupied by non-native species. These observed changes in niche space for the two studied biotic groups confirm hypothesis (ii) that a turnover in species is reflected in shifting niche space. These observations also partially confirm hypotheses (iii) and (iv) as changes in niche space reflected progressing invasions that were initiated by introductions into un-occupied space. However, this has to be taken with caution as the underlying trait information did not cover novel traits (i.e. traits that are entirely unknown to the new system such as anti-predator defensive spines in *Lepomis* sp., Januszkiewicz & Robinson, 2007; or poisonous pectoral spines used for defence and stridulation in *Ictalurus punctatus*, Fine et al., 1997), but rather showed differences in expressed trait modalities among native and non-native species.

One possibility to explain the observed occurrence of non-native species outside the native species’ niche space is that an outside position facilitates its establishment and population growth due to a lower degree of overlap (i.e. competition) with native species. It can also be assumed that these pioneering non-native species introduced new trait modalities. However, it is not yet clear if they facilitated other non-natives by affecting native species (Simberloff, 2006) and lowering the communities’ ‘biotic resistance’ (Alfors & Jackson, 2014; Cuthbert et al., 2018) or by other facilitating interactions (Adams et al., 2003; Crane et al., 2020). The principle of functional redundancy (Rosenfeld, 2002) argues that if a species declines in its abundance, another species ‘takes over’. Therefore, the changing niche space might have made the community more ‘invadable’, because ecological functions within the community could have become vacant, thus ‘opening up’ space that could be more easily claimed by a non-native species due to the limited degree of competition (Pyron et al., 2017). Species introductions can also lead to top-down or bottom-up effects that, in turn, could initiate trophic cascades (Walsh et al., 2016). As such, it is possible that biotic homogenization as a process following successive introductions will also be echoed within niche space given sufficient time.

4.4 | Identification of potential drivers

The turnover within the two biotic groups and the niche spaces occupied by native and non-native species have severe ecological implications: introduced non-native species may compete with native counterparts, but with deteriorating environmental conditions over time certain combinations of traits might become inadequate. In turn, this generates a feedback-loop on prevalent competitions (MacDougall & Turkington, 2005; Pyšek et al., 2010, 2020). Thus, environmental conditions can affect the outcome of the introduction of non-native species. Such disturbance-induced changes may generate an equilibrium in traits despite the presence of non-native
species which can be explained by the principle of functional redundancy. However, as direct measurements of environmental variables over the entire study period were unfortunately unavailable, modeling their effects on the observed temporal turnover and changes in trait modality occurrences was not possible. We therefore infer the effects of environmental change on the biota by analysing historical reconstructions of the studied system and, indirectly, by discussing the changes in species trait modalities as a response to land use change (i.e. observed city and population growth, changing angling activities) and altered hydromorphology.

Non-native fish introductions generally relate to changing customs and angling use (Gozlan, Britton, et al., 2010). This is particularly true for the Arno River that has long been used as a food source and later for recreational activities (Zagli, 2003). The introduction of fish species between 1900 and 1950 matches the strong increase in the city area of Florence and its human population. Accordingly, local fishing associations were founded in that period, introducing non-native fish species to increase angling activities—not primarily by authorized stockings, but intentional and illegal releases by citizens (Bianco, 1995; Bianco & Ketmaier, 2001). Several non-native fish species introduced after 1950 were not able to sustain stable populations and vanished again as, for example, species like Micropterus salmoides (Lacépède, 1802) are bound to certain environmental conditions (i.e. turbidity for predation; Reid et al., 1999). The increase of non-native fish species can therefore be linked to the aforementioned intentional introductions (Su et al., 2019). It is therefore likely that the concomitant observed decline in native fish species was at least partially linked to the increasing presence of non-native fish species (Albins, 2015), indicated by the overlap into niche space. Non-native macroinvertebrate species introductions in the Arno River were, on the other hand, reported to have originated from accidental introductions, downstream spread (Tricarico et al., 2010) or cultural releases to practice native customs (Bodon et al., 2020; Gherardi et al., 1999; Gravili et al., 2010; Occhipinti-Ambrogi et al., 2011) and traditional cuisine (Cianfanelli et al., 2017; Pfeiffer & Voeks, 2008).

With the growth of the city of Florence in the past ~215 years, the hydromorphology of the Arno River changed significantly towards a deeper and more channelized river with increased turbidity and sediment transportation (e.g. impoundments; Adamek & Jurajda, 2001; bed material mining and loss of aquatic vegetation; Billi & Rinaldi, 1997). These changes, accompanied by the construction of weirs, continuously contributed to this change in hydromorphology over time accompanied by shifts in trait modalities and community niche space. Non-native fish have likely been favoured by the new hydromorphological conditions, for example, a decrease in stream velocity and reduced competitiveness of native species (Leavy & Bonner, 2009). This was echoed by a decrease in rheophilic and increase in limnophilic species. This increase in non-native fish species and the consequent incoming transport of larvae of non-native species or of specimens from other populations could have further compromised the genetic identity and survivability of native species (Manganelli et al., 2000; Marrone et al., 2019; Stoch & Bodon, 2014).

Fish traits can also respond to the introduction of weirs and thus a slower flow through changes in the traits ‘shape’ or swimming factor. Indeed, we observed a significant increase in shorter species with higher depth (shape factor 1) and consequently a decrease in longer species with higher shape factors. Furthermore, we identified a decrease in strong swimmers (swimming factor 1) and increase in other classes (particularly swimming factor 3) as defined by the ratio of minimum depth of the caudal peduncle to the maximum caudal fin depth in centimetre (Poff & Allan, 1995). In accordance with the observed increase in bad swimmers (swimming factor 3) within fish, the maximal potential size of macroinvertebrates and species with the ability to move on legs increased. These trait modalities can potentially be advantageous when competing with native counterparts in a slow flowing river, as observed by Vila-Gispert et al. (2005) in small Mediterranean streams. Furthermore, these traits can underlie the ability to spread, which can be a prerequisite for the invasiveness of non-native species (Ricciardi & Cohen, 2007).

