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Revisiting the Invasion: A Success Story of Crayfish Species in Piedmont Plain Lakes (NW Italy)

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Abstract

Crayfish often become invasive when introduced to new waters. The mid-20th-century commercial import of North American species (e.g., *Faxonius limosus, Pacifastacus leniusculus, Procambarus clarkii*) into Europe for food, pets, and restocking after crayfish plague, succeeded due to their adaptability, high reproductive rates, and resilience. Extensive baited-trap monitoring of Piedmont lakes allowed us to confirm the occurrence of the Old Non-Indigenous Crayfish Species (*F. limosus, P. leniusculus,* and *P. clarkii*), and to record *P. clarkii* first-ever in three additional lakes (Pistono, San Michele, and Sirio), thereby expanding our knowledge of their distribution in Piedmont freshwaters. Since all detected species are listed as Invasive Alien Species of Union Concern, protecting the ecological integrity of Piedmont's freshwaters requires coordinated action by member states, regional authorities, policymakers, and water managers to prevent and control their spread, and to improve information sharing. Non-native crayfish occurrence is influenced not only by hydrological and habitat connectivity, and predator–prey interactions, but also by illegal activities that supply the food market.

Keywords: non-native species; lentic habitats; crustacea decapoda; distribution

1. Introduction

Crayfish are often a central component of freshwater food webs and ecosystems. In streams and lakes, crayfish inhabit a wide variety of niches, from shallow vegetated margins and submerged woody debris to deep riffles, burrows, and rocky substrates. They serve as dominant predators and consumers, feeding on benthic invertebrates, detritus, macrophytes, and algae [1,2], while also representing a key prey item for fish, birds, reptiles, amphibians, and mammal species [3,4]. When species are introduced into new ecosystems, whether intentionally or unintentionally, they often face few of the natural halt from predatory species and balances that kept their populations in control in their native ranges. Among these, crayfish are prime examples of organisms capable of becoming invasive when introduced into new water bodies [5,6]. In the mid-20th century several North American species, such as the spiny-crayfish - *Faxonius limosus* (Rafinesque, 1817) previously known as *Orconectes limosus*, the signal crayfish - *Pacifastacus leniusculus* (Dana, 1852), and the red swamp crayfish - *Procambarus clarkii* (Girard, 1852), were introduced into Europe to supply the food market, the pet trade, and to restock the declining noble crayfish - *Astacus astacus* (Linnaeus, 1758) caused by crayfish plague [7–9]. Their success in new environments is driven by their adaptability, high reproductive rates, and resilience to diverse conditions [2,10].

These silent invaders often go unnoticed until their impacts, revealing complex interactions within freshwater ecosystems, or their occurrence become evident to fishermen and the general public [11,12]. Once established, non-native crayfish can rapidly expand their range, outcompete native species, and modify habitat structures, leading to profound ecological shifts and biodiversity loss [13,14].

Because crayfish have been introduced into various environments primarily for human consumption or the aquarium trade [13,15], and due to their detrimental effects on ecosystem services—such as competition, predation, disease transmission, and hybridization—they serve as an ideal model organism for investigating how community structure and ecosystem functions depend on species composition. Long-term or frequent monitoring of these species provides crucial insights into their spreading patterns and ecological consequences—a necessity in a rapidly changing environment under current global changes such as climate change, ecosystem disruption, habitat loss, and pollution [2,16]. The presence of non-native crayfish not only indicates shifts in water quality and ecosystem health but also offers a window into the broader state of freshwater habitats.

This paper therefore examines the historical progression of crayfish invasions in Piedmont plain lakes, highlighting how constant and systematic monitoring over time can improve the effectiveness of habitat conservation and invasive species management strategies.

2. Materials and Methods

2.1. Study Area

The Piedmont lakes in Northwest Italy are a group of fluvial, glacial, and tectonic lakes in origin. Most of them (12 out of 17) belong to the Province of Turin (TO), 1 to Biella (BI), 2 to Novara (NO), 3 to Verbano-Cusio-Ossola (VCO), and 3 to Vercelli (VC) (Figure 1). A few of them span more than one province. Lake Maggiore, due to its large size, lies across two countries—Italy and Switzerland (CH), and spans both the Piedmont (NO, VCO provinces) and Lombardy (VA) regions (Table 1).

