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# The role of species introduction in modifying the functional diversity of native communities

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**Abstract**

Although one of the most evident effects of biological invasions is the loss of native taxonomic diversity, contrasting views exist on the consequences of biological invasions on native functional diversity. We investigated this topic using Mediterranean stream, river and canal fish communities as a test case, at 3734 sites in Italy, and distinguishing between exotic and translocated species invasion in three different faunal districts. Our results clearly confirmed that introduced species were widespread and in many cases the invasion was severe (130 communities were completely composed by introduced species). Exotic and translocated fish species had substantially different geographical distribution patterns, perhaps arising from their differences in introduction timing, spread and invasion mechanisms. We also found a clear decreasing trend of functional dispersion along an invasion gradient, confirming our hypothesis that the invasion process can diminish the relative diversity of ecofunctional traits of host fish communities. Furthermore, our results suggested that exotic species might have a greater negative effect than translocated species on the relative diversity of ecofunctional traits of fish communities. This could also be linked to the fact that translocated species are more ecofunctionally similar to native ones, compared to the exotics. Our multivariate analysis of site-specific combinations of ecofunctional traits highlighted some traits characteristic of all invaded communities, while our discriminant analysis underlined how there was a substantial ecofunctional overlap between native, exotic and translocated species groups in most areas.

**Keywords:** biodiversity, exotic species, translocated species, species invasion, conservation, fish communities

## Introduction

The ecological footprint of human presence falls heavy on worldwide ecosystems, ultimately affecting human well-being itself (Myers, Gaffikin et al. 2013). However, despite increased knowledge on the effects of human action on worldwide ecosystems (e.g. Vörösmarty, McIntyre et al. 2010), the global ecosystem health is apparently still in decline (Collen, Whitton et al. 2014, Sato and Lindenmayer 2018). This trend has reflected correspondingly on biodiversity, which is the diversity of life forms that thrive in different environments. Continued efforts to reverse this decline, usually aimed to preserve and restore key species, have also failed to halt the loss of biodiversity (Butchart, Walpole et al. 2010).

Direct human impacts on biodiversity can go as far as species extinctions, e.g. through excessive harvest (Anderson 1995, Rosser and Mainka 2002). However, also indirect impacts on the biota, e.g. habitat degradation, play a strong role in species extinctions and synergistically interact with each other (Brook, Sodhi et al. 2008). Indirect impacts are usually more subtle, but by no means less significant; for example, the introduction of species produces a powerful pressure on the biological component of global ecosystems (see e.g. Gallardo, Clavero et al. 2016). Introduced species, i.e. species that reach a new ecosystem through human intervention (either intentionally or unintentionally), have been found to be one of the major challenges to preserve biodiversity and ecosystems functioning worldwide (Vitousek, D'antonio et al. 1997, Clavero and García-Berthou 2005). Biodiversity loss is, in turn, a major driver of ecosystem change in itself as it can alter productivity and decomposition, two key processes in ecosystem functioning (Hooper, Adair et al. 2012), and can even affect human health (Díaz, Fargione et al. 2006). The whole human sphere can ultimately be affected as well, through the alteration of ecosystem functioning and its ability to provide the services needed to sustain humankind

(Haines-Young and Potschin 2010, Cardinale, Duffy et al. 2012). As biodiversity and ecosystem functioning are so intertwined, species loss can trigger negative feedbacks on the environment, having cascading effects on biodiversity. However, identifying and understanding the causes and mechanisms of biodiversity loss can be very challenging, as multiple pressures are at play and biodiversity is a multi-faceted concept.

Traditionally, biodiversity has been identified with species diversity, so that biodiversity loss was investigated through the analysis of species loss (Pimm and Raven 2000, Cardinale, Duffy et al. 2012). However, more recent approaches have emphasized the need to progress beyond mere taxonomical diversity, and shift more attention towards functional diversity (see e.g. Poff, Olden et al. 2006, Violle, Reich et al. 2014). The functional diversity approach privileges the ecological functioning role of species over mere species richness, and is generally considered to reflect more closely the interaction between the environment and biotic communities in space and time (see e.g. Baskin 1994). In this perspective, changes in functional diversity can be interpreted through the analysis of the ecological-traits composition of living communities (i.e. ecofunctional diversity), at different spatial scales.

Several studies established that one of the most evident effects of biological invasions is the loss of native diversity (Vitule, Freire et al. 2009, Bellard, Cassey et al. 2016), which naturally leads to the inference that functional diversity could also be undermined. However, contrasting views exist on the consequences of biological invasions on functional diversity: either positive (Toussaint, Charpin et al. 2018) or negative (Shuai, Lek et al. 2018, Milardi, Gavioli et al. 2019) effects on native biodiversity have been found, probably as a result of different choices in functional traits, spatial scales or biological resolution considered (Jarzyna and Jetz 2018). For example, significant differences might exist between the effects of invasions led by exotic (i.e.

originally from a distant geographic area) and translocated (i.e. originally from a nearby geographic area) species (e.g. Leprieur, Beauchard et al. 2008). These differences could arise from the substantially different vectors of introduction, spread and timing of exotic and translocated species, but also from the fact that translocated species are usually more ecologically similar to native species. They can thus ecofunctionally substitute native species, causing a loss of native taxonomical diversity, but not of ecofunctional diversity. However, separating these effects would require datasets where clear distinctions could be made at the geographical and taxonomical level.

To investigate the effects of species introduction on ecofunctional diversity we focused on the Mediterranean region, because previous research identified a high risk to native biodiversity, including several endemic species, from biological invasions (Médail and Quézel 1999, Cuttelod, García et al. 2009, Hermoso, Clavero et al. 2011). We selected fish in inland waters as model taxa, because freshwater fish diversity has been highlighted as one of the most endangered taxa in this region (Crivelli 1995). We further selected Italy as a test area within the Mediterranean region, because it is isolated from the rest of the region by the Alps and includes several insurmountable geographical barriers defining faunal districts, thus allowing for clear distinctions of exotic and translocated species. We used the most detailed information available on community composition, to test the hypothesis that exotic and translocated species would show substantially different geographical patterns of invasion, due to their differences in introduction, spread and invasion mechanisms. We then explored the relationship between biological invasions and ecofunctional diversity, at the community level. First, we used a measure of overall ecofunctional diversity, expressed as the relative variability of traits within a community, to investigate the hypothesis that biological invasions would decrease the

ecofunctional diversity of invaded communities. In particular, we hypothesized that this effect would be more severe when the invasion was led by exotic species, rather than translocated ones, because the latter would be more ecofunctionally similar to native ones. Secondly, we also analyzed ecofunctional diversity, expressed as site-specific combinations of traits, under the hypothesis that some ecofunctional traits would be common in the invaded communities of all districts.

