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A novel approach to quantifying trophic interaction strengths and impact of invasive species in food webs

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Abstract Measuring ecological and economic impacts of invasive species is necessary for managing invaded food webs. Based on abundance, biomass and diet data of autochthonous and allochthonous fish species, we proposed a novel approach to quantifying trophic interaction strengths in terms of number of individuals and biomass that each species subtract to the others in the food web. This allowed to estimate the economic loss associated to the impact of an invasive species on commercial fish stocks, as well as the resilience of invaded food webs to further perturbations. As case study, we measured the impact of the invasive bass *Micropterus salmoides* in two lake communities differing in food web complexity and species richness, as well as the biotic resistance of autochthonous and allochthonous fish species against the invader. Resistance to the invader was higher, while its ecological and economic impact was lower, in the more complex and species-rich food web. The percid *Perca fluviatilis* and the whitefish *Coregonus lavaretus* were the two species that most limited the invader, representing meaningful targets for conservation biological control strategies. In both food webs, the limiting effect of allochthonous species against *M. salmoides* was higher than the effect of autochthonous ones. Simulations predicted that the eradication of the invader would increase food web resilience, while that an increase in fish diversity would preserve resilience also at high abundances of *M. salmoides*. Our results support the conservation of biodiverse food webs as a way to mitigate the impact of bass invasion in lake ecosystems. Notably, the proposed approach could be applied to any habitat and animal species whenever biomass and diet data can be obtained.

Keywords Alien species · Biotic resistance · Competition · *Micropterus salmoides* · Predation · Food web resilience

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Introduction

Invasive species are among the main causes of biodiversity loss and changes in ecosystems (Gozlan et al. 2010; Gallardo et al. 2016), and their impact is expected to increase worldwide due to climate warming and human action (McClelland et al. 2018; Ricciardi et al. 2017). Resource consumption by invaders in relation to resource availability (i.e. the

functional response by invaders, sensu Dick et al. 2017a) is a central element in several hypotheses predicting their success in invaded habitats (Dick et al. 2017a). Nevertheless, measurements of functional responses are often performed under simplified conditions. Specifically, they do not take into account the multiple biotic interactions that constrain invasive species in food webs, and may thus fail to predict their impact in real ecosystems (see Vonesh et al. 2017 for a discussion on this point). Thus, while research in the field has increased during recent years (Dick et al. 2017b; Laverty et al. 2017; Corrales et al. 2019), our ability to measure the ecological and economic impact of invaders in natural communities is still limited (Kulhanek et al. 2011; Crystal-Ornelas and Lockwood 2020).

In this context, the quantification of the impact of biological invasions on complex food webs and key ecosystem services (including the productivity of commercially exploited species) is necessary to formulate effective management strategies (Gozlan et al. 2010; Davies and Britton 2015; Latombe et al. 2017). In parallel, conservation biological control strategies would benefit from a quantitative measure of the resistance by autochthonous and allochthonous species against recently established invaders, thus enabling the identification of meaningful conservation targets (Frost et al. 2019). Indeed, invaders' success can vary greatly depending on the structure of invaded food webs (Dzialowski et al. 2007; Jackson et al. 2013; Smith-Ramesh et al. 2017; Vonesh et al. 2017), through mechanisms of biotic resistance by competitors (competitive resistance) and predators (consumptive resistance) (Britton 2012; Alofs and Jackson 2014; Smith-Ramesh et al. 2017; Rehage et al. 2019). However, field studies comparing consumptive and competitive resistance at the whole food web level are lacking (Alofs and Jackson 2014). Similarly, there is a lack of information about the effects of invaders on the dynamic properties of food webs, including web resilience to further perturbations. This hinders an effective conservation and management of invaded communities, which may be exposed to other environmental stressors (e.g. habitat degradation) that interact with invasion, impairing the persistence of food webs (Didham et al. 2007; Prior et al. 2017; Norbury and van Overmeire 2019).

In recent years, the study of invaded food webs has benefited from the application of stable isotope analysis coupled with Bayesian mixing models to the description of trophic links between species (Bond et al. 2016; Costantini et al. 2018; Ferguson et al. 2018). However, isotopic Bayesian mixing models quantify interspecific interactions as the proportional contribution of each prey to the predator's diet, while they do not provide information on the biomass and/or number of individuals subtracted to prey populations by predators. This represents a crucial limitation when the food web description has to be used to quantify the effect of invasive species on (1) the population dynamics of other species (Ferguson et al. 2018), (2) food web resilience to perturbations (May 1974; Allesina and Tang 2012; Landi et al. 2018), and (3) potential economic losses associated to the reduction of commercially exploited species.

To fill these gaps, we proposed a novel approach for the quantification of trophic interaction strengths in terms of number of individuals and biomass that each predator and/or competitor subtracts to other species in invaded food webs. Based on abundance, biomass and stable isotope data of species, the proposed method allowed us to calculate the resistance against an invasive species at the population and the food web levels, as well as the impact of the invader on the remaining populations. The method also allowed us to estimate the carrying capacity of fish populations and, thus, to calculate food web resilience to perturbations (May 1974; Allesina and Tang 2012).

As a case study, we considered the invasion of lake food webs by the largemouth bass, *Micropterus salmoides* (Lacépède) (Costantini et al. 2018), one of the 100 most invasive species in the world (Welcomme 1992; Brown et al. 2009). We compared two communities invaded by the bass and including both autochthonous and allochthonous fish species introduced into the lake before *M. salmoides*. The two food webs differed in the number of species and trophic links, and we related differences in the impact of the invasive species to their structures. Specifically, we calculated the consumptive and competitive resistance by competitors and predators to the invader, and the biomass that it subtracted to each prey. This also allowed to quantify the potential economic loss associated to the impact of the invader on lake fish stocks, and to simulate the effect of a reduction in its abundance on food web resilience. While we have focused on lake food webs, the proposed approach can be applied to any other habitat and animal species if

biomass and diet data (either obtained through stable isotopes or other methods) can be obtained. This virtually includes all the invertebrate and vertebrate animal taxa.