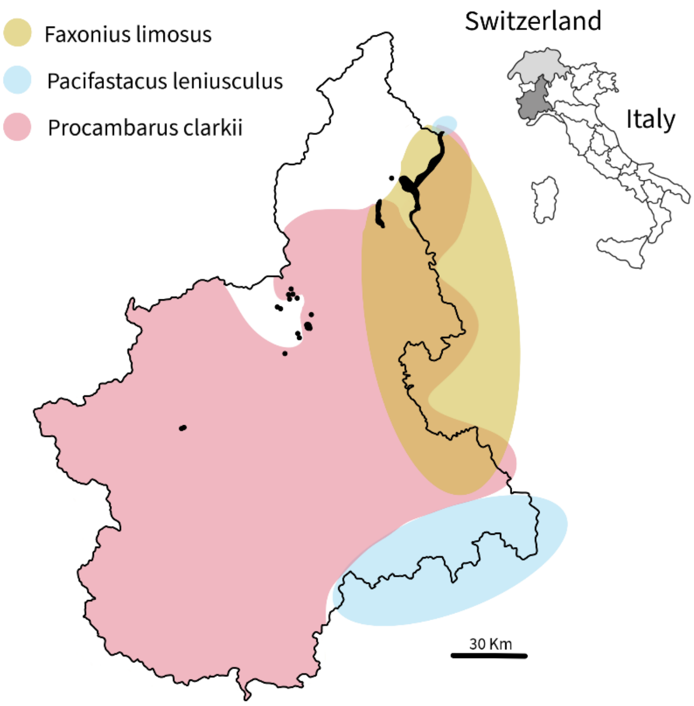

Figure 1. Regional distribution map of *Faxonius limosus*, *Pacifastacus leniusculus* and *Procambarus clarkii*. Overlap between historical and recent records. Lakes in black; Piedmont dark grey; Switzerland pale grey.

Most of them are Special Areas of Conservation (SAC) and/or Special Protection Areas (SPA), part of the European Union's Natura 2000 ecological network or designated by the European Bird Directive to preserve biodiversity (https://environment.ec.europa.eu/topics/nature-and-biodiversity/birds-directive_en), others belong to the Avigliana Lakes Nature Park. The larger ones show along their coasts Natura 2000 sites (Lake Orta) and Emerald zones of protection (Lake Maggiore in Switzerland).

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Surrounded by rolling hills, steep mountain slopes, glacier moraines, and extensive vineyards these submontane lakes (altitude < 800 m a.s.l.) are predominantly characterized by meso- or eutrophic waters. Among them, Lake Maggiore stands out due to its impressive size, with a surface area of 212 km² and a maximum depth of 372 m. Other significant lakes include Lake Orta, with a surface area of 18 km² and a maximum depth of 143 m, and Lake Viverone, covering 6 km² with a depth of 50 m. The remaining natural lakes are limited in size (mean 0.7 km² ± 1.5 SD) and maximum depth (median 11.5 m ± 14.7 SD). They are popular destinations for tourism, water sports, and outdoor recreation.

Table 1. Sampled lakes by State/Province, protected status (SAC: Special Area of Conservation/SPA: Special Protection Area), altitude (m a.s.l.), geographic coordinates (latitude, longitude in DMS), surface lake area (km²), maximum depth (m), and crayfish occurrence. FL: Faxonius limosus; PL: Pacifastacus leniusculus; PC: Procambarus clarkii.

Lake name	State-Province	Protected status	Altitude	Lat N	Long E	Lake area	max Depth	Crayfish
Viverone	BI/TO/VC	SAC/SPA	230	45°24′59.76″	08°02′08″	5.7	50	PC
Alice S.	TO	SAC	575	45°27′44.71″	07°47′43.58″	0.1	11	--
Avigliana G.	TO	SAC/SPA	352	45°03′57.09″	07°23′13.73″	0.9	28	PC
Avigliana P.	TO	SAC/SPA	356	45°03′13′′	07°23′30′′	0.6	12	--
Bertignano	TO	SAC/SPA	377	45°25′56″	08°03′44″	0.1	11	PC
Campagna	TO	SAC/SPA	238	45°29′02.4″	07°53′42″	0.1	5	PC
Candia	TO	SAC/SPA	226	45°19′25″	07°54′43″	1.5	8	PC
Meugliano	TO	SAC	715	45°28′36.33″	07°47′23.36″	0.03	11	--
Nero	TO	SAC/SPA	342	45°30′17.43″	07°52′24″	0.1	27	--
Pistono	TO	SAC/SPA	280	45°29′34.8″	07°52′28.2″	0.1	16	PC
S. Michele	TO	SAC/SPA	238	45°28′37.92″	07°53′16.8″	0.1	19	PC
Sirio	TO	SAC/SPA	266	45°29′13.2″	07°53′02.4″	0.3	44	PC
Mergozzo	VCO		204	45°57′20″	08°28′00″	1.8	73	--
Moncrivello	VC	SAC/SPA	263	45°20′24″	07°59′32″	0.03	2	--
Maglione	VC	SAC/SPA	251	45°20′43″	07°59′44″	0.1	2	--
Orta	VCO/NO		290	45°49′02″	08°24′24″	18.2	143	FL, PC