## **Materials and Methods**

### *Data collection*

We collated, for the first time, all available Italian stream fish community data from official monitoring programs run by provincial/regional administrations. Supplementary table 1 details the sources (and the appropriate acknowledgements) of these data. We collated and often digitized data from 4126 sampling events, but we discarded all sites without fish or those sampled more than once, narrowing our dataset to 3734 sampled sites. Our dataset spanned more than 11 degrees of longitude (~1200 km) and 10 degrees of latitude (~1100 km), covering streams at altitudes between -4 and 2500 m above sea level.

Fish sampling was mainly performed in the warm season, following national monitoring guidelines (APAT 2007), by direct-current electrofishing in shallow areas (e.g. upper stretches of rivers) combined with nets (a combination of trammel nets, gillnets and drop nets) in sites of higher water depth and conductivity (e.g. lower stretches of the rivers), to verify the results of electrofishing. The sampling effort was directed to ensure that all macrohabitats within each site (i.e. river stretch) were covered, and standardized based on sampled area, to allow comparisons between sites. Fish species were classified according to Kottelat and Freyhof (2007), taking into account recent taxonomic determinations and common names as listed in FishBase (Froese and

Pauly 2017). A total of 99 different fish species (37 of which are exotic) were found in Italian streams. Sampling time spanned 1999–2014, but community turnover was not a relevant factor in our study, because fish communities are typically stable over such timescales and the data was collected in a restricted timeframe within each area (Korhonen, Soininen et al. 2010, Gavioli, Milardi et al. 2019).

#### *Data elaboration*

Species were categorized as either native or introduced according to their biogeographic origin, as established through the current scientific literature (e.g. the national IUCN red list of species (IUCN Comitato Italiano 2019)). A species was defined as introduced when introduction was human-mediated, irrespective of the time elapsed since the introduction. Brown trout taxonomy has been under revision in this area throughout the sampling effort, and recently proposals have been put forward to split this taxon into native and exotic species (Zanetti 2017). As surveyors could not establish the exact species at the time of sampling, we conservatively assumed that all brown trout in the dataset were native to all areas. Hybrid specimens or uncertain species were excluded from this study.

Introduced species were divided into exotic species (originally from outside of the Italian geographical barriers) and translocated species (with an origin inside of the national border, but introduced to a new area). To account for native species translocation as a form of introduction, we distinguished 3 faunal districts according to the established literature (Bianco 1987, Bianco 1998); these districts are separated from each other by geographical barriers (i.e. mountain chains or sea stretches) that allowed the speciation of endemic fish taxa in inland waters. With the exception of the islands, in this area translocated species are mostly endemic variants of cyprinids and gobids, which were only recently taxonomically split and are ecofunctionally very



similar to other native species. Our dataset was thus composed by the Padano-Veneto district (PDV, 2418 sites), the Tosco-Laziale district (TL, 1146 sites), and the islands district (ISL, 170 sites (divided equally between the islands of Sardinia and Sicily)). The PDV district includes the largest river basin in Italy, the Po River basin (71,000 km<sup>2</sup>) within the Po River plain, limited in the north by the Alps and in the south by the Apennines. All rivers in this district flow ultimately in the Adriatic Sea. The TL district is characterized by the highest longitudinal extension; the Apennines separate the rivers that flow in the Tyrrhenian Sea, in the west Italian coast, from rivers that flow in the Adriatic Sea and Ionian Sea. The ISL district encompasses the two major Italian islands, completely isolated from the continental lands by sea stretches. Most of the rivers in the southern TL and ISL districts are not permanent, due to summer droughts.

Abundance of each species sampled during the monitoring was recorded with Moyle classes (Moyle and Nichols 1973) ranging from 1 (lower abundance, 1-2 individuals per site) to 5 (higher abundance, more than 50 individuals per site). Unfortunately, direct measures of body-mass were not taken at the time of sampling and Moyle classes (as numerical abundances), tend to overestimate the ecological significance of small-bodied species and underestimate that of large-bodied ones. Attempting to overcome this, and to better describe the ecological allocation of energy in the fish community, a weight was assigned to each species (1=small body up to ~150 g; 2=medium body ~150–400 g; 3=large body over ~400 g) based on the average weight of the adult stage in Italy, based on a combination of FishBase and unpublished data. This weight was multiplied by Moyle abundance classes, in order to obtain a body-mass-corrected abundance, hereafter referred to simply as abundance (Milardi and Castaldelli 2018).

We then calculated an invasion degree, i.e. the share of introduced species in inland waters fish communities, irrespective of their origin, based on the abundance of native and introduced

species. A high invasion degree equals to a high share of introduced species and a low share of native species. Similar calculations, performed using presence/absence or Moyle classes, yielded similar results in term of invasion degree (see Figure A.1 in Appendix A). We also calculated a translocation degree, expressing the share of translocated species among the introduced species, therefore a high share of translocated species translates into a high translocation degree and equals to a low share of exotic species in the introduced community, and vice-versa.

To investigate the ecofunctional composition of fish communities, five different ecological functions were examined: feeding, reproduction, migration, tolerance and habitat use. Within these ecological functions, all fish species were classified in guilds, each representing an ecofunctional trait (Supplementary Table 2, (see also Noble, Cowx et al. 2007)). Ecological functions, guilds and classification for most species in this study were taken from (Milardi and Castaldelli 2018, Milardi, Gavioli et al. 2019, Milardi, Gavioli et al. 2019), where all available information sources were used to identify appropriate guilds for each species. The same methodology was applied to classify species that were not included in previous work (see Supplementary Table 3).

Ecofunctional diversity was investigated through two different metrics based on community-specific fish ecofunctional traits: the functional dispersion metric (Laliberté and Legendre 2010), and the functional identity metric (Mouillot, Graham et al. 2013). We selected these metrics because they could be calculated on all communities (including the species-poor ones) and because they represent two different aspects of ecofunctional diversity.

The functional dispersion metric measures the relative diversity of ecofunctional traits in a community, communities with larger functional dispersion values are more diverse in species traits combinations. This metric should not be overly affected by species richness, can be

computed from any distance or dissimilarity measures and takes into account any number and type of traits (also qualitative traits, as in this study), is not strongly influenced by outliers, and accounts for species abundances (Laliberté and Legendre 2010). We further calculated the contribution of each species biogeographic category (native, exotic and translocated species) to the overall ecofunctional diversity by fractioning the overall functional dispersion according to the abundance of each biogeographic category in the overall community.