Materials and methods

Interspecific interaction strengths and biotic resistance to an invasive species

Using food web data from Costantini et al. (2018), we calculated the strength of all species-pair trophic interactions in the food web. Species' diets were assessed through Bayesian mixing models (SIAR package for R software) based on stable isotope analysis of fish species and their potential food sources. Abundance and biomass of fish were also measured (Appendix S1: Table S1). Analytical methods for the description of species' diet in food webs based on isotopic data have been widely addressed and implemented in recent years, and details can be found in Costantini et al. (2018), Rossi et al. (2019), and in the literature cited therein.

Competition

Following Levins (1968) and Calizza et al. (2017), the strength of interspecific competition between species pairs was calculated with reference to the overlap in resource use, accounting for the proportional contribution of each prey to the diet of each predator. Competition strength is indicated by α_{ij}, i.e. the effect of species j on species i, in accordance with the Levins's formula:

$$\alpha ij = \frac{\sum_h pih \times pjh}{\sum_h (pih)^2} \quad (1)$$

where p_{ih} and p_{jh} are the proportional consumptions of a resource h by species i and species j respectively.

The strength of interspecific competition was corrected for the biomass ratio between competitors, i.e., the measured value of α_{ij} was multiplied for the ratio between the mean body mass of species j and that of species i. Such product will be identified with β_{ij}, intending the competitive effect of species j on species i. This was necessary because competition is expected to decrease with increasing difference in body mass between competitors, i.e. the smaller a competitor j with respect to a species i, the weaker the effect of j on i, due to mass-related differences in energetic requirements, food-size selection and foraging habitat exploration (Basset 1995; Emmerson and Raffaelli 2004; Brose et al. 2006; Neutel et al. 2007). This also has the potential to create asymmetric competition for similar values of α due to body mass differences between species.

Then, the limiting effect of a given competitor j on a species i was calculated as:

$$\text{Limiting effect} = \beta_{ij} \times N_j \quad (2)$$

where N_j is the number of individuals of species j (Calizza et al. 2017 and literature cited therein). According to Eqs. 1 and 2, both α_{ii} and β_{ii} (i.e. the intraspecific interaction terms) give always 1. Thus, the intraspecific limiting effect is directly dependent on the population size, i.e. the number of individuals (N) of species i.

Predation

The effect of a predator species on its prey species was also calculated. To achieve this, the biomass density of each predator species (BD_P) was calculated as:

$$BD_P = N_P \times B_P \quad (3)$$

where N_P and B_P are the mean density and body mass of a given predator P respectively. Then, the biomass of a given prey m subtracted by a given predator P (B_{mP}) was estimated as:

$$B_{mP} = (BD_P \times F_{mP})/\text{Eff} \quad (4)$$

where F_{mP} is the proportional contribution of the prey to the diet of a predator, and Eff is the efficiency of transformation of prey biomass into predator biomass, with Eff varying between 0 and 1 (see below).

Then, the number of individuals of a prey m subtracted by a predator P (N_{mP}) was obtained as:

$$N_{mP} = B_{mP}/B_m \quad (5)$$

where B_m is the mean body mass of the prey.

Carrying capacity and biotic resistance against the invasive species

Based on Eqs. 2 and 5, the carrying capacity of a given species i (K_i) was thus calculated with reference to Lotka-Volterra models (Cohen et al. 1990; Zeeman 1995; Calizza et al. 2017), as:

$$K_i = N_i + \sum_{j=1}^{C} \beta_{ij} N_j + \sum_{P=1}^{S} N_{mP} \quad (6)$$

where $\beta_{ij} N_j$ and N_{mP} are the effects of competitors and predators of species i respectively, as reported above, and C and S are the numbers of competitors and predators of species i.

After the calculation of its K, food web-scale competitive and consumptive resistance against an invasive species can be obtained as:

$$\text{Competitive resistance} = \left(\sum_{j=1}^{C} \beta_{ij} N_j \right) / K_i \times 100 \quad (7)$$

$$\text{Consumptive resistance} = \left(\sum_{P=1}^{S} N_{mP} \right) / K_i \times 100 \quad (8)$$

Hence, resistance to an invasive species is measured as the percentage of individuals that competitors and predators subtract to its population with respect to its carrying capacity.

Table S2 in Appendix 1 includes all the variables used in Eqs. 1 to 9, their units and ecological meaning.

Food web structure and resilience to perturbations

Food webs were described with reference to: the number of species (S), the number of feeding links (L), connectance (Cmin), measured as 2L/(S x (S−1)), and connectivity, measured as S x Cmin. The Shannon diversity (Hs) was used to quantifying the diversity of fish communities excluding the invasive species *M. salmoides*. A bootstrap procedure, available in the Past 3.0 software, was applied to compare Hs values between food webs.