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Maggiore	CH-VCO/NO/VA	193	46°05′53″	08°42′53″	212.5	372	FL, PC, PL

2.2. Field and Laboratory Procedures

During the summer 2025 (late June-early October), a survey on all Piedmont plain lakes (NW Italy) was carried out (see Figure 1) to update the current knowledge on the number of non-native crayfish, and on their distribution. The sampling approach, tailored to each lake's size, was adapted from Garzoli et al. [17] to ensure accuracy and efficiency. This procedure involved using baited cylindrical traps (30 × 60 cm) along the shoreline of each lake, at sites where the occurrence of crayfish was previously confirmed or suspected. A series of 13 interconnected traps was placed in the shallow surface water layers and left overnight to coincide with peak crayfish activity. After 12-hours, the traps were retrieved and, after the identification to species, the number of male and female crayfish in each trap was recorded. Any incidental native species, such as reptiles, rodents, and fish, were identified and promptly released to minimize the impact on local biodiversity. Absolute abundances were estimated using the Catch Per Unit Effort (CPUE), calculated as total crayfish caught per trap per site per day, reported as average CPUE per lake [18].

In the laboratory, crayfish were anesthetized by gradually freezing them at decreasing temperatures (from 4 °C to -20 °C) [19]. Subsequently, identification to species and sex was confirmed based on distinctive morphological features such as body shape, claw (chela) structure, colour patterns and distribution, and sex-specific characters such as gonopod/pleopod presence and morphology, together with other physical characteristics distinguishing them from native species [20].

3. Results

Overall, three non-native crayfish species, *Faxonius limosus* (Rafinesque, 1817): Spiny-cheek crayfish; *Pacifastacus leniusculus* (Dana, 1852): Signal crayfish and *Procambarus clarkii* (Girard, 1852): Red swamp crayfish, have been caught in Piedmont lakes.

Interestingly, seven out of seventeen lakes show no presence of non-native crayfish species. The total number of individuals captured and identified for each species was as follows: 326 (male 195 – female 131) *P. clarkii*, 35 (male 11 – female 24) *F. limosus*, no data are available for *P. leniusculus*, as the species was found only in Switzerland.

Most lakes (eight) harbour only a single species (*P. clarkii*) (Table 1), while Lake Orta hosts two coexisting species (*F. limosus* and *P. clarkii*). Notably, Lake Maggiore is the only lake that supports all three species simultaneously, but only in the Swiss sector (Boggero et al., 2018); therefore, detailed data on *P. leniusculus* are not shown (Table 1). Across the altitudinal range surveyed, *Procambarus clarkii* specimens were found at 193-377 m a.s.l., whereas *Faxonius limosus* occurred between 193 and 290 m a.s.l. restricted to the deepest lakes where it occurred down to 12 m depth (Figure 2).

The mean CPUE (calculated as total crayfish caught per trap per site per day) per each lake per crayfish species showed non-significant differences (Welch Two Sample t-test: T= 0.37, *df*=1.20, *p*= 0.77, [21]) between the two species, with the widest range of variability and highest values for *P. clarkii* (Figure 3).

Overall, random sampling showed near-homogeneous sex distributions: in our data, *P. clarkii* had a slightly male-biased sex ratio (M:F = 1.49), while *F. limosus* was female-biased (M:F = 0.46). Then, sex ratios varied across individual lakes.

In 2025, mean CPUE abundance across lakes varied significantly (Figure 4). Lakes are clearly divided into three groups: those with mean CPUE ≥ 1.5 individuals per lake (lakes Candia, Maggiore, and Pistono), those with mean CPUE between 1.0 and 1.5 (Bertignano, Campagna, and San Michele), and those with mean CPUE ≤ 0.6 (Avigliana G., Orta, Viverone and Sirio).

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Figure 2. Occurrence of *F. limosus* at depths of approximately 11–12 m in the Swiss sector of Lake Maggiore (Locarno: photo by Beatrizzotti S.).

