



Response of functional diversity of fish communities to habitat alterations in small lowland rivers

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Abstract

Functional diversity has proven to be more responsive than traditional taxonomic diversity to alterations for a wide set of communities, especially in aquatic ecosystems. Habitat alterations are among the most relevant causes of biodiversity loss in freshwater ecosystems, nevertheless their effect on functional diversity has been scarcely investigated so far. In this study, functional diversity of fish communities in the River Po basin, north Italy, were related to habitat quality at different spatial scales. Land use and riparian vegetation were identified as the most influent factors on freshwater fish functional diversity. On the other hand, habitat descriptors at smaller scale did not influence functional diversity of fish. The evidenced responses were driven by the contribution of exotic species, which maximized ecological niche occupancy, either by exploiting increased habitat heterogeneity or by interaction with native species. Moreover, traits filtering, disadvantaging large predators such as salmonids, was also observed in the studied communities, but likely this effect was related to other factors than habitat alterations. Overall, this study confirms that land use changes can be considered as valid proxies for anthropogenic alterations. Moreover, possible effects at ecosystem level, also related to the spread of exotic species, could be hypothesized, giving that traits mostly influencing the observed patterns of diversity in communities were related to trophic niche, a factor that has been associated with crucial processes like nutrient cycling or energy transfer.

Keywords Kurtosis · Skewness · Land use · Exotic species · Traits · Riparian vegetation

Introduction

Freshwaters ecosystems are highly affected by habitat loss or fragmentation, eutrophication, flow alteration, chemical pollution and invasive species introduction (Reid et al. 2019), which can result in loss of biodiversity (Dudgeon et al. 2006; Toussaint et al. 2016) and in altered ecosystems' structure and functionality (Alahuhta et al. 2019). Some of the most common pressures are those related to land use changes, including agricultural

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practices, which are often linked to various types of impacts, such as habitat destruction, chemical pollution, nutrient enrichment or even exotic species spread (Dudgeon et al. 2006).

In this context, freshwater fish communities are facing significant changes at different spatial scales, with declining taxonomic (Toussaint et al. 2016) and functional diversity (Villéger et al. 2014), resulting in significant impacts on ecosystem processes (Biswas et al. 2017). The quality of river ecosystems may be affected by direct (e.g. channel reshaping) or indirect (e.g. land use) impacts, acting at different spatial scales (Casatti et al. 2006) and strongly determining community composition. In fact, habitat changes may be consequence of impacts that are not only strictly related to local human intervention on river morphology or hydrology, but also at global (e.g. climate changes modifying hydrological cycles) and regional (e.g. agricultural practices generating increased solid transport) scales (Stoll et al. 2016).

Many protocols assess river habitat quality by analyzing the conservation status of macro and micro habitat components (Belletti et al. 2015). The relationships between these indices and the corresponding fish community composition may be indicative of specific impacts on communities. In particular, functional, instead of taxonomic diversity may be used to evaluate community composition. Functional diversity estimates the magnitude of the overall functional niche of communities, basing on ecological or morphological traits of species. Different metrics have been proposed so far (Mouillot et al. 2013), basing assessment either on presence/absence or abundance data, emphasizing the diversity of most abundant (i.e. functional dispersion) (Legendre and Laliberté, 2010), rare (i.e. functional richness) or functionally rare (i.e. functional originality, functional specialization) species (Grenié et al. 2017; Ricotta et al. 2016). Functional diversity analysis aims at addressing more specifically the relationships between niche availability, their exploitation by species, and their role in ecosystem processes (Villéger et al. 2017).

Functional diversity is itself subject to anthropogenic impacts. However, the influence of habitat quality on freshwater functional diversity has been scarcely investigated to date. Colin et al. (2018) found that habitat alteration increases fish functional specialization and originality, but the study was limited to species-poor communities and to a few general descriptors of habitat features. However, the same study also emphasized that regional factors, such as mean altitude, were largely more influent on functional diversity than habitat alteration.

Functional redundancy, that is the occurrence of multiple taxa sharing the same ecological traits and functions in a community, may improve ecosystem resistance and resilience to perturbations (Rosenfeld 2002). It is expected that, under taxonomic diversity reduction, functional diversity may remain consistent in a community with high redundancy (Biggs et al. 2020). Fish assemblages, in freshwater European ecosystems, comprise a relevant number of functionally unique species, which lower their redundancy and may increase their sensitivity to species loss (Teichert et al. 2017). This is true especially in areas affected by Pleistocene glaciations, or rich in endemisms, such as in the Mediterranean basin (Côte et al. 2019). Fish communities, impacted by anthropogenic factors, might also show an increase of functional homogenization (Toussaint et al. 2016), that is expected to determine the loss of rare or functionally extreme taxa.

Among the vast number of approaches developed so far to assess functional diversity, two conventional statistical moments, i.e. kurtosis and skewness, has been proposed recently to describe the statistical distributions of traits within a community (Enquist et al. 2017). These approaches can be used to infer the main processes shaping functional diversity of sets of communities (Enquist et al. 2017). For instance, environmental filtering,

niche differentiation or rapid response to environmental changes are expected to generate idiosyncratic distribution of traits, whose moments can be compared with the observed ones, by simulation analysis (Gross et al. 2021). The parameters describing traits-abundance distributions have demonstrated to be closely associated to several ecosystem functions, and to respond to environmental drivers (Gross et al. 2017). Thus, this makes statistical distributions of traits a modern and sensitive tool to investigate environmental changes.