In order to account for the effects of both direct and indirect interactions between species, food web resilience to perturbations (i.e., the local Lyapunov stability) was investigated with reference to the inverse of the classical Jacobian matrix (J^{-1}) (May 1974; Montoya et al. 2009; Calizza et al. 2017). Here, we focused on competitive interactions because they represented the majority of interactions between fish species (Costantini et al. 2018), they have a strong destabilising effect on species assemblages (Allesina and Tang 2012) and because invaders are expected to have strong competitive effects in invaded communities (Marchetti et al. 2004; Gozlan et al. 2010). The classical Jacobian matrix (J) is obtained by multiplying species densities with the interspecific interaction matrix containing pair-wise interaction coefficients (see Appendix 1: Fig. S1 for details). The diagonal of the Jacobian matrix contains the intraspecific interaction terms. The inverse Jacobian matrix (J^{-1}) is obtained by multiplying J for its transpose matrix (J'). Each element of J^{-1} describes the net effect of species A on species B, taking into account all indirect pathways that link species A and B via intermediate species (Montoya et al. 2009). This implies that species A may have an effect on species B even if the two species do not interact directly. The stability of a given n-species matrix can be inferred from its eigenvalues, with stability (i.e. resilience) being expected for matrices having only negative eigenvalues (in their real part) (May 1974; Allesina and Tang 2012). Here, stability is defined by Re(λmax) of J^{-1}, which is the real part of the maximum eigenvalue, and by its sign. The system will return to the equilibrium for negative Re(λmax), while it will move away from the equilibrium for positive Re(λmax). In both cases, the rate of return to or 'escape' from the equilibrium is defined by the absolute value of Re(λmax). The mean real part of all eigenvalues of the matrix, Re(λmean), is a function of the mean diagonal elements of the matrix itself. Increasing the absolute value of the negative terms on the diagonal moves the Re(λmean) towards more negative values (Johnson et al. 2014; Jacquet et al. 2016). Given that the diagonal contains the intraspecific interaction terms, and according to the stability criterion applied, i.e. Re(λmax) < 0, the value of Re(λmax) (hereafter referred to as λ) can thus be seen as a measure of the intraspecific regulation that is needed to stabilize the system considering both direct and indirect interactions between species in the food web.

Application to a case study: fish invasion in lake food webs

Study area and sampling activities

Lake Bracciano is located 32 km north-west of Rome (Lazio, Italy), and it is an oligo-mesotrophic volcanic lake (Rossi et al. 2010). It has a perimeter of 31.5 km, a surface area of 57 km^2 and its maximum depth is 165 m. Bass invasion (i.e. *Microoperus salmoides*) was first reported in 1998 (Marinelli et al. 2007).

Two sampling locations were selected in the north-western (hereafter: North) and south-eastern (hereafter: South) littoral areas of the lake. The South location was characterised by a gently sloping bottom, in contrast to the sharper slope observed in North. Previous samplings along 100 m linear transects indicated that the coverage and diversity of both riparian and submerged vegetation were nearly double on gently sloping bottom (Rossi et al. 2010; Costantini et al. 2018). Accordingly, we considered the North and South locations to be characterised by low and high habitat complexity respectively. Consistently, the percentage of organic matter in sediment (2.2 ± 0.2% in North vs. 17.3 ± 4.2% in South) and macroinvertebrate density were higher in South (311.4 ± 34.9 individuals per sampling site in North vs. 711.9 ± 123.8 in South) (Costantini et al. 2018). In both locations, measured temperature, pH and oxygen concentrations fall within the optimal range for the growth and activity of *M. salmoides* (Scott and Crossman 1973; Brown et al. 2009; Costantini et al. 2018). Fish were sampled with the help of professional fishermen from local cooperatives. Catches were performed for three days in each location, in the last week of June. A modified version of a surrounding net without a purse line (40 m linear length) and two fishing traps were used in each location and at each sampling occasion. A very fine mesh (0.5 cm) was used in order to include small fish specimens in the catches. Sampling locations and sampling activities are described in detail in Costantini et al. (2018).

Based on a recent checklist of the Italian freshwater fish fauna (Lorenzoni et al. 2019), fish species were indicated as "autochthonous" or "allochthonous", intending those allochthonous species introduced in central Italy in the past (i.e. before the half of the twentieth century) that naturally persist within the lake (Fig. 1 and Appendix 1: Table S1).

Impact of Microoperus salmoides on lake fish stocks and food web resilience

Original of North America, *M. salmoides* is a successful invader worldwide (Brown et al. 2009), producing severe impacts on biodiversity and ecosystem functioning in invaded habitats (Jackson 2002; Leunda 2010; Ribeiro and Leunda 2012). The bass can survive between 10 °C and 32 °C, while optimal temperature ranges from 24 to 30 °C. It normally inhabits waters with an oxygen concentration > 3.0 mg/l, while a concentration between 1.5 mg/l and 3.0 mg/l can be tolerated at optimal temperature. Optimal pH ranges from 6.5 to 8.9 (Scott and Crossman 1973; Brown et al. 2009). Regarding its diet, *M. salmoides* is known to feed both on invertebrate and fish prey. The bass starts consuming fish when it reaches a standard length of 7–10 cm (Olson 1996; Marinelli et al. 2007), and it is able to adapt its diet depending on habitat complexity and prey availability (Brown et al. 2009; Britton et al. 2010; Costantini et al. 2018).

Various studies provided detailed measurements of physiological parameters of *M. salmoides*. Specifically, an ingestion rate of 3.0% (range: 2.2–3.9%) of its body mass per day, and an efficiency of prey transformation into body mass (Eff) of 27–28% have been reported (Markus 1932; Hunt 1960; Scott and Crossman 1973; Brown et al. 2009). Together, these values allow estimating that a complete turnover of a given standing biomass of *M. salmoides* would take 121.4 days (min: 95.0 days, max: 168.3 days, based on the reported range of ingestion rate). This implies a biomass turnover rate (TO) of 3.0 per year on average (range: 2.3–3.7 per year).

Given the TO of *M. salmoides*, we estimated the year-round body mass that *M. salmoides* subtracted to each prey population m at each location as:

$$B_{mP\text{year}} = B_{mP} \times \text{TO} \qquad (9)$$

where B_{mP} is the biomass subtracted to each prey as calculated with Eq. (4). The calculation was repeated by accounting for the different number of specimens of *M. salmoides* captured at each sampling occasion and location.

