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Fish communities in Italian sub-alpine lakes: Non-native species and anthropogenic pressures increase community dissimilarities

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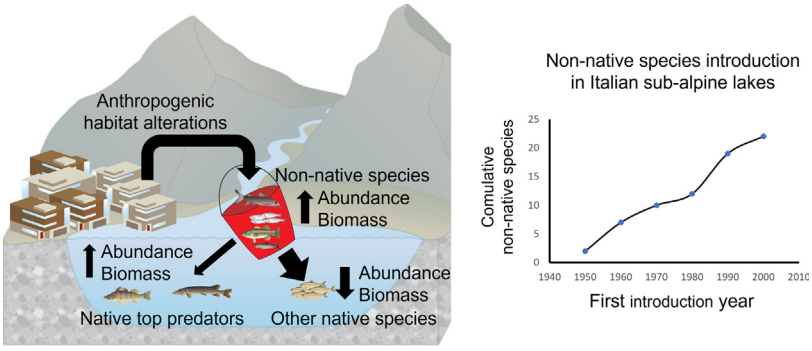
HIGHLIGHTS

- Anthropogenic pressures in Italian sub-alpine lakes increased after the 1950s.
- Non-native species possess higher competitive traits against stressors than natives.
- Non-native fish species are favoured by anthropogenic pressures.
- Non-native species increased the heterogeneity of fish communities in the region.

GRAPHICAL ABSTRACT



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ABSTRACT

In European lakes, anthropogenic pressures have increased significantly since the 1950s, facilitating colonisation by non-native species and increasing the potential for further invasions. Here, we determined the effects of anthropogenic pressures (i.e., habitat alterations and introduction of non-native species) on the fish communities of Italian sub-alpine lakes. We hypothesised that established non-native species would have more competitive traits against anthropogenic stressors, such as habitat alteration, than native species. Thus, we expected that non-native species would dominate lake communities and reduce native species occurrence and abundance depending on the degree of anthropogenic alterations. Overall, we predicted that the increase in anthropogenic pressures after the 1950s had led to homogenisation of the fish communities of the lakes in the region. We tested these hypotheses using data on 15 sub-alpine lakes, covering a broad geographical and morphological gradient, and compared the 2007–2014 fish community composition (sampled according to the CEN protocol plus point-abundance electrofishing) with variables of lake habitat and anthropogenic pressures (based on the Lake Habitat Survey, a method to evaluate the hydromorphological conditions of lakes according to the European Water Framework Directive) and fish communities before 1950, the latter based on bibliographic information. Following our hypothesis, non-native species showed higher prevalence of traits that increase their competitiveness against anthropogenic alterations (e.g., tolerance to pollution). In addition to lake morphology, the community composition of non-native fish determined as abundance (NPUE) and biomass (BPUE) was positively related to anthropogenic pressures. Since the 1950s, 19 non-native species have colonised the Italian sub-alpine lakes, and the occurrence of native species has decreased by ~27%. However, contrary to our expectation, these changes have increased the β-diversity of the fish communities in the lakes.

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1. Introduction

Anthropogenic alterations have affected lake ecosystems in many ways, changing their communities and favouring the establishment of non-native species with competitive traits (Elton, 1958; Catford et al., 2011; Winder et al., 2011). In Europe, mainly after the 1950s, intensification of agricultural land use and increased nutrient effluents from cities have resulted in lake eutrophication (Beeton, 2002; Gerard et al., 2010). Moreover, an increase of human settlements on lake shorelines has reduced the diversity of littoral communities, particularly of macrophytes and woody debris habitats (Francis et al., 2007), which has led to a reduction of invertebrates and fish diversity (Jennings et al., 1999; Brauns et al., 2011).

At a regional scale, fish communities in lakes are mainly determined by lake morphology (i.e., depth and surface area), productivity and geographical position (e.g., Brucet et al., 2013; Arranz et al., 2015). As lakes physically constrain fish dispersion, fish communities exhibit lower spatial changes within a lake in consequence of environmental variations than other organisms (e.g., phytoplankton; Beisner et al., 2006). Besides changes in the water environment, also local modifications of the lake shoreline may affect the species composition by reducing fish refugium possibilities and resources diversity (Jennings et al., 1999; Scheuerell and Schindler, 2004), increasing the risk of fish community homogenisation between lakes, as observed in the case of eutrophication (Menezes et al., 2015). Moreover, the response of fish communities to different anthropogenic stressors is more apparent at smaller geographical scale than at regional or continental scale (Jackson et al., 2001; Brucet et al., 2013).

After habitat modifications, non-native species are considered the main contributor to the biodiversity decline observed worldwide (Lowe et al., 2000). The introduction of non-native species is the second-most significant cause of native fish extinction in North America (Miller et al., 1989), and their joint effects of introduction and anthropogenic stressors (i.e., habitat alterations and pollution) explain as much as 54% of the global fish extinction (Clavero and García-Berthou, 2005). Non-native fish species are responsible for population declines of native fish through direct predation (e.g., Hrabik et al., 1998), niche exclusion (e.g., Bøhn and Amundsen, 2001), environmental changes (e.g., increased lake turbidity; Weber and Brown, 2009), hybridisation (e.g., Splendiani et al., 2016) and introduction of pathogens and parasites (e.g., Peeler et al., 2011).

Sub-alpine lakes in Italy cover a wide morphological range, from small and shallow (e.g., Lake Candia; surface:1.5 km^2; depth: 8 m) to large and deep lakes (e.g., Lake Maggiore; surface: 212.5 km^2; depth: 370 m). Before the 1950s, lacustrine fish communities in Italian sub-alpine lakes were characterised according to morphology and thus divided into shallow and small lakes, characterised by *Esox cisalpinus*, *Scardinius hesperidicus* and *Tinca tinca*, and large and deep lakes, additionally characterised by the pelagic species *Alosa agone* and *Coregonus lavaretus* or cold-water benthic species such as *Lota lota* (Volta et al., 2011). Due to their proximity to the Mediterranean region, isolation and the high latitudinal variation, Italian sub-alpine lakes have a high degree of endemism (e.g., *Salmo carpio* and *Rutilus pigus*; Bianco, 1995; Bianco and Delmastro, 2011). After the 1950s, the region experienced a major increase in human population and anthropogenic land use (Falcucci et al., 2007; Gerard et al., 2010) that, in addition to the permissive environmental legislation before the 1980s, increased lake pressures from multiple sources. For instance, in Lake Orta from the 1930s until the 1980s, pollution, rich in copper and ammonium sulphate, from a rayon factory reduced the lake pH (~ 4), thereby amplifying a negative effect of heavy metals discharged into the water by the tap industries, which almost eliminated the fish community (Volta et al., 2016). Other sub-alpine lakes, such as Lake Candia, underwent eutrophication due to input of non-treated urban wastewater that increased the turbidity, consequently reducing the extent of macrophyte habitats and the potential reproduction and foraging habitats of the native key predator *E. cisalpinus* (Giussani et al., 1990). Additionally, loss of littoral diversity due to morphological pressures, such as concrete shores, on large lakes, had already become a concern during the 1970s (Grimaldi, 1972). Moreover, there has been a significant increase of non-native species in the lakes since the 2000s as evidenced by their dominance, in terms of biomass, of the commercial harvest (e.g., 65.1% of the total biomass fished in Lake Maggiore; Volta et al., 2018). Whereas local effects of single invasions have been previously studied, information is lacking about the relationship between the increased extent of habitats and morphological alterations and the dominance of non-native species, as well as the degree to which fish communities in Italian sub-alpine lakes have changed in consequence of the increased anthropogenic impacts after the 1950s.