The functional identity metric expresses the abundance-weighted average value for each trait in a community, therefore traits with higher values are more represented in the community and those with lower values are less represented. Functional identity analysis produces a complete matrix with abundance-weighted averages for each trait in every community and is thus an expression of site-specific ecofunctional diversity, providing the peculiar combinations of traits present in each community. Functional dispersion and functional identity were calculated through the *dbFD* and the *functcomp* functions, respectively, using R software version 3.4.3 (Laliberté, Legendre et al. 2014).

#### *Data analysis*

We analyzed the spatial distribution of the invasion and translocation degrees, as well as that of the ecofunctional diversity, for all the areas covered by our dataset, through linear kriging in ArcGIS software version 9 (ESRI 2011).

We used non-linear regressions to obtain the curves best-fitting variations in ecofunctional diversity along an invasion degree gradient. The rational model regression ( $y = (a+bx)/(1+cx+dx^2)$ ) was ultimately selected through Akaike's Information Criterion (AIC), and the results were graphically presented (as well as  $R^2$  and AIC reported). Non-linear best-fitting regressions were estimated using the Curve Expert Professional 2.6 software (Hyams 2017).

Locally-estimated scatterplot smoothing (LOESS-smoothing) was used to visualize data trends reducing noise (Jacoby 2000). LOESS-smoothing was applied to clines of ecofunctional diversity (and its components), as well as invasion degree, to show the contribution of each component to the overall ecofunctional diversity.

We performed a linear discriminant analysis to identify differences between exotic, native and translocated species groups based on ecofunctional trait characteristics. Discriminant analysis allows to separate groups of objects based on a combination of features. The analysis derives the coefficients of a scoring function for each category from the input data, and the highest score is used to assign a case to a category (Venables and Ripley 2013). A discriminant analysis was performed for each of the districts, using matrices of species sampled in each area, through the MASS R package. The homogeneity of within-group covariance matrices of the explanatory variables was assessed using the *betadisper* function of the Vegan R package (Oksanen, Blanchet et al. 2017, Borcard, Gillet et al. 2018).

We also carried-out a multivariate analysis, in order to investigate the relationship between ecofunctional traits and invasion/translocation degrees. A secondary aim was to reveal the relationships between invasion and translocation degrees and explore the connections between these variables and major geographical features (altitude, latitude, longitude) and to broad community diversity (species richness). Invasion and translocation degrees, geographical and community diversity variables were selected as independent variables and transformed prior to analysis: percentages were  $(\arcsin X/100)^{0.5}$  transformed, while other variables were  $\log_{10}$  transformed (Legendre and Gallagher 2001). Ecofunctional traits, expressed through the abundance-weighted averages of each trait (calculated through the functional identity metric), were selected as dependent variables. A Detrended Correspondence Analysis (DCA) was

initially performed to select the most appropriate response model for gradient analysis (Lepš and Šmilauer 2003). The dominant gradient length in DCA was always lower than 3 so the Redundancy Analysis (RDA) was finally chosen (Lepš and Šmilauer 2003). RDA is a linear gradient analysis that allows to quantify the variation of a multivariate data set explained by independent variables (Ter Braak and Smilauer 2002). The significance of independent variables was assessed with a forward selection procedure and Monte Carlo permutation tests, however all independent variables selected resulted significant. The collinearity of variables was investigated through the variance inflation factor (VIF), but no collinear variables were found ( $VIF > 8$ ). Multivariate analyses were performed using the CANOCO 4.5 *for Windows* software (Lepš and Šmilauer 2003).

## Results

### *Spatial patterns of invasion*

1940 sites (52% of all sites examined) showed some degree of invasion, and introduced species constituted on average 42.5% of the community in invaded sites, reaching maximums of 100% (i.e. the native community was completely lost in 130 sites, 3.5% of all sites examined). One of the invasion hotspots was located along the Po River, but other highly invaded areas existed in the central and southern part of the Italian peninsula, as well as in the islands (Fig. 1a).

Translocated species were present in 681 sites (18.2% of all sites examined), mostly located in the central and south part of the peninsula. Where present, translocated species were usually part of more invaded communities (44.2% average invasion degree in sites with translocated species presence) and constituted a large part of the introduced community (72.4% average share of the introduced community, 100% of the introduced community in 341 sites), especially in the

TL district. Translocated species were a minor component of the invaded communities of the northern part of the peninsula (in the PDV district), as well as in the islands (Fig. 1b).

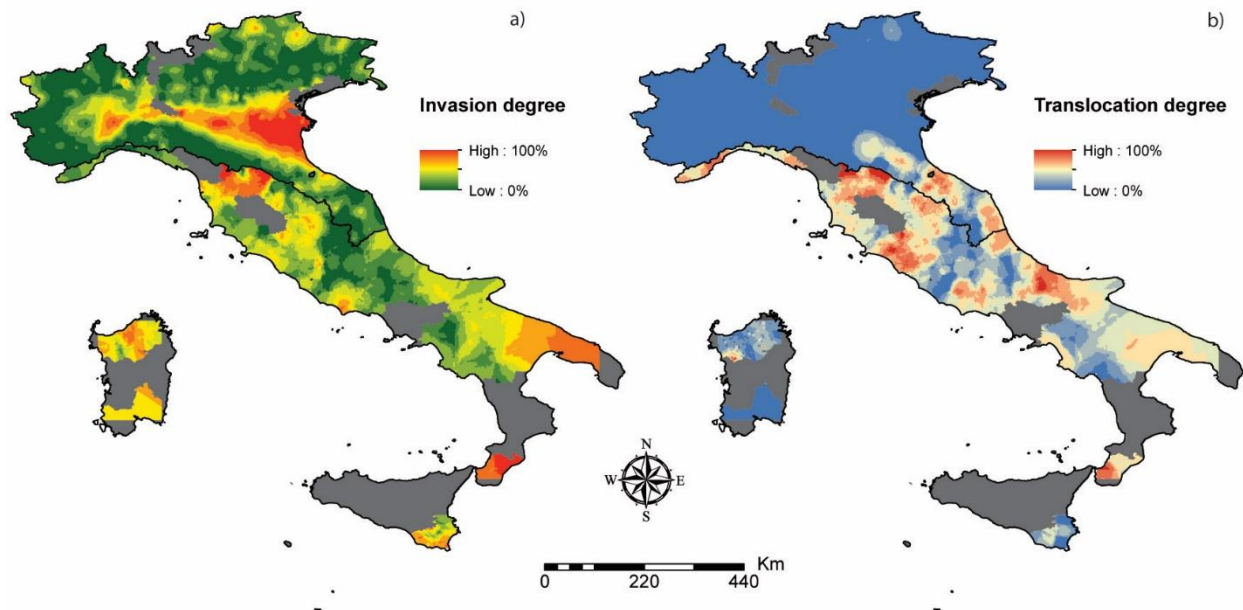


Figure 1 – Invasion (a) and translocation degree (b) in fish communities of Italian inland waters. The solid black line dividing the northern part of the peninsula represents the border of the Padano-Venetodistrict. Grey shaded areas represent zones for which no data could be retrieved.