For *Perca fluviatilis* and *Atherina boyeri*, the two most commercialized fish species of the lake, the biomass subtracted by *M. salmoides* was converted into economic value by considering a cost of 18 €
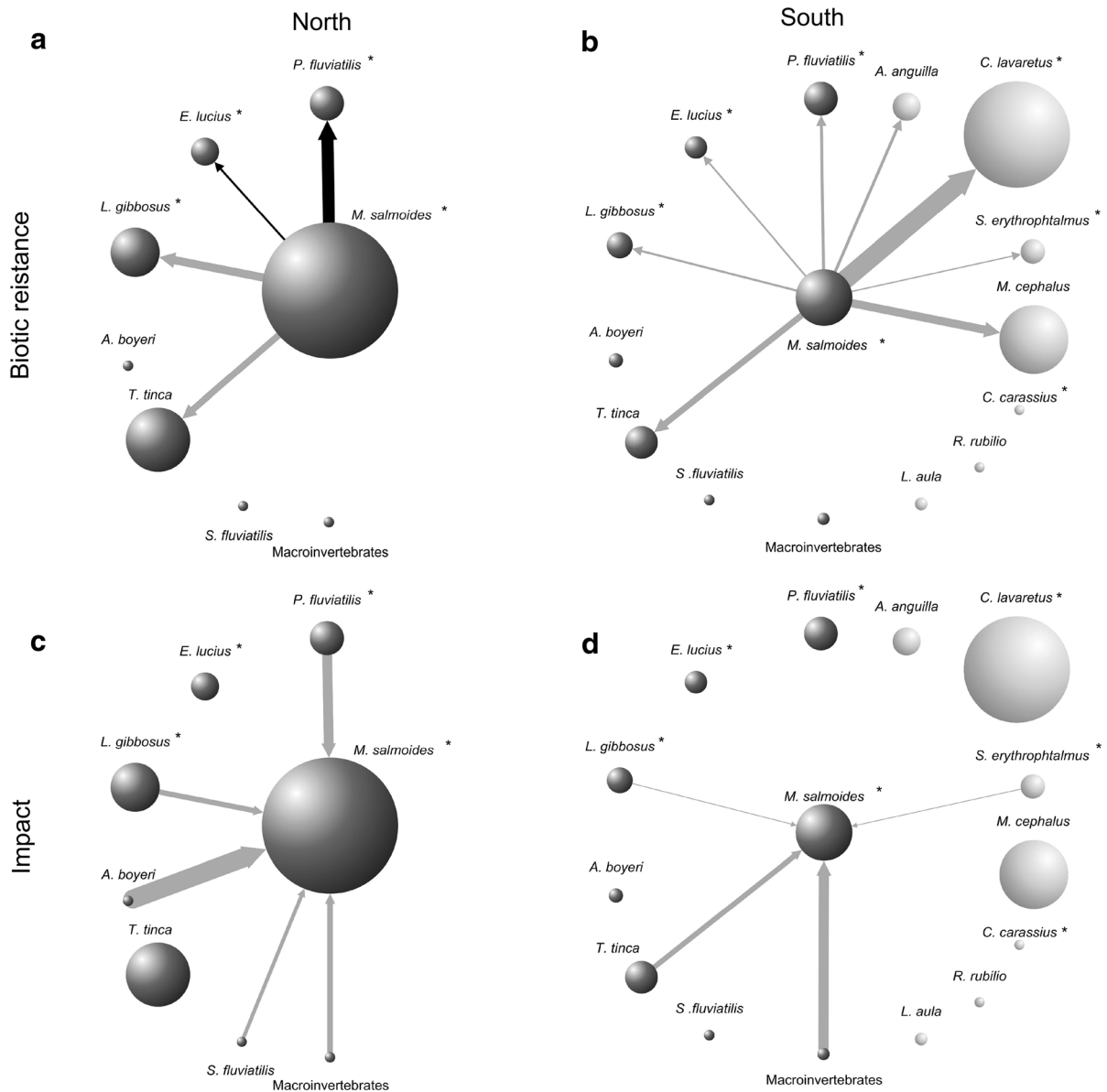
Fig. 1 Panels **a**–**b**: Biotic resistance of fish communities against the invasive species *Micropterus salmoides* in the North and South littoral area of Lake Bracciano (Italy). Arrow width is proportional to the limiting effect, measured in terms of number of individuals subtracted to *M. salmoides* (limiting effects < 1 are excluded). Grey arrows: competition; black arrows: both competition and predation contributed to the limitation on *M. salmoides*. Panels **c**–**d**: Impact of *M. salmoides* on invaded communities. Arrow width is proportioanl to the estimated biomass that *M. salmoides* subtracted to each prey. Nodes' size is proportional to the biomass density of each population. The size of nodes symbolising invertebrates is not to scale with fish. Asterisks denote allochthonous fish species. Dark grey nodes: species found in both locations; light grey nodes: species found only in South. See Tables S1 and S4 in Appendix 1 for details

Kg^{-1} for the former, and 6 € Kg^{-1} for the latter in accordance with the local fish market.

M. salmoides was preyed by *Perca fluviatilis* and *Esox lucius* only in North. Here, the three species shared a very similar trophic position, having a mainly piscivorous diet (Costantini et al. 2018). *P. fluviatilis* had a nearly complete overlap in resource use with *M. salmoides*. In parallel, while *E. lucius* had a relatively

different use of specific prey, the applied Eff falls within values reported for this species (Diana 1983). Accordingly, Eff = 0.27 (known for *M. salmoides*) was applied also to *P. fluviatilis* and *E. lucius* to quantifying the biomass and number of individuals of *M. salmoides* subtracted by the two predators.

In order to test the effect of *M. salmoides* on food web resilience, we simulated a progressive reduction in its abundance up to eradication. Based on Lotka-Volterra population models, at each step, the equilibrium abundances of all remaining fish species were recalculated by taking into account the number of individuals of *M. salmoides* eliminated, and the number of individuals that it subtracted to each competitor (Eq. 2) and/or prey according to the contribution to the diet of *M. salmoides* (Eq. 5). Then, the value of λ was recalculated.