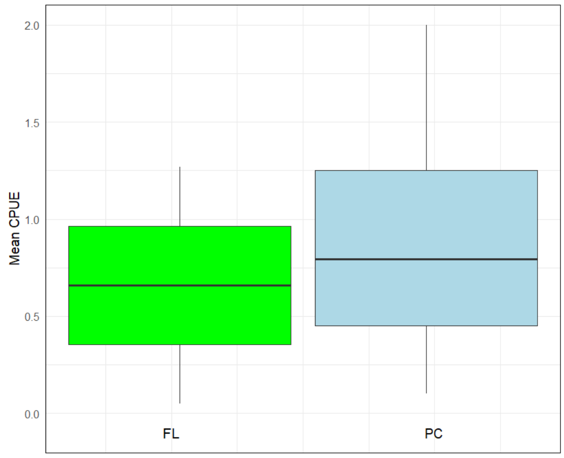

Figure 3. Box plots: distribution of mean CPUE abundances for each crayfish species across those lakes where the species was recorded. FL: *Faxonius limosus (n=35);* PC: *Procambarus clarkii (n=326)*.

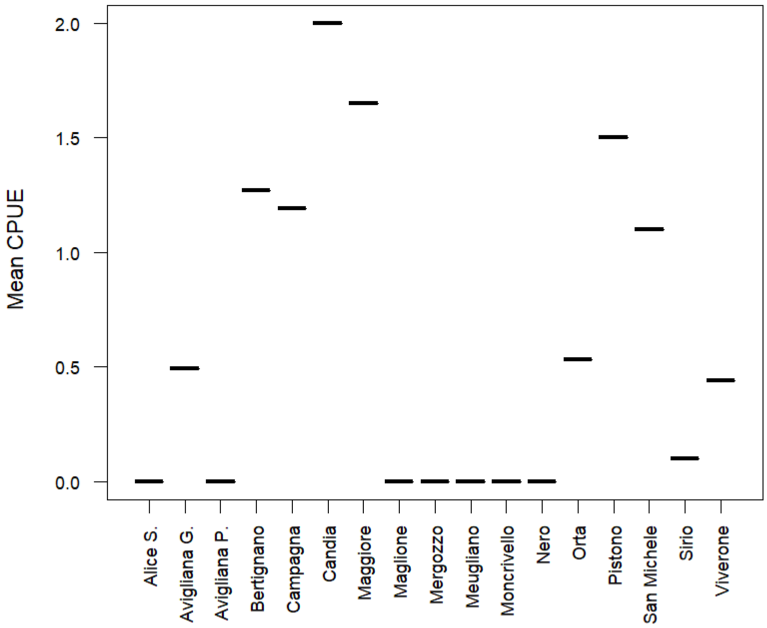

Figure 4. Distribution of mean CPUE abundances across lakes.

4. Discussion

All the detected species are listed as Invasive Alien Species of Union Concern under EU Regulation 1143/2014 [22] enacted in Italy by the Legislative Decree 229/2015. This regulation aims to prohibit their introduction, promote measures for early detection, rapid response, and containment or eradication, foster cooperation among member states for effective prevention and control efforts, and facilitate the dissemination of information to support policymaking and management strategies. All the previous, to protect the ecological integrity of the EU's ecosystems by controlling invasive species that may cause harm [23].

The three non-native crayfish species, known as Old NICS (Non-Indigenous Crayfish Species) [24], are of significant ecological, economic, and social importance due to their impacts on native ecosystems and human activities, and are among the most non-native crayfish globally, and their management is a priority for conservation and resource protection authorities [14].

Our results are consistent with Aquiloni et al. [25], thus based on abundance and distribution data, *P. clarkii* confirms to be the most abundant and widespread crayfish in Piedmont lakes, whereas *F. limosus* is restricted to the Northernmost, deeper lakes. Indeed, Aquiloni et al. [25] reported also *Procambarus clarkii* as the most successful non-native species in Northern Italy, notably dominating the Po River Valley with very large populations.

Our findings on species distribution in Piedmont lakes align with published patterns: *Faxonius limosus* is more frequently recorded in larger, deeper subalpine lakes and in mesotrophic rivers with higher flow and greater depth, favouring cooler, better-oxygenated, structurally complex habitats. *Procambarus clarkii*, by contrast, typically inhabit ponds, lakes and lower stream reaches with eutrophic conditions associated with organic pollution, showing tolerance for warm, turbid, nutrient-rich waters, and often exploiting shallow vegetated margins and anthropogenic habitats. These ecological preferences help explain the observed spatial segregation and potential competitive interactions in Piedmont waterbodies [20,26,27].