#### *Relationship between biological invasion and ecofunctional diversity*

Ecofunctional diversity, measured through the functional dispersion metric, generally increased from higher, species poor, altitudes to lower, species rich, altitudes. However, large areas in the lowlands, corresponding to the most invaded areas (i.e. the Po River course in the

northern part of the peninsula), showed decreased ecofunctional diversity compared to other, less invaded, lowland areas (e.g. in the central part of the Italian peninsula) (Fig. 2a).

That the invasion process likely undermined ecofunctional diversity was further underlined by the distribution of the functional dispersion metric along an invasion degree gradient, which showed a marked decrease in ecofunctional diversity for invasion degrees exceeding ~50% (rational model regression  $R^2 = 0.23$ , AIC = -14639.2, Fig. 2b).

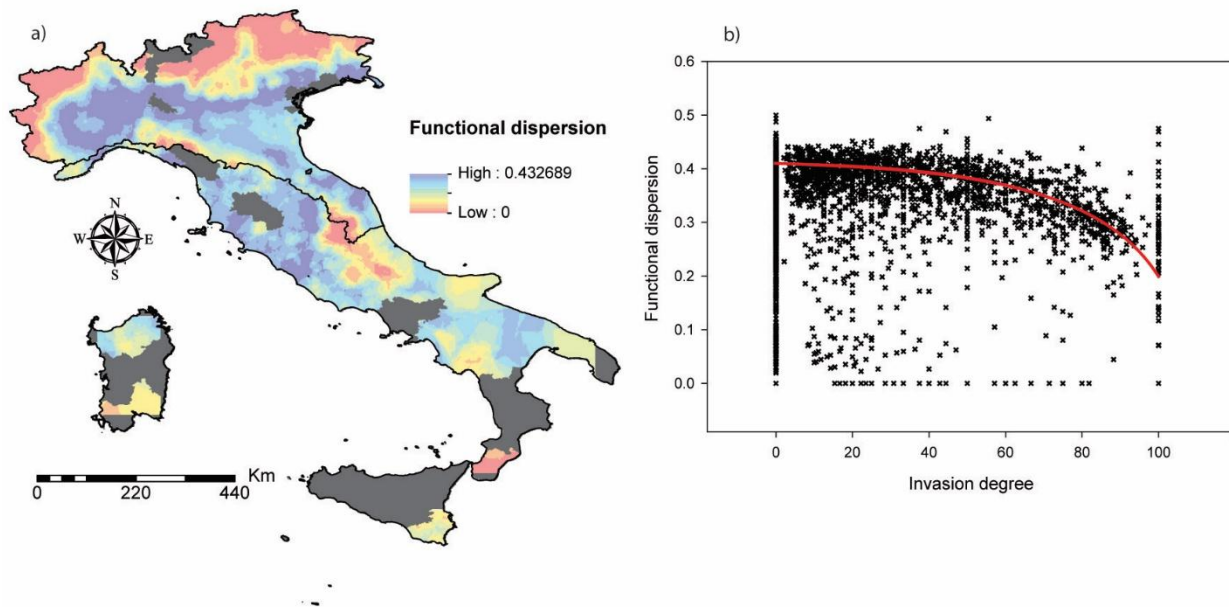


Figure 2 – (a) Spatial distribution of ecofunctional diversity, measured through the functional dispersion metric, in fish communities of Italian inland waters. The solid black line dividing the northern part of the peninsula represents the border of the Padano-Veneto district. Grey shaded

areas represent zones for which no data could be retrieved. (b) Relationships between ecofunctional diversity, measured through the functional dispersion metric, and the invasion degree in fish communities of Italian inland waters. The red line represents the result of the best-fitting regression analysis (rational model).

However, translocated species seemed to contribute less to the decline in ecofunctional diversity: in fact, lower values of functional dispersion were found for high invasion degrees where these were not associated to a high translocation degree (Fig. 3). Some of the highest values of community ecofunctional diversity were reached also in the presence of translocated species, but only at low invasion degrees, whereas a peak in invasion degree was found in sites completely invaded by only one species (rainbow trout), and thus with null functional diversity (Fig. 3).