To explore the effect of increased fish diversity, i.e. increased evenness of fish populations' abundances, on food web resilience, we repeated the above-mentioned simulations by considering an equal abundance of fish species while maintaining stable the overall number of fish specimens sampled at each location. This had the effect to maximize the evenness of fish populations and thus the Shannon diversity value (Hs) of the two fish communities. This allowed us to evaluate (1) the potential effect of lake management strategies aimed at improving fish diversity, and (2) the theoretical effect of diversity on the resilience of invaded food webs.

Lastly, based on the observed relation between the abundance of *M. salmoides* and the value of λ, we used linear models to calculate the increase of *M. salmoides* (as % of the observed abundance within each food web) which should be expected to destabilize the food web (i.e. which led to $\lambda \geq 0$). The Akaike Information Criterion (AIC) was used to select the best model of fit.

Results

Food web structure and biotic resistance against *M. salmoides*

Richness, abundance and diversity of fish species were all higher in South than in North (Table 1 and Appendix 1: Table S1). Accordingly, the total number of trophic links and food web connectivity were both higher in the former location (Table 1). In contrast, *M.*

Table 1 Number (S), abundance (N) and diversity (Hs) of fish species being part of the communities invaded by *M. salmoides* in the North and South littoral lake area of Lake Bracciano (Italy)

	North	South
S	6	13
N§	169 ± 11	267 ± 29
Hs*	1.1 ± 0.4	2.3 ± 0.2
Links	26	68
Cmin	0.26	0.23
Connectivity	2.6	4.1

Values exclude *M. salmoides*. Links, Cmin (i.e. minimum connectance) and Connectivity refer to the number of trophic links and complexity in the two food webs. Superscript symbols indicate a significant difference (p < 0.05, §: Wilcoxon test, *: Bootstrap comparison)

salmoides was more abundant in North (45 ± 7 vs. 18 ± 2 individuals, t-test, t = 6.9, *p < 0.01*). Excluding *M. salmoides*, 3 autochthonous and 3 allochthonous fish species were found in North, while 7 autochthonous and 6 allochthonous species were found in South. Allochthonous species represented the 79.9% of all the individuals sampled in North and the 40.4% in South (χ^2 test, $\chi^2 = 45.1$, p < 0.0001), and their mean body mass was generally higher than that of autochthonous species (Appendix 1: Table S1).

The contribution of fish prey to the diet of *M. salmoides* was higher in North (87% vs. 41% of diet). In particular, *P. fluviatilis* and *A. boyeri* constituted the 23% and 43% of its diet respectively in North, while they were not consumed in South (Fig. 1). In turn, *M. salmoides* contributed to the diet of *P. fluviatilis* (26%) and *E. lucius* (7%) in the former location, while it was not preyed in the latter (Fig. 1). Given the low biomass density of *P. fluviatilis* and *E. lucius* with respect to *M. salmoides* (Fig. 1), and the relatively low contribution of *M. salmoides* to their diet, varying the Eff value had a largely negligible effect on the estimated number of individuals of *M. salmoides* subtracted by the two predators (Appendix 1: Table S3).

Mean competition strength (i.e. α_{ij}) suffered by *M. salmoides* from the other fish species was higher in South (0.71 ± 0.06 vs. 0.34 ± 0.04, t-test, t = 3.2, *p < 0.01*) (Appendix 1: Table S4), and the biotic resistance against the invader was higher in this location (Fig. 2). Indeed, the observed abundance of
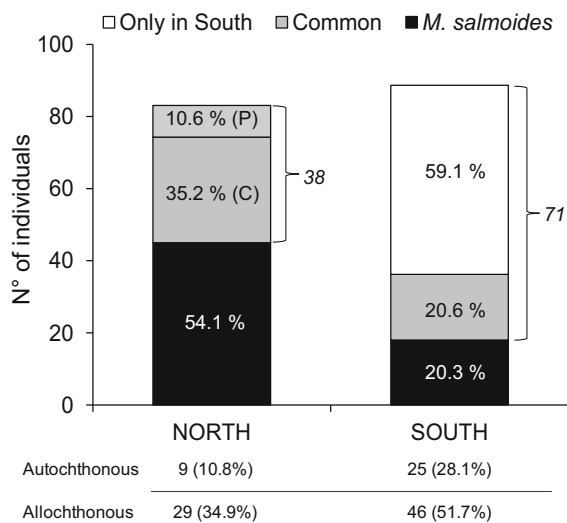
Fig. 2 Abundance of *Micropterus salmoides*, as well as the biotic resistance (i.e. the limiting effect, in terms of n° of individuals as a percentage of its carrying capacity) undergone by the bass in the North and South littoral area in Lake Bracciano (Italy). "Common" refer to the biotic resistance by fish species found in both locations; "Only in South" refers to the biotic resistance by fish species found only in South. P and C refer to the effect of predation and competition respectively. Only competition was observed in South. Numbers within each area represent the percentage of the total, while numbers on the right of brackets quantify the n° of individuals subtracted to *M. salmoides*. The total number of specimens (i.e. the bar height) is the estimated carrying capacity (K) of *M. salmoides*. The n° of individuals subtracted to *M. salmoides* by autochthonous and allochthonous fish species (and the percentage on its K) is shown below the two bars

M. salmoides represented the 54.1% of its carrying capacity (K) in North and the 20.3% in South (χ^2 test, $\chi^2 = 20.5$, $p < 0.0001$). Competitive resistance was the main component of biotic resistance in North, and it was the only component observed in South (Fig. 2). Here, resistance against *M. salmoides* was mainly dependent on those species found in this location only (Fig. 2). The top predator *P. fluviatilis* in North, and the whitefish *Coregonus lavaretus* in South, were the two species that most limited the invader (Fig. 1). In both locations, allochthonous species had a stronger limiting effect than autochthonous ones on *M. salmoides* (Fig. 2, North, $\chi^2 = 13.6$, p < 0.001; South, $\chi^2 = 10.3$, p < 0.01).