In the present study, we compared functional diversity (richness, dispersion, redundancy, kurtosis and skewness of trait-abundance distributions) of fish communities located in small rivers of the River Po valley (North Italy) with the corresponding habitat quality. We considered pressure and effects at basin, at river or at microhabitat scale, and focused on the highly dense network of small, semi-natural watercourses characterizing intensively cultivated lowlands. The presented study was built on the River Po biogeographic district, that hosts highly diverse fish communities, rich of endemisms (Bianco 2014), which have shown to be very sensitive to human impacts (Stefani et al. 2020). More in detail, at least 35 species are considered native to the basin, including 3 euryaline and 6 migratory taxa. Among freshwater obligate taxa, 16 are considered endemic or sub-endemic. Recent surveys, however, indicated that at present no more than 30 riverine native taxa are still presently found, while 19 exotic and two para-autochthonous species have been recorded so far (Autorità di Bacino del Fiume Po 2008). Exotic species has been suspected to be more impacting on native freshwater communities than hydromorphological or chemical water quality (Castaldelli et al. 2013; Gavioli et al. 2018). Exotic taxa invasions have been found to be significantly influenced by regional drivers (i.e. climate and geomorphology), generating different invasion pathways. Thus, interactions between exotic species spread and habitat properties may be also supposed to influence native communities response to perturbations (Milardi et al. 2022a, 2020).

Aims of the present work were: 1) to assess the effects of habitat alteration on functional diversity and trait distribution of fish communities, highlighting trait specific sensitivity at different scales, 2) to find functional unicity or compensatory effects related to redundancy of communities, with a focus on the role of exotic species; 3) to unravel possible cascade effects of functional alterations on ecosystem processes.

Materials and methods

Fish census and habitat quality data

Existing fish census data for small lowland streams, of the central River Po plain (North Italy, River Po basin, Fig. 1), were collected from administrative documents (reports, surveys etc. dating from 2002 to 2008, summarized in Table S1, Supporting Information). Selected datasets were filtered including only censuses for which a parallel characterization of river habitat quality was available. We included data obtained by applying the “Indice di Funzionalità Fluviale” Index (IFF) (Siligardi et al. 2007). The IFF has been largely used in Italy, in the last decades, to monitor the ecological functionality of rivers at different spatial scales. The IFF index calculation estimates scores for 14 parameters at basin level (land use, riparian vegetation structure, width and continuity), at intermediate level (bank naturalness and erosion, transversal section naturalness, pools/riffles/meanders) or at small scale level (substrate composition and stability, organic detritus retention and degradation efficiency, macrophytes coverage, macrobenthos community). A separate score for each river

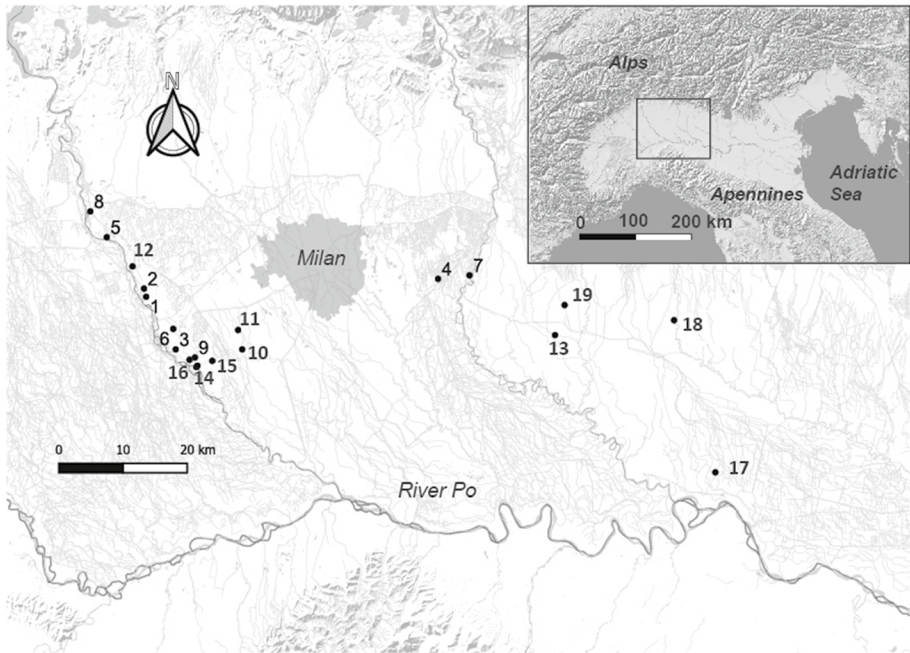


Fig. 1 Map of sampled watercourses for fish censuses and habitat assessment, with main and minor river network. Numeric codes correspond to the sampling sites detailed in Table S1, Supporting Information

bank is calculated, considering the possible differences on each side. In the present study, an average score for each parameter and for the final IFF index was estimated for each site. The analysis of macrobenthic community was omitted from the analysis, since it does not describe specific features of the river, but simply complements the river functionality assessment.

The study area can be considered homogeneous for biogeographical, latitudinal, altitudinal and climatic characteristics and selected streams belongs to the same river type (Bianco 1995), allowing to exclude significant influence of regional natural drivers on functional diversity (Côte et al. 2019). Watercourses are located at an altitude range of 100–150 m a.s.l. and are fed mainly by surficial water and, secondarily, groundwater. All the studied watercourses can be considered as natural or semi-natural small lowland streams. Overall, the dataset included 60 censuses (Table S1, Supporting Information). A total of 16 watercourses were sampled 1 to 4 times between 2002 and 2008 (Fig. 1). In order to account for possible difference in species abundance related to seasonality, we checked for significant effect of season by grouping census for stations with ≥ 3 samples according to the sampling season (i.e. spring, summer, autumn and winter), and testing the significance of the grouping by means of an ANOSIM test in R v. 4.1.0 (function *anosim* in the package *vegan* (Oksanen et al. 2018)). We also tested the significance of grouping according to the locality with the same statistical approach. Fish sampling was always conducted by electrofishing, using standardized protocols and sampling effort (ISPRA 2013). In some cases, two distant stations were considered for the same watercourse. A total of 35 species were recorded in the study area (Table S2, Supporting Information). Species abundance was expressed as percentage of specimens on the total number of fishes caught on each census. Percent abundance of exotic fish species for each census was also calculated. To