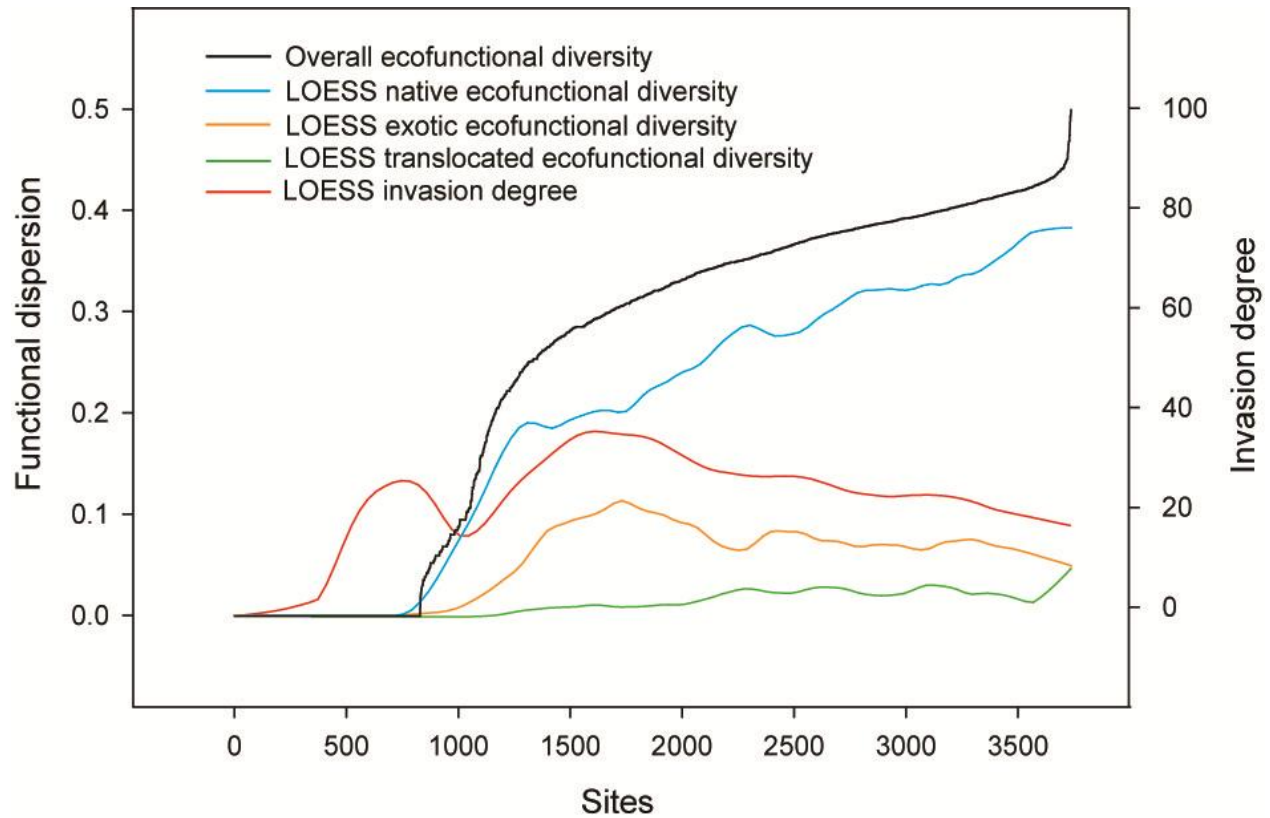


Figure 3 –Native (blue), exotic (orange) and translocated (green) species contribution to the overall ecofunctional diversity, measured through the functional dispersion metric (black line), in fish communities of Italian inland waters. Sites were sorted in ascending order of ecofunctional diversity and the distributions of native, exotic and translocated species contributions were LOESS-smoothed to reduce noise. The red line indicates the LOESS-smoothed invasion degree of each site, scaled on the right vertical axis.

Our discriminant analysis revealed that exotic, native and translocated species ecofunctional traits were highly overlapping in the PDV and TL districts (Fig. 4a and b), whereas a clearer differentiation among the three groups was present in the ISL district (Fig. 4c). The model fits/accuracies were of 80.8%, 71.2% and 87.1%, for the PDV, TL and ISL districts, respectively.

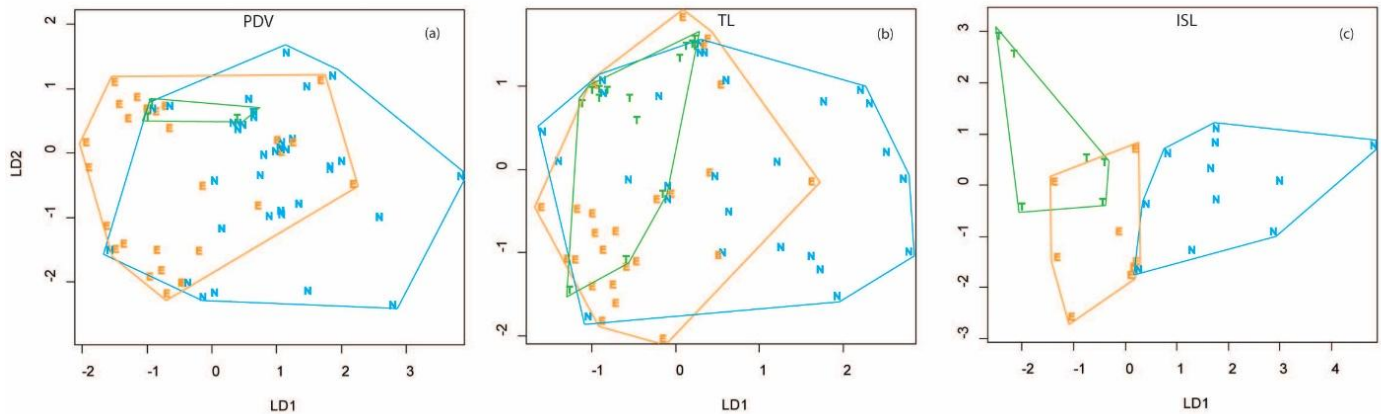


Figure 4 – Discriminant analysis of the ecofunctional overlap between native (blue), exotic (orange), and translocated (green) groups of species present in the Padano-Veneto (PDV, a), the Tosco-Laziale (TL, b) and the Islands (ISL, c) district. Solid lines represent the convex hulls around each of the groups.

#### *Ecofunctional traits typical of invaded communities*

The RDA analysis of site-specific ecofunctional diversity, expressed through the functional identity metric, highlighted some ecofunctional traits of introduced species that were common in all districts (Fig. 5). The total variance derived from the RDA analysis, expressed as the sum of all canonical eigenvalues, was 56.7%, 31.2% and 37.7% for the PDV, TL and ISL districts, respectively. Species adapted to live in turbid waters and reproducing on sand/mud (psammophiles) were common in all invaded zones, irrespective of the district (Fig. 5). In all districts, altitude was inversely related to species richness and, to a lesser degree, to invasion degree (Fig. 5). While a clear relationship between latitude and invasion was apparent in the TL

district (Fig. 5b), the PDV district showed a relationship between invasion and longitude (Fig. 5a).