A balanced sex ratio (~1:1) is generally optimal for crayfish reproduction. Deviations from 1:1 can result from sex-specific behaviours and life-history differences—differential migration, gear catchability, growth rates, and mortality [28]. Males are often more active in summer (outnumbering females), increasing predation risk and mortality, while females may reach reproductive maturity earlier because males allocate more time to growth [29].

It is hypothesized that the occurrence of non-native crayfish in Piedmont lakes is influenced by hydrological connectivity, predator-prey interactions, and illegal activities. **Hypothesis 1**: In Piedmont, lakes that typically lack tributaries and outflows do not contain non-native crayfish, suggesting that these water bodies are relatively isolated and disconnected from the main hydrographic network. Such geographical and hydrological features can contribute to a reduced likelihood of invasive species establishing populations within these lakes, thereby maintaining their native aquatic biodiversity. **Hypothesis 2**: Conversely, lakes hosting predators like *Silurus glanis* Linnaeus,1758, *Trachemys scripta* (Thunberg in Schoepff, 1792), or wading birds (e.g., ardeids, kingfishers, grebes, mergansers, and cormorants) exhibit complex predator-prey interactions that commonly led to the absence or scarcity of non-native crayfish [30–32]. The lakes act as key feeding grounds where crayfish represent a vital prey resource. These dynamic highlights how non-native species can integrate into local food webs, potentially affecting native species and disrupting ecosystem balance [33,34]. **Hypothesis 3**: Field observations and local reports indicate persistent illegal nocturnal fishing at Lake Viverone aimed at harvesting crayfish for commercial sale [35]. Activity typically occurs at night, using baited traps, and torches to ease the capture in shallow waters. This clandestine harvesting appears to be driven by economic demand and undoubtedly evades health controls, increasing the risk of spreading pathogens. This behaviour also hinders management and monitoring efforts and exposes participants and buyers to legal sanctions and food safety risks [35]. Addressing this issue requires coordinated enforcement measures, community awareness, market surveillance, and incentives for product compliance.

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Historical Context

Previous data derive from published literature, technical documents such as action plans, datasets, publications in national journals, theses, and citizen-science observations. Records span from early incidental reports in the 1990s to systematic surveys up to the present (2020s).

Data were collected via several methods such as baited traps, dip and fishing net, electrofishing bycatch, visual surveys along the shorelines, and citizen observations. Visual and citizen observations were valuable for detection of new species but vary in accuracy and were verified by experts to confirm species identity. On the contrary, systematic surveys using standardized trapping provide reliable occurrence and relative-abundance data; however, such studies have only been published in recent years (Table 2) [17,36–38].

Table 2. List of published papers, datasets, technical reports focused on non-native crayfish distribution in Piedmont. Taxon name both cited and updated, type of frequency data format, sampling method, and site names are also provided: A = total number of individuals; D = density (ind m^{-2}); O=occurrence.

Taxon name cited	Update taxon name	Data format	Sampling method	Sites	Reference
O. limosus	*F. limosus*	O	traps	Baldissero pond	Delmastro, 1999 [39]
O. limosus	*F. limosus*	D	fishingnet, traps	lakes Maggiore, Orta	Bazzoni [40]
O. limosus	*F. limosus*	O	literature search, observations	Piedmont freshwaters	Morpurgo et al., 2010 [41]
O. limosus	*F. limosus*	D	traps	Lake Maggiore	Garzoli et al., 2020 [17]
F. limosus	--	O	active search, traps	lakes Maggiore, Mergozzo, Orta	Boggero et al., 2023 [38]
F. limosus	--	D	traps	Lake Orta	Boggero et al., 2025a [42]
F. limosus	--	D	observation, traps	Lake Maggiore	Boggero et al., 2025b [43]
F. limosus	--	D	traps	Lake Mergozzo	Kamburska et al., 2025 [44]
P. clarkii	--	A, O	dip net, elettrofishing, observations	Venesima stream	Delmastro, 1992 [45]
P. clarkii	--	O	observations	Piedmont freshwaters	Delmastro, 1994 [46]
P. clarkii	--	O	observations	Piedmont freshwaters	Delmastro, 1999 [39]
P. clarkii	--	O	literature search, observations	Piedmont freshwaters	Morpurgo et al., 2010 [41]
P. clarkii	--	D	traps	Lake Candia	Donato, 2016 [47]
P. clarkii	--	O	observations	lakes Bertignano, Viverone	Regione Piemonte, 2017a [48]
P. clarkii	--	O	observations	Lake Viverone	Regione Piemonte, 2017b [49]
P. clarkii	--	O	dip net, elettrofishing, fishing net, observations, torches, traces, traps	lakes Avigliana G., Campagna, Candia, Gay-Stroppiana, Maggiore, del Malpasso, Orta, Viverone	Delmastro, 2017 [50]
P. clarkii	--	D	traps	Lake Candia	Donato et al., 2018 [36]
P. clarkii	--	O	observations	Lake Candia	Città Metropolitana di Torino, 2019 [51]