Here, we elucidate the effects that the anthropogenic alterations (i.e., habitat modifications and introduction of non-native species) have had on the Italian sub-alpine lakes. We derived information from the period 2007–2014 on community composition, abundance and biomass from published datasets on 15 lakes. We completed the dataset with environmental data from a parallel study measuring lake habitat and human pressures. In addition, to identify changes occurring after the increase of human pressures (i.e., the 1950s), we compared actual data with a dataset from before the 1950s. We hypothesised that established non-native species would have higher prevalence of competitive traits against anthropogenic stressors, such as habitat alterations, than native species. Thus, we expected that non-native species would dominate the lake fish communities relative to the degree of anthropogenic alterations, gradually reducing native species occurrence and abundance at increasing pressure. Overall, we predicted that the increase in anthropogenic pressures and non-native species after the 1950s had led to regional community homogenisation despite the high variability in the origin and morphology of the lakes.

2. Methods

2.1. Fish species in Italian sub-alpine lakes

To determine the actual state of fish communities in Italian sub-alpine lakes, we used published datasets on fish communities (species abundances and locations within the lakes) from 15 sub-alpine lakes in Italy (Fig. 1 and Table 1; Galafassi et al., 2019; Volta and Galafassi, 2018). These lakes were sampled once during late summer and mid-autumn between 2007 and 2014 (Table S1). Eight of the lakes are categorised as shallow sub-alpine lakes (depth range from 7 to 50 m) and seven as deep sub-alpine lakes (depth range from 70 to 418 m). In each lake, the fish distribution in the littoral zone (depth max = 1.5 m) was evaluated by electrofishing from a boat according to the National Italian Fish Sampling Protocol (ISPRA, 2014). The electrofishing device was a built-in-frame EL64GII (Scubla Acquaculture, 7000 W, 600 V, DC current) setup with a copper cathode (width 2.5 cm, length 300 cm) and a steel ring anode (thickness 0.8 cm; diameter 50 cm). The Point Abundance Sampling Electrofishing method (Copp and Garner, 1995) was used, during which the anode was dipped for 20 s at each sampling point. Fish benthic communities were sampled according to the CEN (2005) protocol with benthic gillnets (1.5 m high x 40 m long) composed of sixteen panels with mesh sizes ranging from 5.5 mm to 135 mm. This method bases the sampling effort (number of nets per lake) on lake area and volume, assuming equal sampling volumes for all the deep zones (see Table S1 for individual lake sampling efforts). All nets and fish captured by electrofishing were georeferenced with a GPS device.

Lake richness was calculated as species present in lakes using captures from both fishing methods, whereas fish biomass per unit of effort (BPUE) and abundance per unit of effort (NPUE) were analysed separately for both sampling techniques. Species whose hybrids could not be identified with certainty were determined at species level according to expert opinion (genus: *Salmo*, *Esox* and *Rutilus*), and individuals of the genera *Salmo* and *Esox* were considered native as differentiation was not possible without genetic information (i.e., *S. marmoratus* vs. *S. trutta* and *E. cisalpinus* vs. *E. lucius*). Differences between shallow and deep sub-alpine lakes in fish richness, abundance and biomass of native and non-native species were determined by Kruskal-Wallis rank sum test (Hollander and Wolfe, 1973). Dissimilarities in the composition of fish communities between lakes were determined by β-diversity using Sorensen similarity index, via the '*betapart*' R package (Baselga et al., 2017). To

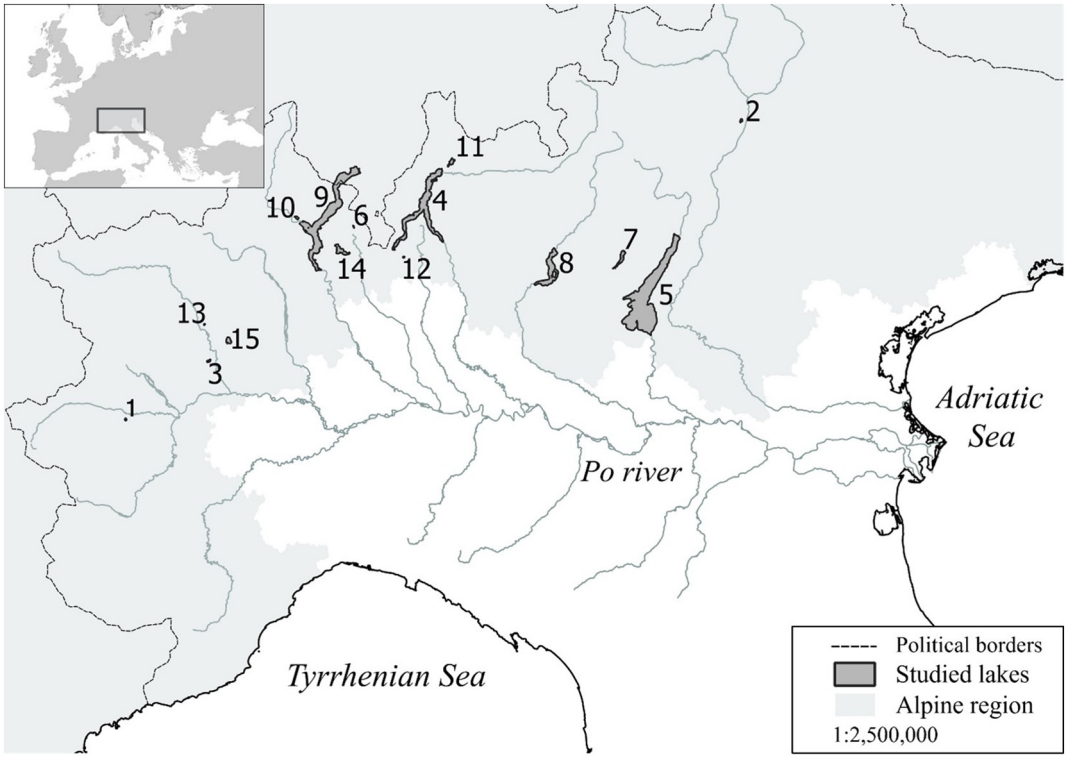

Fig. 1. Studied Italian sub-alpine lakes (grey). Lake: Avigliana Grande (1), Caldaro (2), Candia (3), Como (4), Garda (5), Ghirla (6), Idro (7), Iseo (8), Maggiore (9), Mergozzo (10), Mezzola (11), Montorfano (12), Morasco (13), Serru (14), Sirio (15), Varese (16), Viverone (17).

determine the first introduction record of non-native species (i.e., species introduced after AD 1500) for both Italian sub-alpine lakes and for the Italian Peninsula, we conducted a search on Google Scholar and published lake management plans.