Ecological and economic impact of *M. salmoides*

Based on our sampling effort (i.e. on the standing biomass density of *M. salmoides* sampled), the biomass subtracted by *M. salmoides* to fish prey was markedly higher in North (North: 19.8 ± 0.7 kg vs. South: 3.4 ± 0.2 kg), while that subtracted to macroinvertebrates was higher in South (North: 3.1 ± 0.3 kg vs. South: 5.6 ± 0.3 kg) (Fig. 1 and Appendix 1: Table S4). The two most impacted fish species were *P. fluviatilis* and *A. boyeri* (Fig. 1 and Table 2). Both predation and competition contributed to the impact of *M. salmoides* on *P. fluvaitlis* in North, while only competition (at a reduced level) contributed in South (Table 2). Predation in North represented the main cause of impact of *M. salmoides* on *A. boyeri* (Table 2).

Given the estimated biomass turn-over rate (TO) of *M. salmoides* and an economic value of $18 \, € \, Kg^{-1}$ and $6 \, € \, Kg^{-1}$ for *P. fluviatilis* and *A. boyeri* respectively, it is thus possible to estimate that the biomass subtracted by the invader was equivalent to a potential economic loss of 688.2 ± 21.6 € per year and 144.9 ± 10.2 € per year in North and South respectively (Table 2). All individuals of *M. salmoides* were captured with the linear net (40 m in length), and no individuals were found in fish traps. By standardizing the measured impact over 100-m shoreline, it is thus possible to estimate a potential loss of $1720.5 \pm 53.7 \, € \, 100 \, m^{-1}$ per year in North and $362.1 \pm 25.5 \, € \, 100 \, m^{-1}$ per year in South due to the impact of *M. salmoides* on *P. fluviatilis* and *A. boyeri*.

Food web resilience and simulated eradication of the invasive species

The observed value of λ was comprised between -0.82 (South) and -0.77 (North) (Fig. 3). Increased resilience (i.e. decreased expected time of recovery after a perturbation, for increased absolute value of λ) was observed when simulating the eradication of *M. salmoides*, as well as when simulating a more even distribution of abundances among fish populations (Fig. 3 and Appendix 1: Fig. S2). The tight correlation between the relative abundance of *M. salmoides* and λ allowed to calculate the increase of *M. salmoides* (as % of the observed abundance) which should be expected to destabilize the food web (i.e. which led to $\lambda \geq 0$) (Appendix 1: Fig. S2). Such threshold value

Table 2 Biomass subtracted by *M. salmoides* to the predator *Perca fluviatilis* and the forage fish *Atherina boyeri* in the North and South littoral lake area of Lake Bracciano (Italy) according to our sampling effort, i.e. according to the mean standing biomass of *M. salmoides* sampled

	Biomass Loss (g)			Potential Economic Loss per year (€)		
NORTH	*P. fluviatilis (f)*	*A. boyeri (b)*	Sum (f + b)	*P. fluviatilis*	*A. boyeri*	Sum (f + b)
Predation (P)	5244 ± 178	9918 ± 337	15,162 ± 515	283.2 ± 6.9	178.2 ± 6.3	461.4 ± 13.2
Competition (C)	4096 ± 148	320 ± 11	4416 ± 159	221.1 ± 8.1	5.7 ± 0.3	226.8 ± 8.4
Total (P + C)	9340 ± 326	10,238 ± 348	19,578 ± 674	504.3 ± 15.0	183.9 ± 6.6	688.2 ± 21.6
SOUTH						
Predation (P)	0	0	0	0	0	0
Competition (C)	2321 ± 161	1078 ± 76	3399 ± 237	125.4 ± 8.7	19.5 ± 1.5	144.9 ± 10.2
Total (P + C)	2321 ± 161	1078 ± 76	3399 ± 237	125.4 ± 8.7	19.5 ± 1.5	144.9 ± 10.2

The effect of competition and predation is reported

The values of biomass are converted to a potential economic loss per year according to a commercial value of 18 € Kg^{-1} for *P. fluvatilis* and 6 € Kg^{-1} for *A. boyeri* and the estimated biomass turn-over rate of *M. salmoides* (see methods)
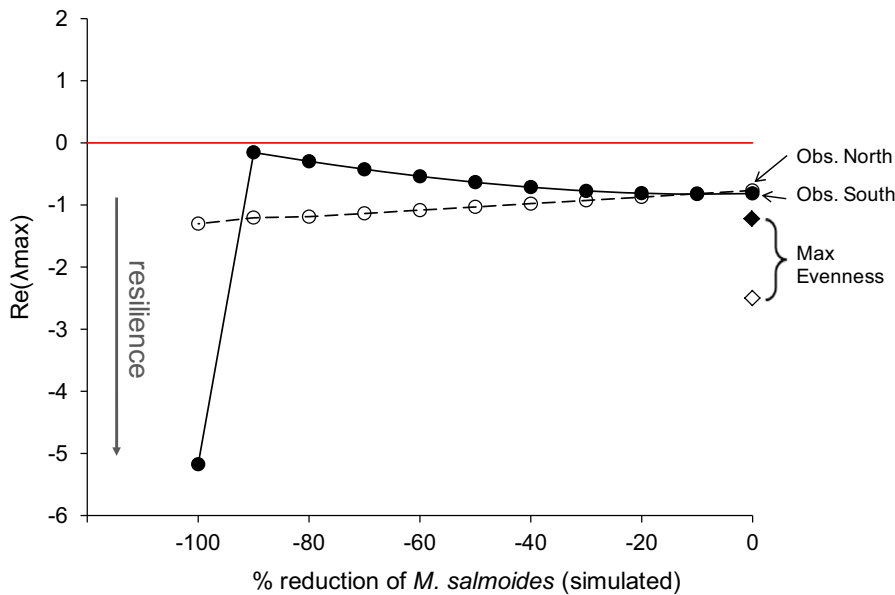