The introduction of weirs, but also the associated straightening of the riverbed and removal of riparian vegetation, can induce particular changes in hydrological and substrate preference traits (Autorità di Bacino dell’Arno, 1996; Becchi & Paris, 1989; Billi & Rinaldi, 1997; Menduni, 2017). Such hydromorphological alterations, but also increased anthropogenic activities and wastewater management due to increasing populations (Karatayev et al., 2009) are commonly associated with an increase in pollution, low oxygen levels or an unnatural enrichment with nutrients (Klein, 1979; Wilson, 2015). Such conditions may be exacerbated by climate change that has increased the frequency of years with extreme water scarcity and low precipitation since the mid-1940s. Indeed, we observed an increase in α-mesosaprobic and polysaprobic macroinvertebrate species, underlining the effect of changes in the saprobity of the Arno River over time and reflecting ongoing environmental degradation. This was further mirrored in the retreating native macroinvertebrate niche space. The changes in trait modality occurrences as a response to changes in the hydromorphology of the ecosystem are mirrored in the disappearance of a major part of the occupied macroinvertebrate niche space without being replaced by non-native species. Compared to fish species, the higher variability in traits and modalities of macroinvertebrates, paired with the higher number of ecological preference traits as opposed to biological traits (e.g. stream zonation, hydrological preferences, substrate and current preferences, saprobity) led to a better representation of environmental changes in the macroinvertebrate niche space. This leads to the conclusion that macroinvertebrates are more adequate to infer environmental changes from changes in community compositions and trait occurrences, while fish traits might not reflect environmental conditions sufficiently.

In summary, whereas recreational activities and the use as a food source may be a substantial factor for introduced fish species globally and even on local scales, it does not suffice to explain the turnover in the macroinvertebrate community. The demise of native macroinvertebrate species might, aside from changes in hydromorphology and an increase in pollution, relate to biotic
interactions or the loss thereof. For instance, the demise of native fish species, and thus the reproductive dependency of various native molluscs (e.g. *Anodonta exulcera*ta Porro, 1838 and species of the genus *Unio* sp.) was shown to lead to the decline of the latter (McNichols et al., 2010). Furthermore for Unionidae, the introduction of fish, and the consequent incoming transport of larvae of native species or of specimens from other populations, can further compromise the genetic identity of autochthonous species (Manganelli et al., 2000; Marrone et al., 2019; Stoch & Bodon, 2014). Given that notable changes in the community occurred earlier for fish than for macroinvertebrate species, it is likely that the macroinvertebrate community will display higher non-native species gains than native species losses in the future, as observed from the fish community.

### 4.5 Management implications

In our study, we suggest that the combined effect of non-native species’ introductions and stream degradation (i.e. hydromor- phology, increased pollution) led to the dominance of non-native species (in line with Früh et al., 2012a, 2012b) and the demise of native species at the Arno River, which underlines the complexity of non-native species management. Indeed, Pyšek & Richardson (2010) highlighted that the management of non-native species has to face various emergent problems. These are (a) ‘secondary introductions’, that is, the rapid replacement of non-native species by other non-native species, (b) the ‘legacy effects’, meaning the long-lasting effects of environmental degradation caused by introduced species due to a measurable impact (e.g. elevated nitrogen levels in the soil following invasions by nitrogen-fixing plants; Yelenik et al., 2004) and (c) the negative effects of non-native species control attempts on native species (e.g. mesopredator releases as biocontrol agents leading to increased densities of intermediate predators with cascading down effects; Bergstrom et al., 2009).

In the light of the identified changes in niche space that accompanied the demise of native and rise of non-native species in the Arno River, we suggest that water managers should address the identified stressors to develop tailored mitigation measures. Management efforts could target environmental and biological conditions as indicated by the changes in trait space to promote the long-term survival of both native and non-native species (Laha & Mattingly, 2006) because these are more likely to coexist when they differ in natural history and microhabitat preferences (Adams & Pearl, 2007). In particular, the maintenance or restoration of suitable habitats may support the recovery of native species and limit the distribution of invaders (Adams, 1999; Adams & Pearl, 2007). The increase in habitat diversity, through the creation of temporal and spatial refugia, may mediate the interactions between native and non-native species by reducing competition pressure on native species and eventually favouring their long-term survival (Adams & Pearl, 2007; Schlaepfer et al., 2005). In areas with refugium and non-refugium habitats, native species could evolve or learn mechanisms surrounding invasions, ultimately persisting on their own within a few generations (Carroll et al., 2007; Wallach et al., 2015). Although rarely observed, such a case was described by Letnic et al. (2008), after 50 years and Kiesecker & Blaustein (1997) after 70 years. A further step, consisting in the temporary reduction of the invaders’ abundance, should be carefully considered to avoid the ecological release of nontarget species (Bissattini et al., 2018).

Our study shows that historical notes can be used to track and explain species replacement dynamics. We further show the worth in considering multiple indicators for the assessment of biodiversity change rather than a few selective metrics like α-diversity or biomass due to the multifaceted nature of community changes over time. For the future, we urgently need harmonized long-term ecosystem monitoring schemes that capture changes in biodiversity and environmental conditions (Haase et al., 2018; Mirtl et al., 2018).

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### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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