2.2. Turnover of in-lake fish communities

To study the community composition within the studied lakes, we used a recently developed network approach to identify communities according to biogeographic regions, integrated in the Infomap Bioregions application (Edler et al., 2017). This method uses the fish capture location to determine a bipartite network between species and geographical grid cells. According to expert opinion, we established the potential species assemblage as the species found within a grid smaller than 1′ (approximately 1.85 km) and larger than 0.25′ (approximately 0.5 km). We used the default settings with maximum cell capacity = 100 and minimum cell capacity = 4 (i.e., cells with less than four different species were not considered potential communities). Then, we used fish presence/absence from both electrofishing and benthic nets on each grid cell to build a community map.

To account for species that contribute to differentiate the communities identified, a similarity percentage test (SIMPER) was performed with a cut-off for low contribution at 90% (Clarke, 1993). Species whose occurrence proved to be unique for each assembly (i.e., indicator species) were tested by multilevel-pattern analyses using the '*indicspecies*' R-package.

Table 1
Characteristics of the study lakes. Lakes sampled during 2007–2014 were used to describe the current communities (Used = 1), lakes with information about lake habitat survey (LHS; Used = 2) and lakes with community information before 1950 from Volta et al. (2011) (Used = 3). Lake typology was determined according to Volta et al. (2011). Lake Habitat Modifications Score (LHMS), which indicates the degree of morphological alterations in the riparian zone, and Lake Habitat Quality Assessment (LHQA), which determines the diversity of the physical structures of the shore and littoral zones, were determined according to the LHS methodology.

Lake	Code	Used	Typology	Maximum depth (m)	Surface (km^2)	Altitude (m a.s.l.)	Shore length (m)	LHMS	LHQA
Avigliana Grande	Avig.	1, 3	Alpine	27	0.8	352	3,780		
Caldaro	Cald.	1, 2, 3	Alpine	7	1.5	214	5,300	20	52
Candia	Cand.	1, 2, 3	Alpine	8	1.5	266	5,380	16	55
Como	Como	1, 3	Deep-alpine	418	145	197	180,000		
Garda	Gard.	1, 3	Deep-alpine	346	368	65	158,400		
Ghirla	Ghir.	1, 2	Alpine	14	0.3	442	3,200	8	52
Idro	Idro	1, 3	Deep-alpine	120	10.9	368	24,000		
Iseo	Iseo	1, 3	Deep-alpine	256	65.3	180	60,000		
Maggiore	Magg.	1, 2, 3	Deep-alpine	370	212.5	193	170,000	40	82
Mergozzo	Merg.	1, 2, 3	Deep-alpine	73	1.8	195	6,150	16	62
Mezzola	Mezz.	1, 3	Deep-alpine	69	5.9	200	13,600		
Montorfano	Mont.	1, 2, 3	Alpine	7	0.5	397	2,660	8	38
Sirio	Siri.	1, 2	Alpine	44	0.3	266	3,110	24	55
Varese	Vare.	1, 3	Alpine	23	14.9	238	24,000		
Viverone	Vive.	1, 2, 3	Alpine	50	5.7	229	1,306	26	68

This method determines the statistical significance of the relationship between species occurrence and sites (Dufrêne and Legendre, 1997; De Cáceres and Legendre, 2009, De Cáceres et al., 2010). We assessed the community turnover within lakes by multiple-site β-diversity (Sorensen similarity index) via the 'beta.multi' function in the '*betapart*' R package (Baselga et al., 2017).

2.3. Habitat and anthropogenic alterations and the fish community

To characterise lake environmental conditions, we used the Lake Habitat Survey approach (LHS; Rowan et al., 2004), which applies hydromorphological characteristics to quantitatively describe habitat features (e.g., substrate, macrophytes), infrastructure and human-induced changes as impacts that can compromise the ecological quality of a lake (e.g., McGoff et al., 2013). The method uses a score system to describe the Lake Habitat Quality Assessment (LHQA), which determines the diversity of the physical structures of shores and littoral zones, and the Lake Habitat Modifications Score (LHMS), which indicates the degree of morphological alterations in the riparian areas, on shores and in the littoral zones (Rowan et al., 2006).

LHS was applied to eight of the studied lakes (Table 1) for the same period as the fish sampling (2007–2014). The survey was done between July and September where macrophytes (if any) are well developed, and lake stratification is at its maximum. The field study was carried out from a boat and by walking along the perimeter of the lake depending on the information to be obtained. For lakes with an area between 0.3 and 14 km^2, 10 Hab-Plots (sections of 15 m width) were distributed equidistantly from each other along the lake perimeter. In the case of presence of particular habitats, we introduced additional Hab-Plots. For lakes with an area > 14 km^2, Hab-plots were placed every 4–4.5 km of the shoreline (e.g., Lake Maggiore, with a shore length of 170 km, required 40 Hab-plots). For each Hab-Plot, a detailed questionnaire was filled out (see Table S2 for details; Rowan et al., 2006). Human pressures were determined according to the LHS method up to 65 m behind the bank top. We additionally calculated the proportion of urban, agricultural and natural land use in each lake basin. The extent of each land use category in each basin was determined with Quantum GIS software (version 2.18.11) based on 2010 or 2012 Corine digital maps (1:100,000) obtained from regional environmental protection agencies. We complemented the information with lake total phosphorous (TP) concentrations as a measure of lake eutrophication, on which data were obtained from samplings done the same year as the fish sampling (see Table S3).

To evaluate habitat and fish community relationships, we built two environmental matrices: (i) one describing the in-lake habitat for each lake using the information from each Hab-plot and lake TP: littoral submerged refugia (% of lake littoral zone), types of littoral refugia, lithophile substrate (% of lake littoral zone), phytophile substrate (% of lake littoral zone) and TP concentration; (ii) and one comprising pressures on the lake surroundings: LHQA, LHMS and lake basin urban and agricultural land uses (%). Environmental relationships with fish descriptors (community composition, BPUE and NPUE) were tested using multivariate co-inertia analysis to study the co-structure between environmental and community data (the whole community and native and non-native species divided) by deriving axes in each dataset with maximum covariance (Dolédec and Chessel, 1994).

2.4. Native and non-native competitiveness

To reveal whether non-native species have traits that can increase their competitiveness compared with the native species, we selected 22 trait categories that capture human preferences (e.g., regional interests in species for commercial or recreational fisheries and use as live bait), reproduction success and tolerance to habitat and dissolved oxygen alterations (see predictions in Table 2). These traits were obtained from Alpine and European fish databases and, when necessary, complemented with species-specific searches (see Table S4 for traits and bibliographic details). Prevalence of traits was established for native and non-native species based on the proportion of species richness from each group relative to each selected trait category, an exception being the "relative fecundity" trait, where we compared the mean values of both groups. We then tested whether each trait affinity tended to be overrepresented in the non-native or native species using Fisher's exact test of independence, adjusted by Bonferroni correction to avoid alpha inflation.