Fig. 3 Impact of *M. salmoides* on food web resilience to perturbations. Resilience is expected for negative real values of the maximum eigenvalue, Re(λmax) of the inverse Jacobian matrix. "Obs. North" and "Obs. South" point to the two values of Re(λmax) measured for the food web in the North and South location of Lake Bracciano, based on the observed abundance of *M. salmoides* at each location. "Max Evenness" (diamonds) refers to the values of Re(λmax) expected under simulated conditions of equal abundances of all fish populations in the food web except *M. salmoides,* which was maintained at the observed abundance. For each food web, a gradual reduction in the abundance of *M. salmoides* was simulated and values of Re(λmax) were recalculated accordingly (symbols from − 10% to − 100% of simulated reduction of *M. salmoides*). Empty symbols: North; Black symbols: South

was higher in North (+ 152%) than in South (+ 88%) ($\chi^2 = 50.5$, $p < 0.0001$), and increased to + 365% (North, $\chi^2 = 24.2$, $p < 0.0001$) and + 199% (South, $\chi^2 = 50.5$, $p < 0.0001$) when simulating a more even distribution of abundances among fish populations (Appendix 1: Fig. S2).

Discussion

Based on abundance, biomass and diet data of species, we proposed a method for quantifying trophic interaction strengths in terms of number of individuals and biomass that each species subtracts to the others through competition and/or predation in invaded food webs. In our study case, this method was useful to measure the impact of an invasive fish species on the invaded communities, as well as the biotic resistance to the invader. Specifically, our approach allowed us to quantify (1) the ecological and economic impact of the invasive species, considering its effect both on commercial fish stocks and on food web resilience, and (2) the competitive and consumptive resistance of autochthonous and allochthonous fish species. This kind of information can provide an ecological theory-based support to the management and conservation of invaded ecosystems.

The knowledge of the ingestion rate and prey transformation efficiency by the invasive species allowed us to estimate the biomass that it subtracted to each prey. Furthermore, the effect of competition on the invader by autochthonous fish species was weighed according to interspecific differences in body mass. This implies that a competitor smaller than the invader will have a small limiting effect on its abundance, regardless of the similarity of resources used by the two species, as expected by ecological theory, model and empirical evidence (Basset 1995; Emmerson and Raffaelli 2004; Brose et al. 2006; Neutel et al. 2007). While ingestion rates and efficiency of prey transformation into body mass of *M. salmoides* were available, this may not be the case for other species. Since metabolic and tissue turnover rates are related to the body mass of organisms (Peter 1983; Brown et al. 2004; Vander Zanden et al. 2015), published allometric coefficients may be used to estimate the parameters starting from body mass data. Noteworthy, the efficiency of prey transformation into body mass is the only metabolic parameter necessary to quantify the impact of a predator on its prey according to the proposed method. It may be calculated as the ratio between the amount of food provided and the net increase in weight of a consumer.

Biotic resistance to *Micropterus salmoides*

Starting from the realized trophic links in the food web, we quantified all the competitive and predatory interactions that limited the invader. In both food webs, competitive resistance had a stronger limiting effect on *M. salmoides* than consumptive resistance. The latter was only observed in the less complex food web. Here, lower habitat complexity and invertebrate prey availability may have increased the predation of *M. salmoides* by other predatory fish (Costantini et al. 2018). Notably, the fish species present only in the more complex and species-rich food web provided an important contribution to the higher competitive resistance observed. This supports a positive relation between species richness and community resistance to invasion, consistently with theory and field observations (e.g. Stachowicz et al. 1999; Kennedy et al. 2002). Increased fish abundance and species richness were associated to higher habitat complexity, as often observed in freshwaters (Willis et al. 2005; Smokorowski and Pratt 2007; Thomas and Cunha 2010). Thus, our results suggest a bottom-up effect of habitat features on the invasibility of lake communities. In parallel, recent modelling and field food web studies have demonstrated that increased food web complexity may decrease communities' invasibility (Hui et al. 2016; Smith-Ramesh et al. 2017; Romanuk et al. 2017). This was ascribed to a higher probability of an invader to undergo competition in highly interconnected webs, as it was observed in our study.

Our approach allowed us also to rank fish species according to their ability to limit the invader that can be considered in biological control strategies. In the study lake, the two species that most limited *M. salmoides* (*P. fluviatilis* and *C. lavaretus*) also represent valuable commercial fish species. This raises management issues since an unavoidable trade-off between the exploitation of these fish species and the maintenance of biotic resistance against the invader exists. Notably, allochthonous species represented half of the fish species sampled and had a strong limiting effect on *M. salmoides*, particularly at low habitat complexity. This can be explained by their higher abundance, mean body mass and competitive effect, consistently with the expected high adaptability and competitiveness of allochthonous species in non-native habitats. Our data are in line with a recent review of the Italian freshwater fish fauna (Lorenzoni

et al. 2019), which found that nearly one out of two species is allochthonous. Thus, our results suggest that the management of invaded ecosystems should carefully consider the ecological role and the potential ecosystem services provided by allochthonous not invasive species.

Impact of *Micropetrus salmoides* on invaded food webs

High habitat complexity and invertebrate prey availability reduced the impact of *M. salmoides*, as biomass subtracted to fish with respect to invertebrates, on the invaded fish communities. This may have strong implication in the top-down control exerted by the invader on lower trophic levels (Mancinelli et al. 2007; Jackson et al. 2013). Indeed, comparative lake studies highlighted important effects of bass invasion on native community composition via predation and competition, with cascade effects on local biodiversity (Jackson 2002; Maezono et al. 2005; Leunda 2010) and key ecosystem processes, including the production of fish stocks (Iguchi et al. 2004; Leunda 2010).

