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Can the introduction of *Xenopus laevis* affect native amphibian populations? Reduction of reproductive occurrence in presence of the invasive species

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Abstract Biological invasions are regarded as a form of global change and potential cause of biodiversity loss. *Xenopus laevis* is an anuran amphibian native to sub-Saharan Africa with strong invasive capacity, especially in geographic regions with a Mediterranean climate. In spite of the worldwide diffusion of *X. laevis*, the effective impact on local ecosystems and native amphibian populations is poorly quantified. A large population of *X. laevis* occurs in Sicily and our main aim of this work was to assess the consequences of introduction of this alien species on local amphibian populations. In this study we compare the occurrence of reproduction of native amphibians in ponds with and without *X. laevis*, and before and after the alien colonization. The results of our study shows that, when *X. laevis* establishes a conspicuous population in a pond system, the populations of *Discoglossus pictus*, *Hyla intermedia* and *Pelophylax* synklepton *esculentus* show clear signs of distress and the occurrence of reproduction of these native amphibians collapses. In contrast, the populations of *Bufo bufo* do not appear to be affected by the alien species. Since the Sicilian population of *X. laevis* shows a strong dispersal capacity, proportionate and quick interventions become necessary to bound the detriment to the Sicilian amphibians populations.

Keywords *Xenopus laevis* · Alien invasive species · Sicily · Amphibians conservation · Biological invasion

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Introduction

Biological invasions are regarded as a form of global change (Ricciardi 2007). Many human activities, such as agriculture, aquaculture, recreation and transportation, are the cause of intentional or accidental spread of species away from their natural ranges of distribution (Gherardi et al. 2008). Although most new species fail to establish viable populations, those that persist can threaten native biodiversity and ecosystem functionality, and may have detrimental effects on human health as well as economic impacts (Kolar and Lodge 2001). Compared to terrestrial ecosystems, aquatic ecosystems have proven particularly vulnerable to invasive alien species (Sala et al. 2000).

The direct link between invasiveness and impact on the host ecosystems of an alien species is not easily demonstrable (Ricciardi and Cohen 2007). Alien invasive species are among the main causes of global amphibian decline (Beebee and Griffiths 2005; Kats and Ferrer 2003). The introduction of predatory fish, crustaceans and non-native amphibians can strongly threaten the native amphibian populations via competition, predation, diffusion of diseases or other interactions (e.g., Garner et al. 2006; Hecnar and M'Closkey 1997; Kats and Ferrer 2003).

After the American bullfrog (*Lithobates catesbeianus*) and cane toad (*Bufo* (*Chaunus*) *marinus*), the African clawed frog *Xenopus laevis* is probably the invasive amphibian species with the greatest worldwide diffusion. It is native to sub-Saharan Africa and is a totally aquatic species that lives in most types of water bodies with preference for stagnant or still waters in ponds or sluggish streams (Tinsley et al. 1996). The African clawed frog has specific adaptations to aquatic life, including retention of the lateral line system in adults, aquatic chemoreceptors (Elepfandt 1996a, b; Elepfandt et al. 2000) and a body structure particularly adapted for swimming (Videler and Jorna 1985). However, it also has a remarkable ability to migrate overland (Eggert and Foquet 2006; Faraone et al. 2008a; Measey and Tisley 1998).

The worldwide spread of the African clawed frog is due to trade started in the 1930s. After the development of a pregnancy assay using African clawed frogs as a test animal, as well as its use as a model in development biology (Gurdon 1996; Keller and Lodge 2007; Weldon et al. 2007). The aforementioned biological characteristics and strong adaptability of the African clawed frog has resulted in its success as an invasive species, particularly in geographic regions with a Mediterranean climate (Lobos and Measey 2002; Tinsley and McCoid 1996). Non-native and invasive populations of African clawed frog are present in the US states of Arizona and California (Crayon 2005), Ascension Island (Tinsley and McCoid 1996), Chile (Lobos and Measey 2002), France (Fouquet 2001), Wales (Measey and Tisley 1998), Sicily (Lillo et al. 2005) and Portugal (Rebelo et al. 2010). Although many studies investigate the biology and the ecology of African clawed frogs in their invasive environments (e.g., Fouquet and Measey 2006; Lobos and Jaksic 2005; Measey and Tisley 1998), to our knowledge no studies examine the effects of this alien species on populations of native amphibians.

The African clawed frog is a proficient generalist predator, implicated in ingestion of endangered and rare species [e.g., *Gasterosteus aculeatus williamsoni* (Tinsley and McCoid 1996); *Eucyclogobius newberryi* (Lafferty and Page 1997)], as well as amphibians. For example, stomach contents of African clawed frogs have been found to have low numbers of *Bufo boreas* (one of 39 stomachs; Crayon 2005). Similarly, in a previous study on Sicilian populations of African clawed frog, we recorded the presence of a *Bufo bufo* tadpole among 306 stomachs examined (Faraone et al. 2008b). The African clawed frog is also considered as the probable origin of the spread, and a vector of, the chytridiomycosis fungus *Batrachochytrium dendrobatidis* (Weldon et al. 2004). Despite the aforementioned observations that lead to a legitimate concern for native species, few studies provide details of the impact of African clawed frogs on host ecosystems, particularly local populations of amphibians. Since the discovery of African clawed frogs in Italy in 2004 (Lillo et al. 2005), the need for an in-depth investigation on the possible consequences of its introduction on ecosystems is vital.