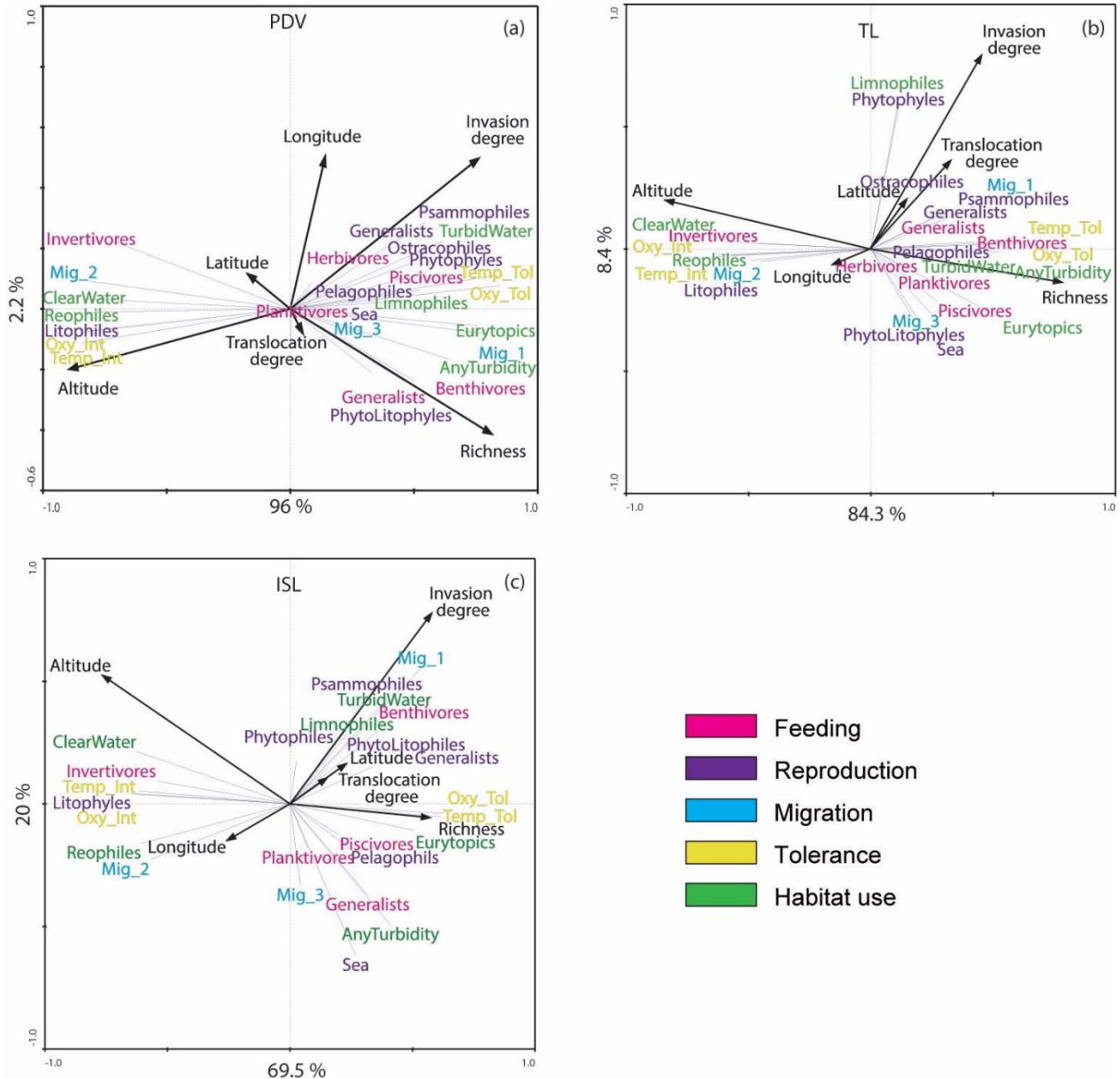


Figure 5 – Plots of RDA of site-specific ecofunctional diversity (colored labels, explored through the functional identity metric) of fish communities in Italian inland waters using geographical variables, species richness, as well as invasion and translocation degrees as explanatory variables (black arrows and labels). Each panel describes sites in a different district: the Padano-Veneto

(PDV, a), the Tosco-Laziale (TL, b) and the Islands (ISL, c) district. Percentage values along each axis illustrate the proportion of variance of the traits-environment relation explained along that axis. Ecofunctional traits are color-coded to separate them in ecological functions, Supplementary Table 2 contains longer descriptions of each trait.

## Discussion

Our results clearly confirmed our hypothesis that exotic and translocated fish species had substantially different geographical distribution patterns, perhaps arising from their differences in introduction, spread and invasion mechanisms. We also found a clear decreasing trend of functional dispersion along an invasion gradient, confirming our hypothesis that the invasion process can diminish the relative diversity of ecofunctional traits of host fish communities. Furthermore, our results suggested that exotic species might be more invasive and thus have a greater negative effect than translocated species on the relative diversity of ecofunctional traits of fish communities. This could also be linked to the fact that translocated species are more ecofunctionally similar to native ones, compared to the exotics, at least in the PDV and TL districts. Our multivariate analysis of site-specific combinations of ecofunctional traits highlighted some traits characteristic of all invaded communities, but some differences and nuances were present in different districts, perhaps due to their species assemblages or their peculiar geographical characteristics. Overall, our results depicted a dire situation for native freshwater fish communities.

*Spatial patterns of invasion*

Possibly, the most striking outcome of our work was the detection of the dramatic situation of native freshwater fish communities, with 130 sites where communities were solely composed by introduced species. Albeit a small percentage (3.5%) of the total sites examined, the invasion process is unlikely to be reversed in these sites, at least in the short term. Furthermore, this count is even more vivid, when considering that local extinctions in connected freshwater ecosystems have been rarely reported for fish (with few exceptions, Townsend 1996, Kitchell, Schindler et al. 1997) and that previous studies over a smaller area had underlined a critical situation for a smaller subset of sites (Lanzoni, Milardi et al. 2018). However, the situation could be much worse nowadays, compared to the survey period. At this level of detail, our analysis was unable to detect smaller community variations before/after the invasion. Another possible limitation of the invasion degree calculated in the present study was that it could not discriminate between mass occurrences of a single invader or the presence of many invading species with few individuals each. Future studies that aim to disentangle the effects of species and abundances could shed further light on this crucial element of invasion dynamics. However, our results have the merit of representing a broad picture of the invasion degree gradient, using the most updated and detailed data available. The invasion was staggeringly widespread in space, spanning the entire area examined and affecting 52% of all sites. The average invasion degree in sites where introduced species were present was also considerably high (42.5%), suggesting that the invasion was not only widespread, but also very pervasive. Previous studies on brown trout genetics in the Apennines range point out that several native Mediterranean trout populations might be genetically compromised by stocking, at least in this area (i.e. most brown trout seem to be of Atlantic or Danubian origin, Caputo, Giovannotti et al. (2004)). Our conservative choice to consider all undetermined brown trout (*Salmo trutta complex*) as native, because of lack of

detailed information, likely decreased the severity of our results. A similar analysis, conducted considering all reported brown trout as introduced, would have worsened our results on the invasion degree by more than 50%, especially at higher altitudes (Milardi, unpublished data).