To determine the extent to which non-native species presence, total abundance and total biomass could determine native species metrics, we fitted pure latent variable models (using spatial but not environmental covariates) using Bayesian Markov Chain Monte Carlo (MCMC) to account for any residual correlation between species ('*boral*' package; Hui, 2016). For the analysis, we selected those species present in 10 or more assemblages, thus avoiding zero representation and correlations between rarely occurring species pairs. We ran the MCMC according to the default settings: burn-in 10,000 iterations, total number of iterations including burn-in = 40,000, thinning rate = 30, very weakly informative normally distributed priors with mean zero and variance 10. We applied binomial distributions to the p/a datasets and Tweedie distributions, a log-normal distribution usually used to model biomass and abundance (Foster and Bravington, 2013). This analysis determines the effect of latent variables (e.g., species interaction), highlighting possible positive/negative relations between native and non-native species.

2.5. Community change from 1950 to 2010

Information about the community composition (presence/absence) before the 1950s from 13 of the 15 lakes (Table 1) was extracted from Volta et al. (2011), who reconstructed the fish communities based on a literature survey. As in the fish dataset containing communities between 2007 and 2014, the genera *Salmo* and *Esox* were considered native (i.e., *S. marmoratus* and, *E. cisalpinus*). Dissimilarities in community compositions were tested using Sorensen, presence-absence and beta diversities (Baselga, 2017, Baselga, 2010) using the '*betapart*' package (Baselga et al., 2017). Temporal changes on lake communities from before 1950s to 2007–2014 were estimated following the method proposed by Tatsumi et al. (2021), which allows partitioning of the temporal changes of beta diversity into components that reflect local extinction ($\Delta\beta_E$) and colonisation ($\Delta\beta_C$). Consequently, this method allows to determine the contribution of local extinctions and colonisations to the community homogenisation or heterogenization.

3. Results

3.1. Fish species in Italian sub-alpine lakes

A total of 40 fish species (20 native and 20 non-native) were found in the 15 lakes studied (Table S5). Fish richness per lake ranged from 9 to 26 species, increasing with lake depth (log-regression: $R^2 = 0.770$, $p < 0.001$) and surface area (log-regression: $R^2 = 0.590$, $p < 0.001$). In four of the lakes non-native species dominated the community richness (≥ 50% of the community species; Table S5). Native species were more dispersed than non-native species (occurrence: 49.3 ± 28.0% and 32.0 ± 26.3%, respectively; Kruskal-Wallis test: H = 4.164, d.f. = 1, $p < 0.05$; Table S5). Indeed, introduction rates of non-native species in Italian sub-alpine lakes were higher during the 1990s (~ 20 years before the 2007–2014 sampling), mainly produced by non-native species already present on the Italian peninsula (Fig. 2; see Table S6 for species introduction years). The native *Perca fluviatilis* and *S. hesperidicus* and the non-native *Lepomis gibbosus* were the only species present in all the studied lakes (Table S5), while the native species *Chondrostoma soetta* was present in only two lakes (L. Avigliana Grande and L. Mezzola) and seven non-native species in only one (Table S5).

The community composition in the lakes differed between shallow and deep sub-alpine lakes (Fig. 3a), species richness being the highest in the deep sub-alpine lakes (22.8 ± 2.6 sp. and 12.1 ± 2.3 sp. respectively;

Table 2
Frequency of different traits for native and non-native species in Italian sub-alpine lakes. The selected traits were linked to high or low competitiveness (see 'expectation'). Bold numbers indicate that the trait was significantly over-represented (*P*-values <0.05; Fisher's exact test, adjusted by Bonferroni correction). "Human preference" is determined from regional interest. Species may belong to more than one category (see Table S4 for species traits).

Trait	Expectation	Category	Prevalence of native	Prevalence of non-native
Human preference	Advantage: Higher human preference increases the probability of species dispersion and/or care.	Yes (commercial fisheries target)	38.1%	15.8%
		Yes (recreational fisheries target)	28.6%	31.6%
		Yes (live bait)	23.8%	21.5%
		No	23.8%	36.8%
Age at sexual maturity	Advantage: Short age increases the probability for population expansion.	< 2 yr	16.7%	13.0%
		≥ 2 yr	72.2%	87.0%
Relative fecundity (1000 eggs/kg)	Advantage: Higher fecundity increases the probability of population expansion.		284.6 ± 621.8	267.7 ± 571.3
Spawning season	Disadvantage: Co-occurrence of spawning period and summer, where the frequency of human use of lakes is high, may stress the fish and reduce the availability of spawning habitats.	Reproduction during summer	19.4 ± 25.0%	25.4 ± 34.3%
Spawning habitat	Disadvantage: Reproduction on lithophile substrates may be inhibited by increased eutrophic conditions.	Lithophile	56.3%	40.0%
		Lithophytophile	18.7%	30.0%
		Phytophile	25.0%	30.0%
Parental care	Advantage: Reduces the competitiveness among juveniles and increases egg survival.	Yes	16.7%	**40.9%**
Main feeding source	Advantage: Omnivorous strategy increases the food resources range.	Piscivorous/insectivorous	27.8%	17.4%
		Insectivorous (benthic)	44.4%	39.1%
		Planktivorous	**11.1%**	0%
		Omnivorous	16.7%	**43.5%**
Tolerance to habitat alteration	Advantage: Tolerance increases the resistance to anthropogenic habitat modifications.	Non-tolerant	**50.0%**	13.6%
		Intermediate	33.3%	13.6%
		Tolerant	16.7%	**72.7%**
Tolerance to dissolved oxygen reduction	Advantage: Tolerance increases the resistance to the predicted reduction of dissolved oxygen in sub-alpine lakes due to the climate change.	Non-tolerant	**43.8%**	18.2%
		Intermediate	37.5%	27.2%
		Tolerant	18.8%	**54.5%**

Kruskal-Wallis test: $H = 9.183$, d.f. $= 1$, $p < 0.01$). Lake β-diversity was primarily explained by nestedness component (72.7 ± 22.2%), being 51.2 ± 24.8% of the species present in L. Como (Fig. 3b). The turnover component (27.3 ± 22.2%) was explained by 12 non-native species (mean occurrence: 2.4 lakes) and one native species (*C. soetta* present in L. Mezzola and L. Varese; Table S5 and S7a).

Despite having the highest species richness, L. Como had the lowest diversity value in the littoral zone due to the high abundance of the native *Alburnus arborella* ($H' = 0.67$; Table S8). The highest total abundances (NPUE) and biomasses (BPUE) in the littoral and benthic zones were found in the small and shallow L. Caldaro and L. Candia, respectively (Table S8).