P. clarkii	--	O	literature search	Piedmont freshwaters	Lo Parrino et al., 2020 [52]
P. clarkii	--	D	traps	Lake Orta	Kamburska et al., 2024 [53]
P. clarkii	--	D	traps	Lake Orta	Boggero et al., 2025a [42]
P. clarkii	--	D	observations, traps	Lake Orta	Boggero et al., 2025b [43]
P. leniusculus	--	O	active search, observations	Valla stream	Candiotto et al., 2010 [54]
P. leniusculus	--	O	observations	Lake Maggiore	Boggero et al., 2018 [55]
P. leniusculus	--	D	active search, traps	rivers Valla and Erro	Larson et al., 2022 [37]
P. leniusculus	--	D	observations, taps	Lake Maggiore	Boggero et al., 2025b [43]

Spatially, non-native crayfish (e.g., *Faxonius limosus, Procambarus clarkii*) are recorded across lowland and submontane water bodies in several provinces and neighbouring areas. Temporally, records show initial introductions in 1989 for *P. clarkii*, and at the beginning of the 2000s for *F. limosus* and *P. leniusculus*, followed by expansion and occasional local declines linked to environmental and climate changes, such as unprecedent heatwaves throughout 2022 in many European countries [56].

Comparison across past and current studies is thus hindered by uneven spatial coverage, often limited to accessible or already monitored sites, variable sampling effort, and temporal gaps. Historical records frequently lack standardized efforts compared with modern monitoring, making trend analyses unreliable or even impossible. Ongoing standardized monitoring (regular trapping at fixed stations with precise geographic coordinates) improves comparability, detection sensitivity, and trend assessment.

Previous scientific and technical reports on non-native crayfish in Piedmont lakes did not provide data on abundances or shoreline distribution, while our results fill this knowledge gap thanks to the extensive monitoring carried in summer 2025. Furthermore, for the first time *P. clarkii* in three additional lakes (lakes Pistono, San Michele, and Sirio) was detected. This may indicate a recent range expansion but could also result from historically inadequate monitoring of small peripheral water bodies, delayed reporting, or improved detection techniques in recent surveys.

5. Conclusions

- An inventory of non-native crayfish for Piedmont lakes had never been conducted prior to 2025, making this the first comprehensive effort to document the occurrence and to assess the distribution of non-native crayfish species within the region. Extensive baited-trap monitoring allowed us to confirm the occurrence of the Old Non-Indigenous Crayfish Species (*F. limosus, P. leniusculus*, and *P. clarkii*), and to record *P. clarkii* first-ever in three never monitored lakes (Pistono, San Michele, and Sirio).
- Isolated lakes or those with complex predator–prey networks host few or lack non-native crayfish because limited connectivity restricts dispersal while high predator pressure and biotic interactions hinder establishment and recruitment.
- Presence of non-native crayfish alters community structure and stability by reducing prey availability and modifying predator dynamics; understanding these interactions is essential for invasive-species management and freshwater biodiversity conservation.
- Standardized monitoring of crayfish populations is not only crucial for assessing the ecological health of freshwater ecosystems, but also to enable comparison of data and trend analyses.
- This baseline is crucial for informing managers to develop effective strategies to prevent further spread, and to protect Piedmont's freshwaters. Therefore, coordinated measures are required to prevent and control the ecological threats posed by invasive species.

- Moreover, improving information exchange across stakeholders and water managers, to halt illegal harvesting for food and pet trade since all these activities highly contribute to crayfish spread.

In summary, our results highlight lakes as valuable cultural and economic attractions, facing not only heavy anthropogenic activities from urbanization, recreational, wastewater, and irrigation [57,58], but also from biological pollution. Altogether, these pressures disrupt the chemical, physical, and ecological balance of lakes demanding for urgent and for a frequent non-native species monitoring, currently not included in any national action plans.

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Conflicts of Interest: The authors declare no conflict of interest.

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