account for possible differences in sampling effectiveness among stations, for each single census completeness (i.e. the proportion of observed species in the population) (Chao and Chiu 2016) was estimated by using the iNEXT.4steps Online tool (https://chao.shinyapps.io/iNEXT_4steps/) (Chao et al. 2020). Completeness estimates are obtained from functions, which are parameterized by an order $q \geq 0$, where q is an exponential parameter that determines the function's sensitivity to species abundances. Completeness was obtained for $q=0$, 1 and 2. For $q=0$ (corresponding to species richness), species abundances are not considered and disproportionate weight to rare species is given. For $q=1$ (corresponding to Shannon diversity) species are weighted by their abundance, without disproportionately favoring either abundant or rare species. Finally, for $q=2$ (corresponding to Simpson diversity), each species is weighted by its squared species relative abundance, so that completeness gives disproportionate influence to highly abundant species. We also obtained the estimated asymptotic diversity profiles for the three q values, and compared it to the observed values. We performed an exploratory PCA on the IFF scores matrix by using the software Statistica v.8.0.3 to identify the main contributions of each habitat variables to the overall variability of watercourses.

Functional diversity of fish communities

To estimate functional diversity, a set of 14 morphometric numerical parameters, related to diet preferences, habitat preference and speed ability was considered (Côte et al. 2022). Details of traits definition, measurement and collection can be found in Stefani et al. (2020) and resumed in Table S3 and Figure S1, Supporting Information. Briefly, reference species' morphological traits were measured on at least 5 images of different specimens, and expressed as mean values, after standardization to the length of each fish. For each species, we selected images taken at different times and locations, in order to overcome the risk of bias related to phenotypic plasticity changes through time (Pease et al. 2018; Raffard et al. 2019).

To analyze functional diversity, the standardized effect size Functional Richness ($SESF_{ric}$) and functional dispersion ($SESF_{dis}$) (Legendre and Laliberté, 2010; Villéger et al. 2008) were calculated for each fish community. Standardization was done to overcome the intrinsic correlation of F_{ric} and, partially, F_{dis} with species richness (Mason et al. 2013). Briefly, the observed values were standardized to the mean and the standard deviation of null model indices, obtained preserving species occurrence frequency and sample species richness, by adapting the script provided by Plass-johnson et al. (2016). To calculate functional indexes the species trait matrix was firstly analyzed with a Principal Component Analysis (PCA), then an Euclidean distance matrix was calculated on the basis of the first two PCA axis and indexes estimated. Calculations were performed by referring to the workflow and functions implemented in the mFD package (Magneville et al. 2022) in R version 4.1.0. We also compared the mean values of each trait for exotic ($n=12$) and native ($n=23$) species by mean of a Student's t test. All statistical analyses were run in R version 4.1.0, using the packages *FD* (Laliberté et al. 2014).

Kurtosis and skewness of traits-abundance distributions

Observed kurtosis (K) and skewness (S) of trait-abundance distributions were calculated for each community, and according to the inequality SKR that relates the two moments series (Gross et al. 2017), the slope β and the intercept α estimated. We also calculated the

deviation of the observed kurtosis (K_{obs}) respect to K_{min} calculated for each community as $D = K_{obs} - K_{min}$. We compared the observed descriptors with 1000 simulated communities obtained under neutral selection of traits, to highlight processes favoring trait diversity (e.g. competition), or filtering them in the observed datasets. In case of competition, multimodal, or more skewed distributions are expected respect to neutral distribution. This indicates the presence of few species with extreme traits, eventually even respect to the bulk of species. Kurtosis, otherwise, indicate the peakiness of traits-abundance distribution. More peaked distributions than those expected under neutral selection are indicative of environmental filtering, which occurs when many species in a community are selected for the same traits values. The opposite case (i.e. lower than expected kurtosis) indicates the co-dominance of diversified species with regard to the trait investigated. At this scope, four values of migration rates m from a reference pool population were tested in four different simulations sets ($m = 0.1, 0.25, 0.5$ and 0.9) to generate simulated communities drifting differently from the original pool. Specific details of the analysis are reported in Appendix S1, Supporting Information.

Assessing the role of habitat quality on functional diversity

Response of diversity indexes to habitat quality was modelled with linear mixed-models, considering: a) the observed functional indexes and moments as response variables; b) each of the 13 habitat influent parameters of IFF as predictors; c) the watercourse as random effect for the intercept. Calculations were done using the package *nlme* (Pinheiro et al. 2020) and the function *lme* in R v. 4.1.0. Prior to estimation, the predictors were unit-based normalized ($X_0 = (X - X_{min}) / (X_{max} - X_{min})$). Response of diversity indexes was also evaluated in respect of the relative abundance of exotic species, using the same approach as above.

Results

Fish census and habitat quality

Sample completeness resulted not always fulfilled for $q=0$ among the different censuses (completeness < 0.95 in 35 out of 60 censuses), however indicating that in most cases (41 out of 60) not more than 2 rare species resulted undetected (Appendix S2). For $q=1$ and $q=2$, sample completeness resulted almost ≥ 0.95 , and estimated and observed diversity highly congruent. Giving that the different functional indexes here employed can be alternatively sensitive to rare species, or weighted by species abundance, the interpretation of results obtained with the former ones has taken into account the possible effect of incongruent sample completeness. However, abundance weighted functional indexes, for which sample completeness appeared satisfied, were the most informative in the following model testing (Sect. "Relationships between functional diversity, habitat quality and exotic species abundance").

Seasonality did not result a significant factor shaping species censuses in each station, according to ANOSIM ($R = 0.0289$, $p = 0.158$), on the contrary, locality significantly influenced community composition ($R = 0.442$, $p < 0.01$). Hence, sampling locality was set as a random factor in the following modelling analysis.

Habitat quality variability (Figure S2, Supporting Information) was represented by PCA along two main axes (Figures S3, Supporting Information). Axis 1 (33.03% explained

variance) mostly represented large scale variables (land use, riparian vegetation amplitude or transversal section naturality). Axis 2 (18.12% explained variance), on the contrary, mainly described the variability associated with mesoscale habitat (substrate composition, abundance and composition of the detritus and the banks erosion). Sampling sites (Figure S4, Supporting Information) resulted distributed mainly along the PCA axis 1 gradient. However, a grouping related to PCA axis 2 was evident as well.