Conversely, the lowlands showed the highest rates of invasion, with a multitude of introduced species present in the terminal parts of rivers, a distribution that was clearest in the Padanian plain of northern Italy. In this area, the invasion was mostly composed by exotic species, with a very low rate of translocation, if compared to the other districts. On the contrary, translocation rates were higher along the Apennines range, in the TL district, but in this area the overall invasion was relatively low. Translocated species in this area were introduced from the northern part of the Italian peninsula: for example the Padanian goby (*Padogobius bonelli*), an endemic species that has been unintentionally translocated, has become invasive and detrimental to another endemic goby, the Arno goby (*Padogobius nigricans*), (see e.g. Pompei, Giannetto et al. (2018)). The different spatial distribution of exotic and translocated species could partly be due to national mechanisms of fisheries management dating back to the early 20<sup>th</sup> century. It is around this time that some exotic species were first introduced in northern Italy and the state created aggregated farms to stock (both exotic and native) fish species of recreational value throughout the peninsula in an effort to enhance fisheries (Milardi, Aschonitis et al. 2018).

#### *Relationship between biological invasion and ecofunctional diversity*

From our results (e.g. Fig. 2b), it was clear that species introductions, notwithstanding their origin, undermined the ecofunctional diversity of host communities. Similar detrimental effects of exotic invasions on functional diversity were found by Shuai, Lek et al. (2018), by looking at different functional traits. Furthermore, a previous study in Italy had already underlined this mechanism, in a limited area where native and exotic species overlapped, and attributed it to the

intrinsically lower ecofunctional diversity of exotic species, and partly to homogenization processes caused by the invasion process (Milardi, Gavioli et al. 2019). Our present results greatly expand the basis for such conclusion and confirm such a mechanism exists over a much larger spatial scale. Local extinctions of native species, and a general decline of native abundance, have been previously linked with the interaction between native and introduced species in parts of the study area (Castaldelli, Pluchinotta et al. 2013, Lanzoni, Milardi et al. 2018, Milardi, Aschonitis et al. 2018). Native extinctions and decline of native abundance could be partly responsible for the decline in ecofunctional diversity detected at highly invaded sites, but further work and data comparing the communities before/after invasion would be needed to confirm this. In the PDV district, the most invaded area in our dataset, richness and altitude were less inversely linked than in other districts, implying that homogenization processes underlined in a sub-area of this district (Gavioli, Milardi et al. 2019) could be typical of the whole area. Biotic homogenization at the faunal district scale leads to communities dominated by few exotic species (Rahel 2000, Leprieur, Beauchard et al. 2008), which are consequently less ecofunctionally diverse. Our analysis further suggested that ecofunctional diversity loss could be led by exotic, rather than translocated species (see Fig. 3). A possible explanation could be that translocated species could be ecofunctionally more similar to native species (at least in some districts, see Fig. 4a and b), because their evolutionary divergence is usually recent (i.e. the abovementioned case of endemic Italian gobies), and thus might tend to cause less ecofunctional diversity losses. Another possible explanation is that invasions led by translocated species generally reach lower levels of invasion and homogenization, thus affecting less the ecofunctional diversity of impacted communities. However, even low invasion rates of translocated species are likely to influence native taxonomic and genetic diversity, so the impact

of translocation on native biodiversity should not be underestimated. Communities with diminished taxonomical or ecofunctional diversity could be less resilient to further pressures, e.g. those of climate change, if key functional groups of the communities are lost (Dunne, Williams et al. 2002). Further studies, using detailed temporal information, would be needed to assess whether biodiversity losses in the Mediterranean region have impaired the resilience of freshwater communities. Furthermore, it would be important to evaluate the respective contributions of habitat degradation and invasion processes on the functional diversity of communities (Colin, Villéger et al. 2018). Site-specific data on pristine communities would be needed to investigate the change in ecofunctional composition resulting from the invasion process (and other, multiple, pressures). Unfortunately, we could only analyze the introduction gradient over a large number of sites, which does not equal an assessment of the variation before/after the invasion in each site.

#### *Ecofunctional traits typical of invaded communities*

By analyzing this invasion gradient we were able to underline that some ecofunctional traits are dominant in highly invaded communities in all districts, for example adaptations to live in turbid waters and reproducing on sand/mud. However, our analysis could not discriminate whether some of these traits were typical of pristine communities in different invaded areas, as we lacked complete data on pristine or unimpacted communities. Not all traits highlighted in invaded communities are typical of generalist species, as suggested by previous studies (Marr, Olden et al. 2013, Milardi, Gavioli et al. 2019), perhaps indicating a higher complexity of traits associated with fish invasions than previously thought. Furthermore, the differences in invasion rates among the districts, and the differences in the prevalence of some of the other traits associated with high invasion in each district (see Fig. 5), suggest that pinning down the linkages



between these changes and invasion could be a rather complex task. Some of the differences that we found among districts could be attributed e.g. to the different translocation rates, or to the climatic and geographical differences between the districts. For example, the prevalence of short migration species in invaded areas of the TL and ISL districts seems to suggest that habitat degradation (e.g. habitat fragmentation by artificial barriers) could play a role in the invasion process. However, streams in these areas are generally shorter in length and naturally fragmented due to drought events in summer, so that these traits could be more associated to environmental rather than invasion factors. Furthermore, anthropogenic habitat fragmentation has been previously found to block the spread of invading species in rivers (Gavioli, Mancini et al. 2018). Dissimilarities in ecological traits between native and introduced species have been previously suggested as a potential key factor of invasiveness (Divíšek, Chytrý et al. 2018), but our discriminant analysis underlined that, at least in the PDV and TL districts, translocated, exotic and native species ecofunctional traits had little dissimilarities. Potentially, this could be a relevant factor in the ISL district, where species groups were most ecofunctionally distinct. Despite the fact that our analysis was able to outline some of the ecofunctional traits dominant in invaded communities of different districts, the relationship between invasion success and ecofunctional traits of successful invaders would need to be further explored in dedicated studies, aiming to assess more quantitatively the differences existing among different areas. Furthermore, the validity of our conclusions should be explored in other taxa and other regions.

### *Conclusions*

In summary, our results underline new aspects of a potential threat to native biodiversity, which possesses a widely-recognized conservation value (Humphries, Williams et al. 1995). However, while biodiversity is regarded as a key characteristic of the Mediterranean region,

native biodiversity has not been extensively evaluated, especially from a socio-economic perspective. Social support for native biodiversity could be too low, especially in the case of fish (see e.g. Tiberti (2018)), to develop and apply multi-species conservation actions that could be costly and unpopular. Conversely, the increasingly-popular role of several exotic and translocated species in recreational fisheries has provided a powerful stimulus in the opposite direction: the species of recreational interest are actively stocked, further spread by anglers and, in several cases, also benefit from protection measures (Milardi, Aschonitis et al. 2018, Milardi, Lanzoni et al. 2018). Perhaps as a consequence of these socio-economic pressures, national ministries of some Mediterranean countries do not strictly apply the national and international legislation aimed at limiting the presence and spread of exotic invasive species, or even allow the introduction of exotic species when they can bring economic benefits (see e.g. Anastácio, Ribeiro et al. 2018). Despite potential economic gain, exotic species invasion can have multiple and cascading impacts on the host environment (some of which are relatively difficult to explore, see e.g. Milardi, Petäjä et al. 2019), with potentially major consequences (Maceda-Veiga, López et al. 2017, Milardi, Soana et al. 2019), besides negatively affecting native biodiversity. Our work could contribute to underline the critical state of native biodiversity and the relevance of the invasion process in Mediterranean inland waters, but further actions would be needed to disseminate its significance to the general population and build political support for conservation solutions.