The aim of this study is to clarify if the establishment of an invasive population of African clawed frogs influences native amphibian populations. Specifically, we aimed to evaluate:

1. The difference in the reproductive occurrence and population structure of native amphibians in ponds with and without African clawed frogs
2. The change in reproductive occurrence of amphibian assemblages during the colonization process of the African clawed frog
3. The trophic overlap between an aquatic native amphibian and the African clawed frog.

Materials and methods

Study area and amphibian species

We conducted our study in the catchment basins of the rivers Belice Destro and Jato, Sicily, Italy. This area is 15 km wide (37°52′–38°0′N) and 27 km long (12°56′–13°14′E) and is mainly agricultural land, cultivated with vineyards, olive groves and cornfields. It also includes a large reservoir (Lake Poma) and hundreds of agricultural ponds with surface areas ranging between 100 and 2,000 m^2. Faraone et al. (2008a) showed that this region has a large invasive population of African clawed frog, with a distribution surface of $\sim$225 km^2 in 2005.

The catchment basins include five native amphibians: the common toad *Bufo bufo*, the endemic Sicilian green toad *B. siculus*, the painted frog *Discoglossus pictus*, the Italian tree frog *Hyla intermedia* and the Italian complex of green frog *Pelophylax* synklepton *esculentus*. The agricultural ponds are important sites for reproduction of all these amphibians except for the Sicilian green toad that is rare in agricultural ponds and prefers temporary ponds for reproduction (Sicilia et al. 2006), so our study focuses on the other four native amphibians.

Sampling and analysis

On 34 occasions between 2005 and 2008, we conducted sampling trips at 68 ponds within the study area. Each pond was sampled at least one time for season. During each sampling period we recorded (1) the presence/absence of African clawed frogs in the ponds, (2) the occurrence of reproduction of the native amphibians in the same ponds, and (3) the colonization of new ponds by African clawed frog from year to year. The presence of amphibians was evaluated through visual observation and with the aid of dipnets. The detection of the presence of African clawed frog is facilitated by its respiratory behaviour: African clawed frogs spend in fact, most of their time underwater, periodically performing rapid surfacing in order to breathe (Ihmied and Taylor 1995). The surfacing individuals are easily identifiable by observing the surface of the ponds. Each pond was sampled for at least 30 min by two experienced observers. In the case of doubtful observations, the sampling was repeated a few days later, otherwise the pond was discarded for the analysis.

During 2007, to evaluate the consequences of the presence of African clawed frogs in the ponds, we selected, between the 68 ponds sampled, 45 ponds that appeared optimal for reproduction of native amphibians. These ponds was divided in two groups: one group of ponds included those impacted by the presence of African clawed frogs (IMP; n = 26) and one group of control ponds without the alien species (CTR; n = 19). We compared the IMP and CTR ponds (*t* test) about their environmental variables (Table 1).

We used a χ^2 test to compare the different occurrence of reproduction of native amphibians between IMP and CTR ponds. The number of ponds sampled for each species was the following: 26 IMP ponds and 18 CTR ponds for green frogs; 18 IMP ponds and 10 CTR ponds for common toads; 18 IMP ponds and 11 CTR ponds for painted frogs; 17 IMP ponds and 14 CTR ponds for Italian tree frogs. In the case of no significant differences between IMP and CTR ponds we evaluated the difference of relative abundance of tadpoles collected by dipnets as described by Scott and Woodward (1994). The method consists of dragging the net (25 × 20 cm) for a note tract (1.5 m) proportionally to the length of the pond edge (every 10 m). A one-way ANOVA was applied to examine the difference of the relative abundance of tadpoles between the pond groups.

To evaluate the yearly variation of the reproductive occurrence of native amphibians we focused observing a focal pond for four consecutive years (2005–2008). The focal pond was *Xenopus*-free in 2005 and colonized for the first time in 2006. To verify the presence of African clawed frogs we conducted yearly repeated samplings between May

Table 1 Comparison between the environmental characteristics of pond with *Xenopus laevis* (IMP) and ponds without the alien species (CTR)