Relationships between functional diversity, habitat quality and exotic species abundance

Functional diversity indexes (i.e. $SESF_{ric}$ and $SESF_{dis}$) were calculated based on the first two axis of PCA. The first axis scores resulted mostly correlated with fish body depth parameters (Table S3, Supporting Information) while the second axis to the upper jaw and the head length. Thus, axis 1 (figure S5, Supporting Information) represented the transition from rounded, gibbous species, such as *Lepomis gibbosus* (L. 1758) or other rounded cyprinids to the elongated species, such as the reophilic cyprinids or cobitids, up to the exotic *Misgurnus anguillicaudatus* (Cantor, 1842). The second axis represented the transition from predators, such as *Salmo marmoratus* (Cuvier, 1829), *Esox* sp., characterized by large head and mouth, to the other species. Interestingly, according to PCA scores plot (figure S5, Supporting Information), exotic species resulted consistently located as outliers or at the extreme of the functional space.

Three trait values (*body depth at the position of the eye*, *caudal peduncle depth* and *insertion of the pectoral fin—dorsal side distance*) resulted significantly higher (Student's t , $p < 0,05$) in exotic species, indicating a prevalence of gibbous traits in non-native species (Figure S6, Supporting Information). Hence, PCA axis 1 variation can be associated to variation between exotic and native species (except for *M. anguillicaudatus*).

Large scale parameters resulted more strongly related with functional indexes (Table 1, Figure S7, Supporting Information). In particular, the overall land use was a significant predictor for $SESF_{ric}$, $SESF_{dis}$, kurtosis, skewness and D of PCA axis 1, but not of the axis 2.

Interestingly, relationships were inverse for the two functional indexes, indicating a decrease of functional diversity with increasing land use naturality (Table 1, Figure S7). Similarly, kurtosis and skewness increased with naturality, indicating the shift to specific selected traits in more natural habitats (Table 1, Figure S7). This trend was confirmed for the parameters describing the width and continuity of the riparian vegetation belt, while vegetation structure and complexity seemed to be not influent on fish functional diversity.

Narrowing the scale of habitat assessment, the bank conformation resulted a significant predictor for $SESF_{dis}$ and D of the axis 1 of PCA, while river section naturality was significant only for $SESF_{dis}$. None of the small-scale descriptors was significantly associated with functional metrics. The overall IFF index was significantly related to $SESF_{dis}$, kurtosis and D of the axis 1 of PCA.

Exotic species abundance resulted a significant predictor for $SESF_{dis}$ ($\beta = 0.232$, $t = 2.473$ (d.f. = 40), $p = 0.018$), indicating an increase of diversity where the exotic species were more abundant. On the contrary, kurtosis ($\beta = -6.301$, $t = -2.168$ (d.f. = 40), $p = 0.03$) and D ($\beta = -2.884$, $t = -2.248$ (d.f. = 40), $p = 0.03$) for the PCA axis 1 resulted inversely associated with exotic species abundance, namely exotic species tend to unflatten the distribution curve of community traits and to maximize diversity, giving the observed skewness. Otherwise, no significant relationships were found for $SESF_{ric}$ ($\beta = 0.075$, $t = 0.502$

Table 1 Significance of linear-mixed models between functional diversity indexes, moments and habitat descriptors