3.2. Turnover on in-lake fish communities

Analyses on Infomap Bioregions, using fish distribution within lakes led to five fish communities on Italian sub-alpine lakes (Fig. 4a). Differences in the composition of fish communities within a lake increased with increasing lake depth and surface area ($R^2 = 0.463$, $p < 0.001$; $R^2 = 0.231$, $p < 0.05$ respectively; Fig. 4b; Table S7b). These community changes were mainly explained by species turnover (mean turnover weight on β-diversity: 75.1 ± 19.5%; Table S7b) that increased according to lake dimensions (depth: $R^2 = 0.514$ $p < 0.01$; surface: $R^2 = 0.233$, $p < 0.05$; Fig. 4c). "Community 1" was the most common, occurring in 13 of the 15 studied lakes. This community was characterised by 10 indicator species (60% of which were non-native) and showed community aggregates with a mean richness of 6.5 ± 2.1 species, *Micropterus salmoides*, *L. gibbosus* and *S. hesperidicus* being the most common species. "Community 1" occurred in a variety of littoral habitats with and without anthropogenic pressures; "Community 2", which appeared in 9 of the 15 studied lakes, was mainly characterised by native species (83% of the richness) and occurred in shallow waters with submerged macrophytes but was rarely found in urbanised areas; "Community 3" comprised only non-native indicator species. Despite that this assemblage had a lower occurrence than communities 1 and 2 (4 of the 15 studied lakes), when present, it was the dominant (74.4%) in-lake community (e.g., Lake Maggiore). "Community 3" was mainly found near stream discharges (80%) and beach habitats (58.3% of the cases) but was rare if the shore area was urbanised, agricultural or forested; "Community 4" dominated by native species (75%) and "community 5" dominated by non-native species (75%) were present in one of the lakes each (Fig. 4c).

3.3. Habitat, anthropogenic alterations and fish community

From the eight lakes with LHS data available, Lake Habitat Modifications Score (LHMS) and Lake Habitat Quality Assessment (LHQA) scores ranged between 8 and 40 (mean: 19.4 ± 9.3) and between 38 and 82 (mean: 53.7 ± 15.4), respectively (Table 1; Table S9). The first axis of the lake surrounding pressures-PCA accounted for 33.3% of the total explained variance, of which agricultural land use accounted for 86.2% and urban land use for the remaining 13.8%. The second axis accounted for 33.3% of the total explained variance, mainly explained by LHQA (37.8%), urban land use (29.1%) and LHMS (26.2%). Both, first and second axes from the in-lake habitat-PCA accounted for 25% of the total explained variance. The first axis was explained by lithophile (70.7%) and phytophile (21.6%) substrates and lake total phosphorous concentration (7.7%) and, the second axis by lake total phosphorous concentration (86.1%) and the proportion of submerged refugia (13.9%).

The species composition in lakes (presence/absence) was neither related to the in-lake habitat nor surrounding pressures (i.e., in-lake habitat-PCA and lake surrounding pressures-PCA, respectively). Relative abundance of the fish communities caught by benthic nets (NPUE) was related to the in-lake habitat conditions (co-inertia: $R^2 = 0.711$; $p < 0.05$; Table S10), whereas relative biomass (BPUE) of the fish caught in both the benthic nets and by electrofishing in the littoral zones was related to lake surroundings pressures (co-inertia: $R^2 = 0.669$; $p < 0.01$; and $R^2 = 0.685$; $p < 0.01$, respectively). When the community was divided into native and non-native species, no relations between native species and in-lake habitat or surrounding pressures were found (Table S10). However, the relative abundance of non-native species was correlated with the in-

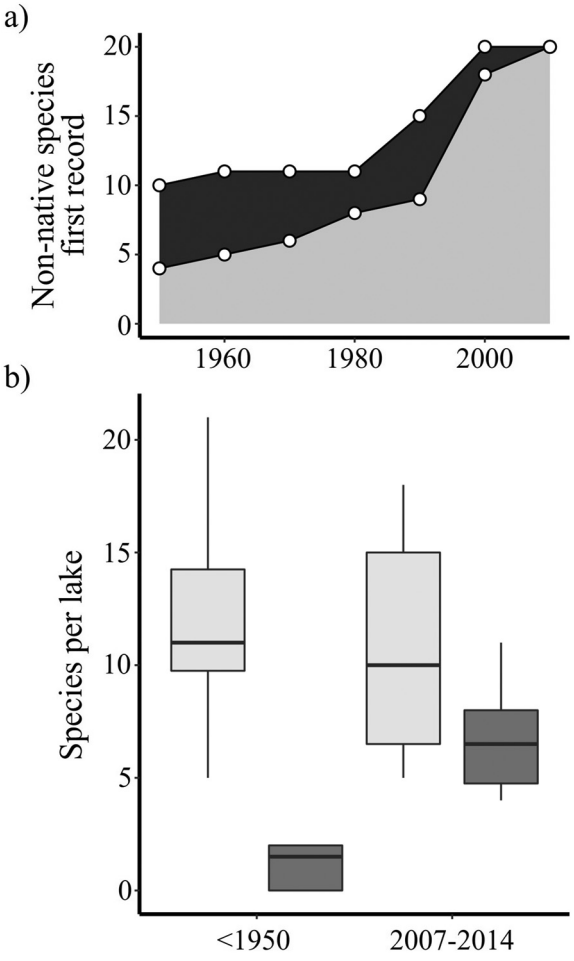

Fig. 2. Non-native species introductions in Italian sub-alpine lakes. (a) First record of non-native species in the sub-alpine lakes in Italy (black) and in Italian sub-alpine lakes (grey). (b) Native (grey) and non-native (in black) species per lake. See Table S6 for species information.

lake habitat (NPUE in benthic nets, co-inertia: $R^2 = 0.673$; $p < 0.05$), and non-native species relative biomass was correlated with surrounding pressures (BPUE in benthic nets, co-inertia: $R^2 = 0.688$; $p < 0.01$, and BPUE electrofishing, co-inertia: $R^2 = 0.700$; $p < 0.05$).

3.4. Native and non-native competitiveness

Comparison of human preferences (i.e., anthropogenic services of fish species) for native ($n = 21$) and non-native ($n = 19$) species did not show significant differences (Fisher's exact test, adjusted by Bonferroni correction; Table 2); however, non-native species are mainly linked to recreational fishing activities (e.g., *M. salmoides*), whereas native species are mainly linked to commercial fishing activities (e.g., *A. agone*; Table 2). There were no significant differences between native and non-native species regarding reproductive traits (Table 2) despite a higher mean value of fecundity and use of lithophile substrates for reproduction of native species. Non-native species had higher values of traits that might increase their competitiveness such as higher parental care ($p < 0.001$), higher omnivory ($p < 0.001$), higher tolerance to habitat alterations ($p < 0.05$) and higher tolerance to reduction of dissolved oxygen concentrations ($p < 0.001$; Table 2).

Occurrence, biomass (BPUE) and abundance (NPUE) of native species were generally negatively correlated with the relative metrics of non-native species (pure latent variable models using MCMC; Fig. 5). However, native predators (*P. fluviatilis* and *E. cisalpinus*) abundance and biomass were instead favoured positively by the increase of total abundance and biomass of non-native species (Fig. 5). These results should be interpreted with caution, though, due to the low co-occurrence of the two species.

3.5. Community change from 1950 to 2010

Lake community compositions before 1950s were characterised by a total of 24 native and 2 non-native species (Table S11). Native *A. arborella*, *E. cisalpinus*, *S. hesperidicus* and *T. tinca* were common in all lakes. As presently, shallow and deep sub-alpine lakes held differentiated communities (Fig. 3c). Total species richness increases with increasing lake surface ($R^2 = 0.752$, $p < 0.001$), L. Garda having the highest richness (23 species; lakes richness range: 5–23; Fig. 3d).