While the abundance of invertebrates generally increases with vegetation coverage in freshwaters (Godinho et al. 1994, 1997; Olson et al. 1995; Batzer and Wissinger 1996; Dala-Corte et al. 2020), the higher consumption of invertebrates by *M. salmoides* in the more complex habitat should not be solely related to their higher abundance. Indeed, the abundance of fish (an energetically richer prey type) increased in a similar manner in this location. According to optimal foraging theory (Pyke et al. 1977; Rossi et al. 2015), we thus hypothesis that the interaction between increased availability of invertebrates and increased energetic cost of fish predation underlies the shift from a fish- to an invertebrate-dominated diet by *M. salmoides* in the more complex habitat. Consistently, reduced consumption of fish with increasing habitat complexity due to reduced attack success rate (Gotceitas and Colgan 1989), increased handling time of fish prey (Alexander et al. 2015), modification of habitat use by fish prey (Jackson 2002) and increased invertebrate abundance (Godinho et al. 1994, 1997) has been reported for *M. salmoides* as well as for other invasive fish (Moyle and Light 1996; MacRae and Jackson 2001; Nasmith et al. 2010; Hanisch et al. 2012). The results presented in this case study may thus provide useful information

for the management of habitats invaded by alien predatory fish and by *M. salmoides* in particular, which represents a worldwide ecological and management issue (Welcomme 1992; Jackson 2002).

In the study lake, the measured impact of *M. salmoides* on other fish species has important economic implications. Indeed, the two most profitable commercial fish in the lake (*P. fluviatilis* and *A. boyeri*) were also the two most impacted fish species, and local professional fishermen reported drops in catches following invasion by the bass. Our approach made it possible to estimate the impact of *M. salmoides* on these two species over a year-round basis. Although our estimations assume no changes in the relative importance of prey to the diet of *M. salmoides* over the year, they are based on the description of diet composition over a medium-long term period (4–5 months) thanks to the stable isotope analysis of fish muscle (Weidel et al. 2011; Winter et al. 2019). The difference in the potential economic loss observed between locations ($\sim 1360 \, \text{€} \, 100 \, \text{m}^{-1}$ per year) may thus be considered a useful measure to quantifying the specific ecosystem service provided thanks to the presence of a biodiverse and complex food web.

Scaling from the population- to the food web-level, we quantified the expected resilience to perturbations of invaded communities. To our knowledge, this is the first attempt to quantify food web resilience, as firstly proposed by May (1974), starting from the isotope-based description of realized trophic links between species. Notably, observed values of λ lie in the range expected for real and model ecological networks (Allesina and Tang 2012), implying that resilience after a perturbation can be expected in both food webs, but at a relatively slow rate of recovery (i.e. λ was negative but relatively close to 0).

Simulated eradication of *M. salmoides* led to increased resilience. In parallel, increased evenness in the abundances of populations also led to increased resilience, and our simulations showed that increased evenness was associated to a higher potential of invaded food webs to maintain stability at high density of *M. salmoides*. The stability criterion applied (i.e. λ < 0) implies that food web resilience is achieved if all the populations can be expected to recover following a perturbation (May 1974; Allesina and Tang 2012). The differences between simulated (i.e. increased evenness) and observed communities may

be explained by considering that under observed conditions poorly abundant species may experience weak intraspecific regulation and thus local extinction after a perturbation due to interspecific competition (Arnoldi et al. 2016). This can also explain the observed slighter increase in the value of λ in South at simulated low abundances of *M. salmoides*, given the strong interspecific competition suffered by the bass in this location.

The successful eradication of *M. salmoides* has been reported in small and well-defined habitats, e.g. ponds (Tsunoda et al. 2010) and streams (Ellender et al. 2015), while it is often considered unfeasible in large ecosystems (Britton et al. 2011). In Lake Bracciano, *M. salmoides* is subject to professional and recreational fishing, and the releasing of captured specimens is not allowed. Nevertheless, this is the only method applied for the control of the bass, and its successful eradication from the lake seems unrealistic. In this context, while the simulated eradication of the bass allowed us to estimate its effect on the stability of invaded food webs, the proposed approach may allow to estimate the economic and ecological impact of *M. salmoides* at progressively reduced abundances, thus supporting the identification of science-based thresholds for its regulation.

Concluding remarks

Improvements in the quantification of trophic interaction strengths in real ecosystems represent an important step towards a better understanding of the structure and functioning of invaded and pristine ecological communities. Indeed, theoretical and experimental evidences show that the effects of one species on the population dynamics of others (Levins 1968; Montoya et al. 2009; O'Gorman et al. 2010; Calizza et al. 2017) and key food web properties, including resilience (May 1974; Allesina and Tang 2012), robustness to biodiversity loss (Eklöf et al. 2013), energy transfer (Bellingeri and Bodini 2016), and vulnerability to disturbance propagation (Montoya et al. 2009; Calizza et al. 2019), are tightly related to the strength and distribution of interspecific interactions.

Here, the quantification of trophic interactions in invaded food webs provided important insights into ecological mechanisms behind the ability of autochthonous and allochthonous species to resist invasion

by a recently introduced species, as well as on the direct and indirect effects of the invader on ecological communities. Notably, our results provided quantitative evidence supporting the conservation of biodiverse and complex food webs, associated to vegetated and productive littoral lake habitats (Costantini et al. 2018), as a way to mitigate bass invasion, its impact on commercial fish stocks and on food web stability.

Species invasions are increasing worldwide, boosted by human activities and climate change (McClelland et al. 2018; Ricciardi et al. 2017; Frost et al. 2019). In parallel, applications of stable isotopes in food web studies are flourishing, and include an increasing number of taxa and habitats, from small invertebrates to aquatic and terrestrial megafauna, from temperate to polar regions (Vander Zanden et al. 2004, 2015; Fry 2006; Michel et al. 2019; Rossi et al. 2015, 2019; Sporta Caputi et al. 2020). Thus, the proposed approach could be applied to a broad array of ecosystems and species if biomass and diet data (either obtained through stable isotopes or other methods) are available, improving our ability to conserve and manage invaded food webs.

Data availability Data will be made available on reasonable request.

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