Habitat descriptors	SESFRic	SESFDis	Skewness PCA1	Skewness PCA2	Kurtosis PCA1	Kurtosis PCA2	D PCA1	D PCA2
land use (d.f. 40)	$\beta = -0.198$ $t = -2.08$ $p = 0.044$	$\beta = -0.262$ $t = -3.659$ $p < 0.001$	$\beta = 0.934$ $t = 2.172$ $p = 0.036$	$\beta = -0.223$ $t = -0.909$ $p = 0.369$	$\beta = 7.208$ $t = 2.450$ $p = 0.019$	$\beta = -0.712$ $t = -0.687$ $p = 0.496$	$\beta = 2.590$ $t = 2.158$ $p = 0.037$	$\beta = -0.206$ $t = -0.655$ $p = 0.516$
riparian veg. structure (d.f. 40)	$\beta = -0.056$ $t = -0.581$ $p = 0.564$	$\beta = -0.037$ $t = -0.375$ $p = 0.710$	$\beta = 0.708$ $t = 1.551$ $p = 0.129$	$\beta = -0.440$ $t = -1.952$ $p = 0.058$	$\beta = 5.879$ $t = 1.940$ $p = 0.060$	$\beta = -0.909$ $t = -0.874$ $p = 0.387$	$\beta = 1.1.71$ $t = 0.913$ $p = 0.367$	$\beta = -0.190$ $t = 2.158$ $p = 0.545$
riparian veg. width (d.f. 40)	$\beta = -0.178$ $t = -1.806$ $p = 0.078$	$\beta = -0.190$ $t = -2.200$ $p = 0.034$	$\beta = 0.946$ $t = 2.244$ $p = 0.030$	$\beta = -0.212$ $t = -0.878$ $p = 0.385$	$\beta = 8.481$ $t = 3.175$ $p = 0.003$	$\beta = -0.757$ $t = -0.744$ $p = 0.461$	$\beta = 2.513$ $t = 2.119$ $p = 0.040$	$\beta = 0.138$ $t = -0.611$ $p = 0.662$
riparian veg. continuity (d.f. 17)	$\beta = -0.113$ $t = -1.143$ $p = 0.269$	$\beta = -0.228$ $t = -2.719$ $p = 0.015$	$\beta = 0.678$ $t = 1.516$ $p = 0.148$	$\beta = -0.395$ $t = -1.752$ $p = 0.100$	$\beta = 1.789$ $t = 0.533$ $p = 0.600$	$\beta = -0.856$ $t = -0.858$ $p = 0.403$	$\beta = 0.813$ $t = 0.603$ $p = 0.554$	$\beta = 0.213$ $t = -0.444$ $p = 0.494$
bank conformation (d.f. 17)	$\beta = -0.202$ $t = -1.736$ $p = 0.101$	$\beta = -0.352$ $t = -4.875$ $p < 0.001$	$\beta = 0.331$ $t = 0.726$ $p = 0.478$	$\beta = 0.272$ $t = 1.169$ $p = 0.259$	$\beta = 6.265$ $t = 2.100$ $p = 0.05$	$\beta = 1.609$ $t = 1.715$ $p = 0.105$	$\beta = 2.735$ $t = 2.321$ $p = 0.033$	$\beta = -0.138$ $t = -0.699$ $p = 0.662$
detritus retention (d.f. 17)	$\beta = 0.066$ $t = -0.602$ $p = 0.555$	$\beta = -0.013$ $t = -0.121$ $p = 0.905$	$\beta = -0.004$ $t = -0.008$ $p = 0.994$	$\beta = -0.269$ $t = -1.120$ $p = 0.278$	$\beta = 1.750$ $t = 0.525$ $p = 0.606$	$\beta = -1.102$ $t = -1.082$ $p = 0.294$	$\beta = 0.549$ $t = 0.414$ $p = 0.685$	$\beta = -0.340$ $t = -1.097$ $p = 0.288$
bank erosion (d.f. 40)	$\beta = -0.294$ $t = 1.843$ $p = 0.073$	$\beta = -0.048$ $t = 0.337$ $p = 0.738$	$\beta = 0.084$ $t = -0.189$ $p = 0.851$	$\beta = -0.615$ $t = -3.026$ $p = 0.004$	$\beta = 2.745$ $t = 0.835$ $p = 0.489$	$\beta = -2.776$ $t = -3.356$ $p = 0.002$	$\beta = 1.065$ $t = 0.784$ $p = 0.438$	$\beta = -0.106$ $t = -0.356$ $p = 0.723$
section naturality (d.f. 17)	$\beta = -0.178$ $t = -1.560$ $p = 0.137$	$\beta = -0.343$ $t = -4.586$ $p < 0.001$	$\beta = 0.407$ $t = 0.911$ $p = 0.375$	$\beta = 0.222$ $t = -0.957$ $p = 0.352$	$\beta = 6.195$ $t = 1.989$ $p = 0.06$	$\beta = -0.617$ $t = -0.629$ $p = 0.538$	$\beta = 3.305$ $t = 2.731$ $p = 0.014$	$\beta = -0.022$ $t = -0.073$ $p = 0.943$
substrate composition (d.f. 17)	$\beta = 0.141$ $t = 1.012$ $p = 0.326$	$\beta = -0.099$ $t = 0.755$ $p = 0.460$	$\beta = -0.263$ $t = -0.580$ $p = 0.570$	$\beta = 0.430$ $t = -2.038$ $p = 0.058$	$\beta = 0.468$ $t = 0.142$ $p = 0.889$	$\beta = -0.035$ $t = -0.035$ $p = 0.972$	$\beta = 1.094$ $t = 0.844$ $p = 0.411$	$\beta = 0.256$ $t = 0.843$ $p = 0.411$

Table 1 (continued)

Habitat descriptors	SESEFric	SESEFDis	Skewness PCA1	Skewness PCA2	Kurtosis PCA1	Kurtosis PCA2	D PCA1	D PCA2
pool/riffles/meanders (d.f. 17)	$\beta = -0.039$ $t = -0.383$ $p = 0.706$	$\beta = -0.117$ $t = -1.200$ $p = 0.247$	$\beta = -0.171$ $t = -0.363$ $p = 0.721$	$\beta = -0.145$ $t = -0.594$ $p = 0.560$	$\beta = 2.160$ $t = 0.659$ $p = 0.519$	$\beta = -0.246$ $t = -0.238$ $p = 0.815$	$\beta = 1.450$ $t = 1.149$ $p = 0.267$	$\beta = 0.069$ $t = 0.218$ $p = 0.830$
macrophytes (d.f. 17)	$\beta = -0.073$ $t = -0.633$ $p = 0.535$	$\beta = 0.011$ $t = 0.101$ $p = 0.921$	$\beta = 0.245$ $t = 0.524$ $p = 0.607$	$\beta = 0.109$ $t = 0.445$ $p = 0.662$	$\beta = -2.536$ $t = -0.767$ $p = 0.454$	$\beta = 0.885$ $t = 0.866$ $p = 0.399$	$\beta = -2.048$ $t = -1.638$ $p = 0.120$	$\beta = -0.042$ $t = -0.135$ $p = 0.894$
detritus degradation (d.f. 17)	$\beta = 0.186$ $t = 1.430$ $p = 0.171$	$\beta = -0.149$ $t = -1.137$ $p = 0.271$	$\beta = -0.0006$ $t = -0.001$ $p = 0.999$	$\beta = -0.289$ $t = -1.158$ $p = 0.263$	$\beta = 3.941$ $t = 1.207$ $p = 0.244$	$\beta = -0.122$ $t = 0.114$ $p = 0.911$	$\beta = 2.068$ $t = 1.660$ $p = 0.115$	$\beta = 0.443$ $t = 1.438$ $p = 0.169$
IFF (d.f. 40)	$\beta = -0.140$ $t = -1.403$ $p = 0.168$	$\beta = -0.258$ $t = -3.200$ $p = 0.003$	$\beta = 0.722$ $t = 1.577$ $p = 0.123$	$\beta = -0.407$ $t = -1.733$ $p = 0.09$	$\beta = 7.734$ $t = 2.641$ $p = 0.012$	$\beta = -0.848$ $t = -0.812$ $p = 0.421$	$\beta = 2.755$ $t = 2.292$ $p = 0.027$	$\beta = -0.198$ $t = -0.619$ $p = 0.540$

Significant relationships are indicated in bold, with their slope coefficients (β), the t-test value (t) and p-values (p), and the degree of freedom (d.f.). Skewness, kurtosis and distance to the lower boundary (D) have been modeled separately for the PCA axis 1 and 2 coordinates, from the morphometric matrix of traits

(d.f.=40), $p=0.618$), skewness ($\beta=-0.529$, $t=-1.535$ (d.f.=40), $p=0.133$ for PCA axis 1 and $\beta=-0.218$, $t=-1.225$ (d.f.=40), $p=0.228$ for PCA axis 2) and, limited to PCA axis 2, kurtosis ($\beta=-0.596$, $t=-0.841$ (d.f.=40), $p=0.405$) and D ($\beta=0.123$, $t=0.516$ (d.f.=40), $p=0.609$).