Changes in community composition were driven by both species extirpation (extirpation-resultant, $\Delta\beta_E = 0.083$, the 25.1% of the β-diversity) and colonisation (colonisation-resultant, $\Delta\beta_C = 0.247$, the 74.9% of the β-diversity). From the 1950s to the 2010s, the loss of native species in the studied sub-alpine lakes was 27.0 ± 15.2%, *A. alborella* (−6 lakes) and *S. squalus* (−5 lakes) being the most frequently lost species. Also, *Barbatula barbatula*, *Chondrostoma genei*, *Gasterosteus aculeatus*, *Phoxinus phoxinus*, and *S. carpio* were not found during the 2007–2014 samplings (Fig. 2b; Table S5). Higher extirpation of widespread than rare species ($|\Delta\beta_{E+}(0.34)| > |\Delta\beta_{E-}(-0.26)|$; see Table S12 for species details) has contributed to the enhanced heterogeneity of lake communities. Species colonisation was mainly driven by non-native species (69.2 ± 17.1% of the colonisation events since 1950s; Table S12), leading to an increase of species richness of 4.7 ± 2.3 species per lake, except for Lake Garda (−2 sp.) and Lake Montorfano (−1 sp.). Some colonising species contributed to community homogenisation (e.g., *L. gibbosus* and *Carassius* sp., occurring in 100% and 86% of the lakes, respectively). However, most of the colonising species had lower occurrences (Table S5 & S11), increasing the communities heterogeneity ($|\Delta\beta_{C+}(0.56)| > |\Delta\beta_{C-}(-0.31)|$). Shallow lakes presented the greatest temporal change (i.e., higher values of β-diversity, $R^2 = 0.4783$, $p < 0.01$; Table S7). However, Lake Idro, a deep sub-alpine lake, exhibited the greatest community change due to the extirpation of seven native species and colonisation by four native and five non-native species. These community changes increased the community similarities between Lake Idro and shallow sub-alpine lakes (Fig. 3c).

4. Discussion

Non-native species colonisations since 1950 have doubled the fish richness in Italian sub-alpine lakes, which is similar to findings from 1866 to 2013 in the rest of the Italian Peninsula (Bianco, 2014). Despite that, the main introductions occurred recently (52.4% of the species were introduced during the 1980s and 1990s; Fig. 2; Table S6), the abundance of most non-native species increased a few years after their introduction, and they now dominate the lake fish communities in many of the Italian sub-alpine lakes (e.g., Volta and Jepsen, 2008; Volta et al., 2018). Here, we have described the combined effects of non-native species and anthropogenic habitat alterations on fish communities in Italian sub-alpine lakes.

4.1. Anthropogenic habitat alterations and fish communities

Anthropogenic habitat alterations (i.e., anthropogenic land use and shoreline modifications) reduce the habitat diversity of littoral areas and increase the amount of dissolved organic matter in lakes (Brauns et al., 2011). For instance, Jennings et al., 1999, have found that these changes can reduce fish richness by diminishing habitat complexity. However, our results suggest that in the Italian sub-alpine lakes, morphology (i.e., depth and surface), and not habitat alterations, was the main driver of lake species composition and richness of fish communities. Similar results were reported for German lakes by Mehner et al. (2005), who hypothesised that shore alterations (affecting less than 35% of the lake shore), through its effect on fish reproduction, fecundity and behaviour, might not be enough to determine the fish species composition. Nevertheless, shoreline alterations can change the relative proportion of the numerical dominant species by

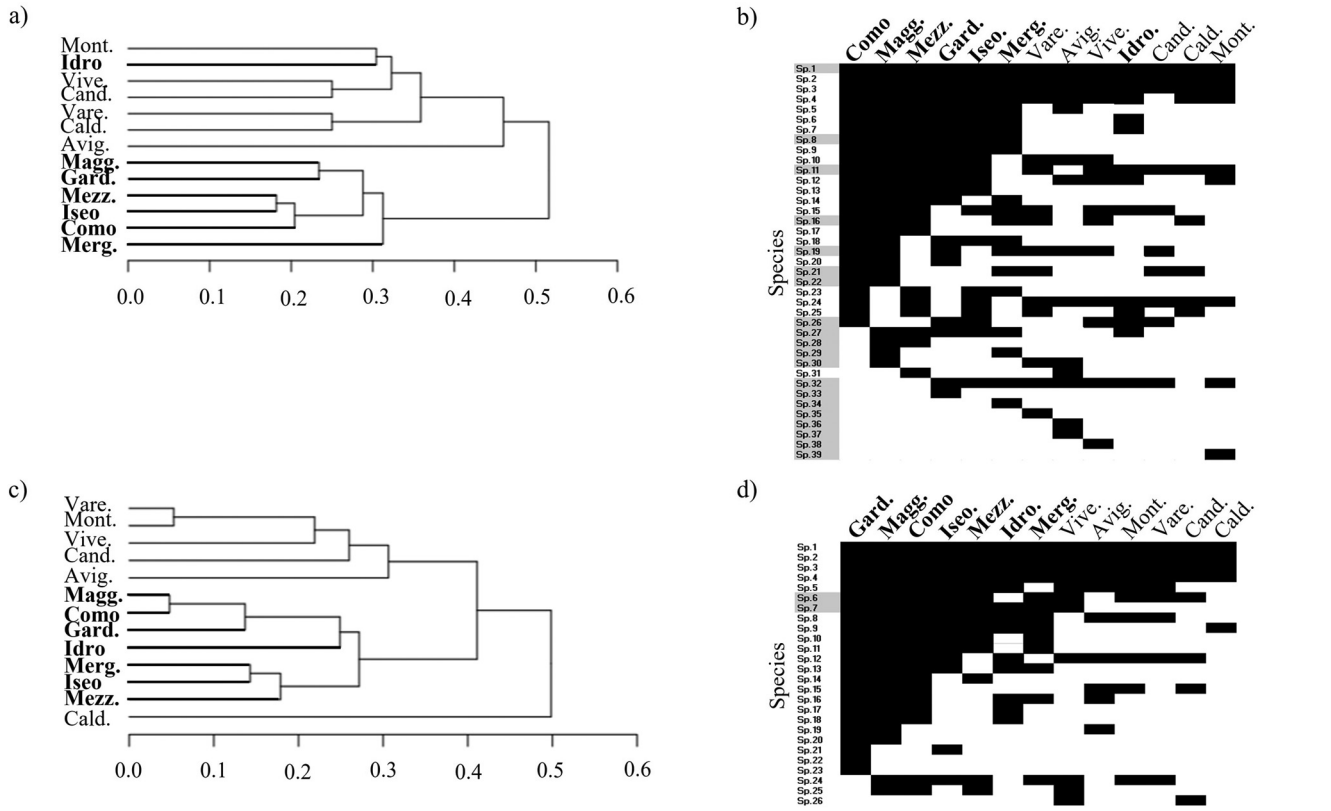

Fig. 3. Fish community similarities in Italian sub-alpine lakes. (a) Actual community (2007–2014) similarity using Sorensen, presence-absence data. (b) Species presence/absence in actual communities (2007–2014). (c) Past (before the 1950s) community similarity in the lakes and (d) species presence/absence. Deep sub-alpine lakes are highlighted, and non-native species are indicated by grey background.

limiting feeding resources and habitat refugia against predators (e.g., Perrow et al., 1999; Romare et al., 2003). Thus, as we found, anthropogenic environments favour species that are more competitive such as non-native species, that increase their relative biomass according to anthropogenic alterations. These results are consistent with trends observed in French lakes, where the increase of pollution fluxes was related with an increase on the probability of non-native species establishment (Irz et al., 2004).