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## Author contributions



M.M. conceived the study and M.M. and A.G. collected and analyzed the data. All authors critically contributed to the drafting of the manuscript.

## Appendix A

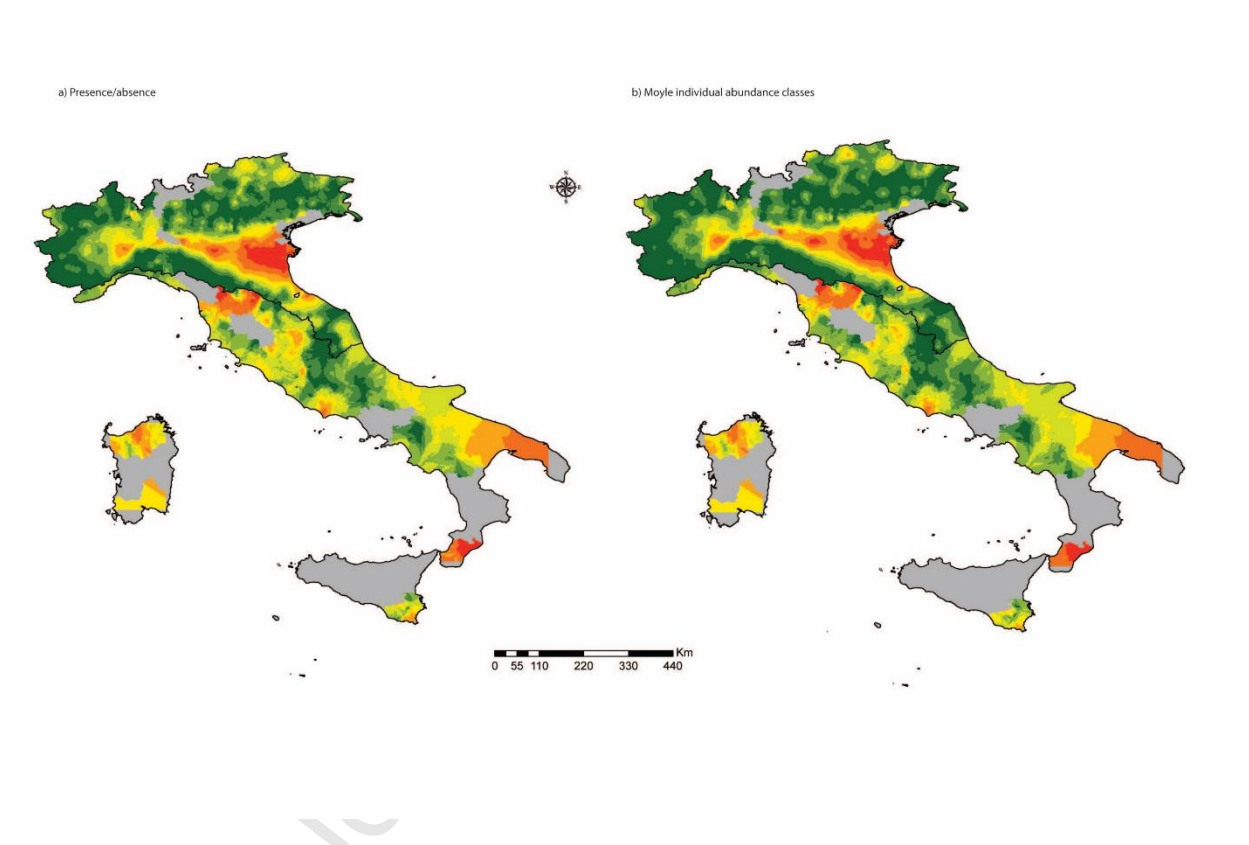
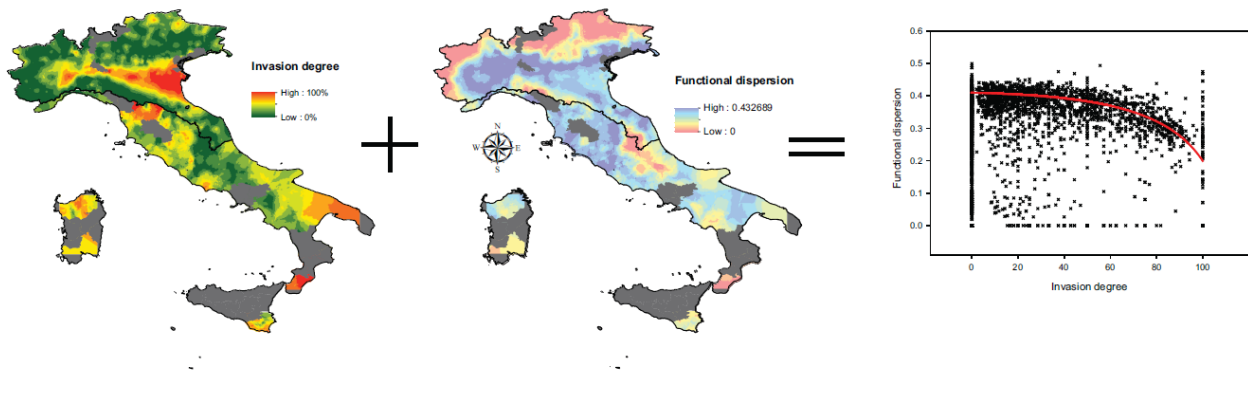


Figure A.1 - The left (a) panel shows the invasion degree calculated on species presence/absence, while the right (b) panel represents the invasion degree estimated using Moyle individual abundance classes uncorrected for body size.

## Graphical abstract



### Highlights for “The role of species introduction in modifying the functional diversity of native communities”

- Introduced species were widespread, and in many cases the invasion was severe, in Italy
- Exotic and translocated fish species had different geographical distribution patterns
- Invasion can diminish the ecofunctional diversity of host fish communities
- Exotic species might have worse effects than translocated ones
- Some traits were typical of invaded communities, but with regional differences