Simulation analysis of neutrally selected communities

Simulated values of α and β for neutral communities resulted, as expected, more dispersed when setting lower migration parameters, since drift from the reference pool

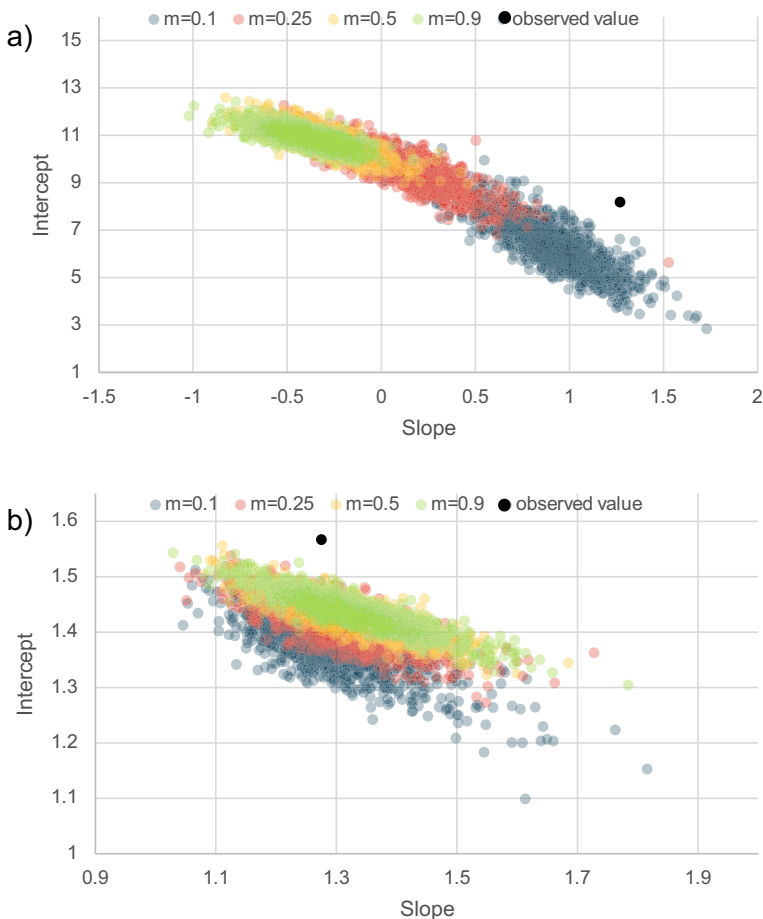


Fig. 2 Comparison between observed and 1000 simulated intercept α and slope β , as obtained by relating kurtosis and skewness of traits. Simulated values were obtained under neutral selection of traits and different rates of migration m from the reference pool to the generated communities. Comparisons were made separately for the traits encoded by the PCA axis 1 (a) and 2 (b) obtained from the species \times traits matrix

population is favored with low migration (Fig. 2). Significance of observed moments respect to neutral simulated values was influenced by this behavior and resulted more stringent when compared with the low drifting communities (Table 2). The observed values of α resulted non significantly different from neutral values in high drift conditions, nearly significant with moderate drift, and significantly small with low drift. Hence, in all but the most extremely drifting case kurtosis was lower than expected by chance, indicating the co-dominance of diversified species along the PCA 1 traits space. The observed values of β showed a similar behaviour, but resulted not significantly different from neutral values up to moderate drift ($m=0.25$, Table 2). That is, even when increase skewness, kurtosis increased more slowly than in a neutral scenario, again indicating a tendency of the community to host diversified species. D index provided less straightforward outputs. Indeed, D resulted significantly large at low migration rates, and not significantly different at high migration, a contrasting behavior indicating that at medium and low drift traits evenness is similar to values found in a community under neutral selection of traits, while evenness is lowered at low drift. The comparison seems to indicate that for most of cases, except when drift is particularly high, the communities express higher functional diversity than in neutral communities, suggesting the presence of factors favoring traits diversification within communities.

Differently, in the case of the PCA axis 2, observed α and D resulted always significantly larger than simulated values regardless of the level of drift, while β was always not significantly different. These results seem to indicate a pattern of functional diversity distribution more peaked and restricted than by chance, suggesting in this case a possible environmental filtering.

Discussion

One of the main objectives of the present study was to explore the relationships between functional diversity for freshwater fish communities and the morphological and habitat quality of the small lowland watercourses. This study indicated that the functional response can be trait specific, and that habitat alterations act synergically with other pressures in shaping the functional space of communities (Huang et al. 2021).