Non-native species of Italian sub-alpine lakes have four traits that yield a higher competitiveness against anthropogenic alterations than native species. Non-native fish had a higher frequency of species tolerant to habitat alteration and decreased dissolved oxygen concentrations than native species. These traits, combined with the usually opportunistic feeding behaviour of non-native species, might explain their invasion success (Ruesink, 2005) and their dominance of biomass and abundance according to habitat perturbations. Indeed, some non-native species became dominant in the Italian sub-alpine lakes only a few decades after their introduction. This was the case for coregonids (*Coregonus* spp.), which dominated commercial catch in Lake Garda just 20 years after their introduction (Grimaldi, 1972), and roach (*R. rutilus*), introduced to Lake Maggiore in the early 1990s, which became the most abundant species in the 2000s (Volta and Jepsen, 2008) in this lake and in the nearby Lake Orta and Lake Mergozzo in the 2010s (Volta et al., 2016, 2018). Non-native species apparently increase zoobenthivory in the lakes of the region (Volta et al., 2011, 2013a, 2013b). Increased parental care by non-native species can reduce egg predation, thereby limiting the impact of voracious egg predators such as the widespread L. *gibbossus* (García-Berthou and Moreno-Amich, 2000; Trochine et al., 2018) and thus enhance non-native species survival. Stronger parental care among non-native species was also observed in Californian streams and in the Danube basin, and this was considered a key contribution to species establishment and invasion success (Marchetti et al., 2004; Erös, 2005).

The increase of non-native species abundance and biomass may reduce the abundance of native species through predation and competitive exclusion (e.g., Cucherousset and Olden, 2011). Despite that disentangling the direct effects of non-native species in the Italian sub-alpine lakes can be a challenging task due to the co-occurrence of multiple stressors (e.g., historical eutrophication, overfishing; Volta et al., 2018), potential impacts of non-native species have earlier been shown to correlate with their abundance (Ricciardi, 2003). This agrees with our results showing that the abundance of non-native omnivorous and intermediate predators (e.g., zooplanktivorous, insectivorous) positively correlated with the reduction of native species abundance. This might change the community size structure, favouring relatively large fish predators (Arranz et al., 2021), and may explain the abundance increase of native piscivorous species (*P. fluviatilis* and *Esox* sp.) in the studied lakes. The observed increase of non-native species abundance could otherwise favour the success of new colonisers (Simberloff and Von Holle, 1999), a trend already observed on a European lake study (Trochine et al., 2018). Overall, increasing the risk of communities to become dominated by non-native species.

4.2. Anthropogenic changes since 1950 have increased fish community beta-diversity

Contrary to our hypothesis, anthropogenic impacts (i.e., habitat alterations and species introductions) did not decrease but increased the heterogeneity of fish communities. Lake fish communities before the 1950s had a high nested pattern possibly resulting from Holocene colonisation, mainly from the lower parts of the Veneto-Po basins (Bianco, 1995; Bianco and Delmastro, 2011), restricting native species abundance (Bianco, 1995). The pattern might also be due to historical selection by humans (e.g., for fishing; Volta et al., 2018), favouring dispersion of species with a commercial or angling interest. Non-native species introduced before the 1930s (*L. gibbossus*, *A. melas* and *M. salmoides*; Table S6) occurred abundantly in