Table 2 Significance of observed intercept (α), slope (β) and distance to the lower boundary (D) respect to simulated values under neutral selection of traits and different proportion of migrants from the community pool to the generated ones (m)

	PCA axis 1			PCA axis 2		
	$p(\alpha\beta)$	$p(\beta\alpha)$	D	$p(\alpha\beta)$	$p(\beta\alpha)$	D
$m=0.1$	$p=0.930$	$p=0.940$	sl ($p < 0.001$)	$p=1.00$	$p=0.419$	sl ($p < 0.001$)
$m=0.25$	$p=0.058$	$p=0.938$	sl ($p < 0.01$)	$p=1.00$	$p=0.393$	sl ($p < 0.001$)
$m=0.5$	$p < 0.001$	$p < 0.001$	ns ($p=0.37$)	$p=1.00$	$p=0.325$	sl ($p < 0.01$)
$m=0.9$	$p < 0.001$	$p < 0.001$	ns ($p=0.98$)	$p=1.00$	$p=0.28$	sl ($p < 0.01$)

Conditional p-values are calculated as in (Gross et al. 2017), and indicate the probability of simulated values to be lower than observed ones

sl significantly large; ns not significant

Land use and riparian vegetation size influence the functional diversity of freshwater fish

The functional space of the fish communities can be synthesized by a few factors. On one hand, a main source of variation (PCA axis 1) was represented by the shift from rounded species to elongated ones, which can be roughly interpreted as the gradient from communities typical of lentic habitats to those inhabiting more lotic environments. However, hydrodynamic variations cannot explain the different patterns of freshwater fish ecomorphology alone (Baldasso et al. 2019), and other factors can play a relevant role in shaping functional diversity. Interpreting the influence of habitat quality on this gradient resulted intriguing, as we obtained counterintuitive responses. Indeed, kurtosis, skewness and D for the PCA axis 1 increased with naturalness of the large-scale descriptors of habitat quality (i.e. land use and the amplitude and continuity of riparian vegetation), indicating the shift to specific selected traits in more natural habitats. This trend was confirmed by the observed reduction of functional diversity indexes ($SESF_{dis}$ and $SESF_{ric}$) with the same large scale descriptors, and thus it may be considered the main response obtained in this study. Taking all this together, functional diversity resulted maximized at lower scores of the large-scale variables, and that main trend probably determined the response of the overall IFF scores too.

Fish assemblages functional richness was showed to increase in ecosystems impacted by agricultural land as well (Barbosa et al. 2020; Teresa and Romero, 2010; Virgilio et al. 2018). Such results could be explained by the increased microhabitat availability produced by the reduction of the canopy continuous tree cover, intermixed with forested land parcels. More again, it was observed that areas with or without canopy within the same basin presented different fish assemblages (Teresa and Romero 2010). In the cases analyzed by the present manuscript, the gradient of land use and canopy cover ranges from close forested areas to open, cultivated areas, with many intermediate cases in between. The heterogeneity of habitats could have favoured the coexistence of species with different ecological traits, thus determining the increase of functional diversity. Many cascade effects, for instance on trophic niche availability for fish, may derive by changes occurring on land use and riparian vegetation integrity (Wahl et al. 2013). Riparian forests can indeed influence physical, chemical, and biological variables of streams and mediate terrestrial-aquatic linkages.

The apparent scarce relevance of meso- and microhabitat

No significant relationship was found between functional diversity indexes and moments with specific descriptors of habitat and microhabitat heterogeneity. This does not come fully unexpected, as land use and riparian vegetation alterations have been found to influence more significantly the functional and community descriptors in many freshwater ecosystems (Alvarenga et al. 2021; Filgueira et al. 2016; Tanaka et al. 2016) than smaller scale descriptors. For instance, the alteration of land use can have stronger influence on water physicochemical properties than on habitat structure and complexity (Marzin et al. 2013). Moreover, fish communities response to alterations has already been found to be more influenced by large scale factors (e.g. climate change, land use) and habitat fragmentation than by local changes, differently from freshwater invertebrate communities (Haase et al. 2013; Kail et al. 2015; Verdonschot et al. 2016).

However, we could not disregard that small scale habitat properties may undoubtedly be influential for many ecological needs (reproduction, resources, refuges) (Plichard et al.

2020; Kirk et al. 2022). Consequently, our results cannot be generalized, but should be read as necessity to adopt a case by case approach investigating functional response of communities to anthropogenic stress. As an example, the watercourses analysed in this study showed changes mostly related to large scale descriptors (land use and riparian vegetation size), and to a lesser extent to meso- and microhabitat parameters (Figure S3 and S4, Supporting Information). Moreover, basing on sampling protocols, the fish censuses were averaged over the entire set of microhabitats of the studied stretch. This may be relevant considering also that local environmental parameters and pressures, coupled with biotic responses, are usually challenging to detect, being them subject to high stochasticity and dependent on local specific influences or fish dispersal limitations (Radinger et al. 2017).

Exotic species contribute to enlarge functional trait distributions

The morphological PCA axis 1 gradient from elongated to round body shape described the main difference between native and exotic species (except for the elongated *M. anguillicaudatus*), a pattern already observed at global scale (Toussaint et al. 2018; Xiang et al. 2021). The significant positive response of $SESF_{dis}$ (and inverse for PCA axis 1 kurtosis and D) with the abundance of exotic species calls for a significant role for invasive species, alone or with native ones, in shaping and increasing the functional diversity of communities (Milardi et al. 2019; Moore and Olden 2017; Renault et al. 2022). This is corroborated by the simulation of statistical moments, demonstrating that observed functional diversity may be higher than expected by chance for the PCA axis 1 traits. Other studies addressing the relationships between functional diversity of coexisting native and exotic fish species found often non-random assemblages of traits, favouring trait divergence within communities (Xiang et al. 2021; Su et al. 2020; Azzurro et al. 2014; Toussaint et al. 2018). In other cases, however, the ecological traits (and functions) of native prey species were extirpated by the introduction of large predatory fish (Matsuzaki et al. 2016), reducing functional diversity.

Having established that exotic species play an active role in shaping the functional diversity of the studied communities, what remains challenging is disentangling the ecological processes behind invasion dynamics. Disentangling active interaction with native species, or simply correlation of their responses respect to drivers, is a challenging task. Biotic interaction, such as niche partitioning due to competition, is considered among the main factors maintaining high functional diversity and divergence in communities, a dynamics often exacerbated in invaded communities (Weiher et al. 2011). On the other hand, anthropogenic disturbance can increase environmental heterogeneity favouring in general more diversified communities, but often supporting exotic species invasion (Lorion and Kennedy 2009; Teresa and Casatti 2012). One element in support of the latter hypothesis comes from the assumption that empty niches could emerge in a heterogeneous catchment, where land use is a mix of open and forested areas (Didham et al. 2005), a scenario commonly found within the River Po valley. In this perspective, habitat heterogeneity may favour in general traits divergence, regardless of the native or exotic status of the species. We could not, however, exclude an active role of exotic species in modifying the functional structure of native communities, by competing with native taxa. Whether these changes can happen regardless of habitat status, or whether habitat perturbation may decrease native species resistance and resilience to invasions still remains an open question (Didham et al. 2005; Farnsworth 2004), which would require ad hoc functional analysis.

Finally, an influence of exotic fish species on traits represented by PCA axis 2 traits did not find support in this study. Exotic species modulation of functional diversity can be trait

specific and scale dependent, while processes filtering invaders can vary according to the invasion stage (Carboni et al. 2013; Gallien and Carboni 2017). Consequently, it cannot be excluded that effects of exotic fish invasions on functional diversity, which can be considered low to mild in our study cases, could become more pervasive at later stages of the invasion processes, or considering other traits (Stavert et al. 2017).

Trait specific responses to anthropogenic disturbance

The second PCA axis represents species with large head and jaw size, associated to specific ecological traits: late female maturity, winter reproduction, salinity tolerance and piscivorous diet (Côte et al. 2022; Stefani et al. 2020). These are typical of big predators, such as salmonids (*S. marmoratus* and the exotic *Salmo trutta* L., 1758 in our case). Interestingly, descriptors of trait distribution for this axis (i.e. kurtosis, skewness and D) were influenced only in a few cases by habitat variables, either at large or small scale (Table 1), so that any sounding conclusion about habitat influence on PCA trait 2 cannot be drawn. However, community trait distribution resulted significantly different from those obtained under neutral dynamics, indicating a possible filtering of traits under directional selective pressures.

For instance, a past study addressed the long term trend of fish community functional diversity in the same geographical context of the present work (Stefani et al. 2020). A significant role of global warming was found in determining the rarefaction of cold adapted predators (i.e. *S. marmoratus*), which share the same morphological traits here represented by the PCA axis 2. Hence, it is possible that morphological traits resulted filtered because of their covariation with thermal preferences and tolerance of cold adapted predators (Raffard et al. 2019). In the same study area, hydro-chemical quality worsening was found to be significantly associated with changes in some ostracods communities (Rossetti et al. 2020). Chemical pollution, mainly due to fertilizers, and pesticides, is indeed another main pressure acting on lowland freshwater within the River Po basin (Mascolo et al. 2019; Viaroli et al. 2018). This suggests that other factors may acting synergistically with thermal changes in fish communities.

In conclusion, the different response to habitat drivers, shown by the two main PCA components, likely indicates that multiple natural or anthropogenic non-stochastic factors might have shaped the observed distribution of traits, while not excluding synergistic dynamics (Su et al. 2019; Ge et al. 2021; Milardi et al. 2022a, b).

Possible implications for ecosystem processes and functionality maintenance

This study demonstrated that functional diversity of fish communities, measured along a gradient of land use and riparian buffer vegetation, may increase with increasing intensity of anthropogenic perturbation, in contrast with theoretical expected outcomes (Buisson et al. 2013; Cavalcante et al. 2022). This trend resulted correlated to the spread of exotic species, that probably contributed to introduce novel traits within communities subject to land use intensification.

It must be said, however, that when a community is disrupted by introducing novel functionally divergent taxa, eventually being exotic species, the functional response to stress and further perturbations may be significantly altered (Stavert et al. 2017).

When one or more species are subtracted from a community, that community is altered and disaggregated. The disassembly process follows the non-random loss of certain species

and it is based on species sensitivity distribution (Zavaleta et al. 2009). Disassembly can lower ecosystem functioning and increase vulnerability of ecosystem processes to human pressures, as most high sensitive species has been found to be those with higher contribution to functionality (Larsen et al. 2005; Zavaleta et al. 2009). In the case of freshwater fish communities, however, Moore and Olden (2017) found that small fish species were more sensitive, but less important for the nutrient recycling dynamics. In that case, however, the spread of exotic species compensated for the loss of functionality. On the other hand, European surveys of fish communities found low functionality redundancy and hence high risk of functional losses in case of extinction, especially in rivers (Teichert et al. 2017), regardless of the spread of exotic taxa. What emerges is a strong dependence of the final response of communities on case specific conditions and ecogeographic constraints.

In the present study we did not associate traits to any putative ecological functions at ecosystems level. We focused on the interaction of the fish autoecology with altered habitat. However, functional diversity, based on the most influent traits in our analysis (large jaw size and body shape), can be considered a good proxy for diversity of ecological traits such as trophic niche (Côte et al. 2022). The modification of those niches could impair the ecosystem functioning, altering nutrient cycling (Sereda et al. 2008) or energy transfer (Svřaranta et al. 2011) or trophic position shifts (De Santis et al. 2021).

Conclusions

Functional diversity can be described by a wide set of parameters. In the case of freshwater fish communities, the integration of index of functional niche occupancy and moments of traits distributions proved to be highly effective in evidencing idiosyncratic responses to land use and riparian buffer size. This study confirms that these two main descriptors of the environment surrounding small watercourses can be considered valid proxies for anthropogenic alterations. Interestingly, the evidenced responses resulted modulated by the contribution of exotic species, which maximized niche occupancy, either by exploiting increased habitat heterogeneity or by interaction with native species. The counterintuitive observed inverse relationship between functional diversity descriptors and habitat quality should warn about the need to carefully evaluate the use of functional diversity indexes to assess ecological quality of watercourses. Indeed, their responses may result to be trait dependent, inverse or non-linear.

Finally, inferring possible effects of habitat alterations on ecosystems functionality and services, mediated by community traits changes, was outside the main aims of this study. However, possible compensatory dynamics at community level could be hypothesized.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-024-02809-w>.

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Author contributions FS, LM, SG and SB conceived the ideas and designed methodology; FS, PT and AS collected the data; FS, EF, PT and AS analyzed the data; FS and EF led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Declarations

Competing interests The authors have no relevant financial or non-financial interests to disclose.

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