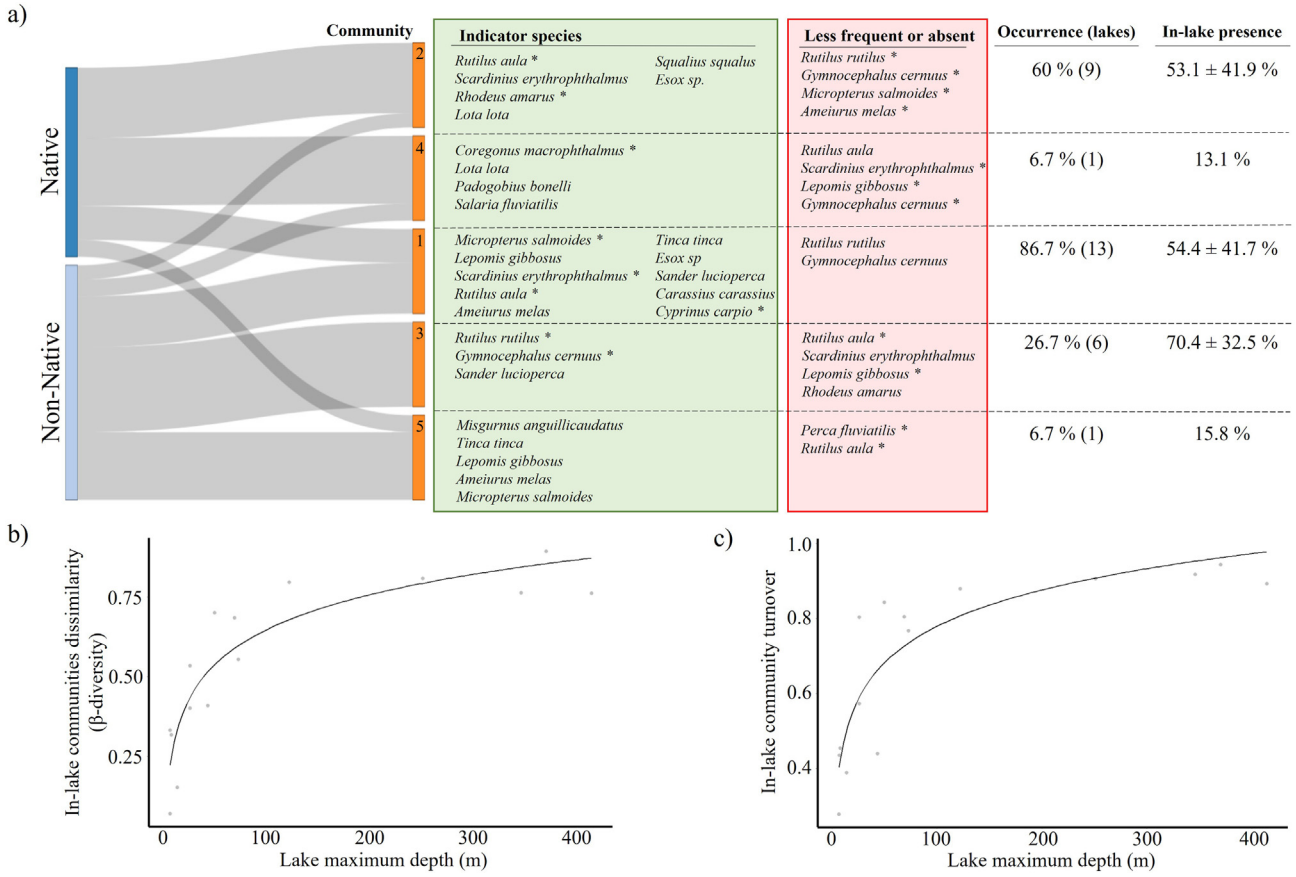

Fig. 4. Fish assemblages in Italian sub-alpine lakes. (a) Contribution of native and non-native species to the main fish communities characterising the lakes. "Occurrence" denotes the presence of a community in a lake, and "In-lake presence" denotes the community dominance within a lake, when present. (b) Differences in in-lake communities (β-diversity) increase with lake depth ($R^2 = 0.463$, $p < 0.001$), (c) with changes in the community composition mainly explained by the species turnover (75.1 ± 19.5%; $R^2 = 0.231$, $p < 0.05$). * denotes significant contribution (multilevel pattern analyses, p-value <0.05).

Italian sub-alpine lakes, contributing to the homogenisation of the fish communities. However, local extinction of widespread native species has increased community dissimilarities (e.g., the severe mortality events of *A. arborella* during the 1970s due to lake eutrophication, resulting in fungal and bacterial diseases; Grimaldi, 1972; Giussani et al., 1976). Additionally, the occurrence of non-native species introduced during the 1980s–1990s

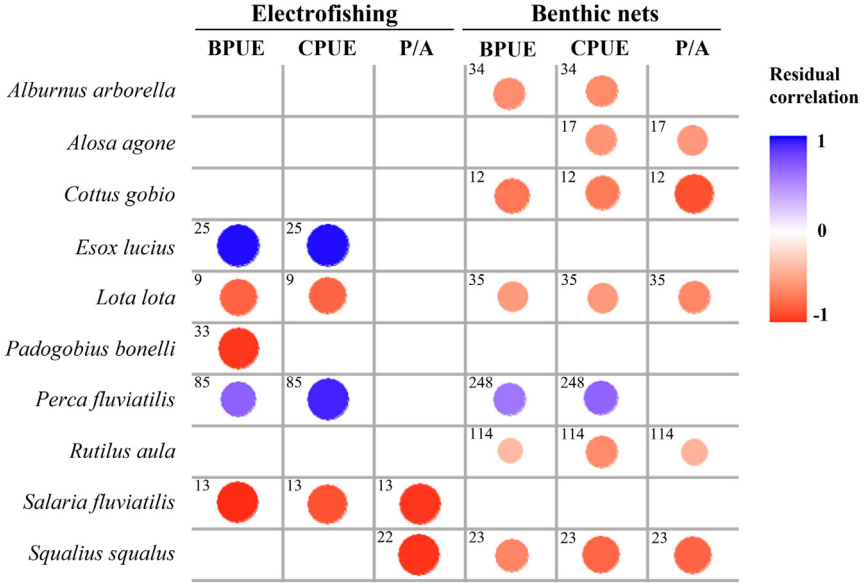

Fig. 5. Residual correlation between total non-native and native fish species. The colour intensity and dot size reflect the strength of the correlation – from positive correlations (blue) to negative correlations (red). All correlations are shown when significant (p-value <0.05). Corner numbers reflect the total number of assemblages used for the analysis of each native species.

(the greatest addition period; Fig. 2; Table S6) was lower, increasing the differences between lake community compositions (i.e., increasing β-diversity). The increase of species introductions during the last decades have been also observed on other isolated areas, as UK and Ireland (Winfield et al., 2011) and Iberian Peninsula, where non-native fish species has doubled from 1991 to 2001 (Clavero and García-Berthou, 2006).

Clavero and García-Berthou (2006) pointed out that the colonisation process by fish species on the Iberian Peninsula is dynamic and characterised by community heterogenisation immediately upon colonisation and by homogenisation when the colonising species are established. Thus, the current situation in Italian sub-alpine lakes suggests that non-native species might drive a general homogenisation of fish communities in the region, as seen in river basins of northern Italy (Bianco, 1995). The risk of homogenisation is substantiated by the decline of rare (e.g., *B. barbatula*, *G. aculeatus*, *C. genei*) and endemic species (e.g., *S. carpio*) due to pollution, habitat alteration and introduction of non-native species (Zerunian, 2007). A clear example is the decline of *S. carpio*, an endemic species of Lake Garda, whose population decreased in the 1960s because of habitat degradation and overfishing in reproductive periods (Zerunian, 2007). The high occurrence of species related to recreational fishing in Italian sub-alpine lakes (e.g., *P. fluviatilis*), as well as in other mountain regions in Europe, increases the risk of anthropogenic dispersion and biotic homogenisation (Clavero and García-Berthou, 2006). An example of this trend is the rapid expansion of non-native *Carassius* sp. This omnivorous species has a high tolerance to different environmental conditions (e.g., habitat alterations, water turbidity, pollution; Abramenko et al., 1997), a winning trait that might justify its spread and high abundances (in 86% of the lakes). Furthermore, it is not a target both of commercial and recreational fishing and, therefore, its exploitation is likely very low. Overall, as observed by Milardi et al., 2020, on Italian rivers, community homogenisation driven by non-native species can reduce the functional diversity of fish communities, increasing the risk of functional loss despite different lake morphology and origin.

4.3. Final remarks

The present study highlights the risk of fish community change in Italian sub-alpine lakes driven by anthropogenic stressors (e.g., habitat change, anthropogenic land use), may facilitate the establishment and community dominance of non-native species. However, our study has some potential caveats. First, although two different sampling methods were used (gillnets and electrofishing), reducing the potential bias due to the sampling technique, the lakes were sampled only once, likely preventing detection of rare species (e.g., *S. carpio* in L. Garda; Lunelli et al., 2012). Second, the method used to determine the relationship between native and non-native species is recent in fish ecology studies (Mehner et al., 2021) and warrants further tests. Despite the significance of our results, a wider larger of samples would have been preferable to increase the robustness of the analyses.

In the present situation with climate warming, lakes can respond differently to fish invasions, not only in consequence of differences in community compositions but also differences in anthropogenic stressors that often interact with the climate change (Jeppesen et al., 2012; Volta and Jeppesen, 2021), and this may boost the spread of non-native species and lead to their successful establishment. Thus, to support effective management actions and enhance the conservation status of native fish populations, lake management and conservation plans should consider a broad spectrum of factors, including in-lake specific factors (e.g., lake trophic status, substrate, shore zone; Ciampittiello et al., 2017) and external factors of the area of interest (e.g., anthropogenic land use; Pelletier et al., 2020), as well as their possible interactive effects (i.e., non-native species and anthropogenic stressors, including climate warming).

CRediT authorship contribution statement

JRM conceptualization, analysis, interpretation of results, writing. MC sampling, interpretation of results, review and editing. SB interpretation of results, review and editing. EJ interpretation of results, review and editing. PV conceptualization, supervision, interpretation of results, writing, review and editing, funding acquisition.

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.154959.

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