Pond characteristics	IMP (n = 26)	CTR (n = 19)	*t* test			All ponds (n = 45)	
	Mean ± SE	Mean ± SE	*t*	*df*	*P*	Mean ± SE	Range
Surface area (m^2)	824.0 ± 36.5	831.6 ± 27.9	0.15	43	0.88	827.2 ± 23.9	600–1500
Maximum depth (m)	3.7 ± 0.2	3.5 ± 0.2	0.53	43	0.60	3.6 ± 0.1	2–5
Riparian vegetation (%)	34.4 ± 2.0	35.8 ± 2.3	0.44	43	0.66	35.0 ± 1.5	25–50
Altitude (m asl)	316.7 ± 9.7	327.7 ± 13.3	0.68	43	0.50	321.4 ± 7.9	200–450
Surrounding area (% vineyards)	68.3 ± 4.7	72. 4 ± 5.4	0.57	43	0.57	70.0 ± 3.5	25–100

and August using a plastic dredge (see Faraone et al. 2008a; 100 cm × 100 cm × 50 cm, L × W × H). The occurrence of reproduction of all amphibians in the pond was evaluated by presence/absence of spawning, larvae and postmetamorphs. Furthermore we recorded the relative abundance of tadpoles for each amphibian species, as the number of tadpoles observed during a complete turn of the pond edge. We used a scale of abundance as follows: abundant (>50 in at least one sampling during the year), low (10–50), present (1–9), absent (0).

To evaluate the possible trophic competition between the native amphibians and the African clawed frog we compared their with that of the green frog. The green frog has the strongest aquatic ecology, living in close contact with the water throughout the year (Lanza et al. 2007). The painted frog, Italian tree frog and common toad only use the aquatic ecosystems during their reproductive period. During five sampling periods between July and September 2006, we collected stomach contents of African clawed frog and green frog in two neighbor and similar ponds. To avoid interferences we selected a *Xenopus*-free pond to collect green frogs. The African clawed frogs were collected by using a plastic dredge and green frogs using dipnets. The stomach contents were collected through the stomach flushing method (Solé et al. 2005), and prey items identified using a stereo-microscope. We distinguished prey types at the level of Order. Furthermore, we distinguished the prey types as adults, larvae, nymphs or pupae and for their aquatic and non-aquatic ecology. The Orders that occurred in stomach contents of both amphibians were identified to the level of Family. The percentage of every prey type was calculated. To estimate the overlap of the diets of two amphibian species we used the Pianka Index. The values of this index vary from 0 (no overlap) to 1.0 (complete overlap) with 0.75 indicating high overlap and values less than 0.4 indicating low overlap (Pianka 1973).

Results

During the firs year, 35 ponds of 68 (51.5%) was colonized by African clawed frog. In 2008 we found the species in 47 ponds (69.1%). The timing of occurrence of spawns, larvae and metamorphs of all five native species in the study area is shows in Fig. 1.

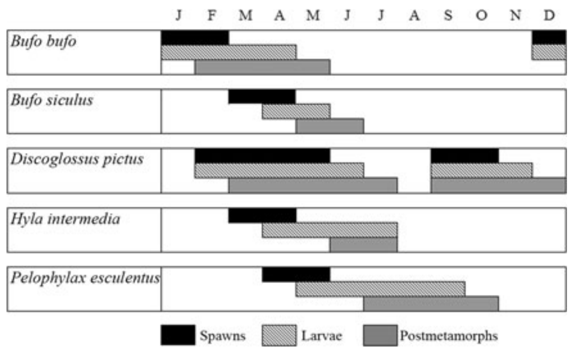

Fig. 1 Timing of occurrence of spawns, larvae and postmetamorphs of all native species in the study area

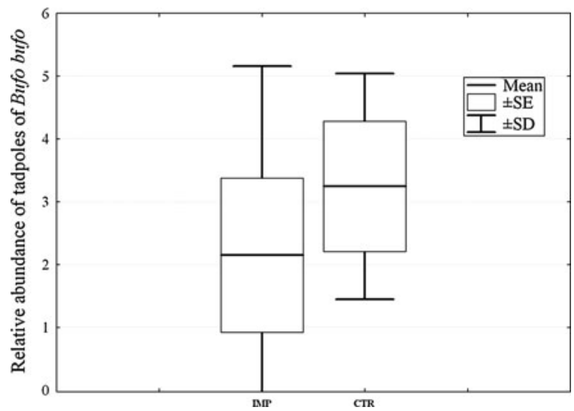

Fig. 2 Mean, SE and SD of relative abundance of *B. bufo* tadpoles in IMP and CTR ponds

The comparison between IMP and CTR ponds showed no statistically significant differences for all their environmental variables. Occurrence of reproduction was higher in CTR ponds than IMP ponds for green frogs ($\chi^2 = 14.65$; $P < 0.001$), painted frogs ($\chi^2 = 23.52$; $P < 0.001$) and Italian tree frogs ($\chi^2 = 6.1$; $P = 0.013$). However, the occurrence of reproduction of common toads did not differ in ponds with and without African clawed frogs ($\chi^2 = 0.003$; $P = 0.96$) (Fig. 2). Similarly, the relative abundance of tadpoles of common toads, evaluated by one-way ANOVA, did not differ between ponds with and without African clawed frogs ($\text{Average}_{IMP} = 2.15$ ($SE = \pm 1.23$), $\text{Average}_{CTR} = 3.24$ ($SE = \pm 1.04$); $F_{6,93} = 1.39$, $P = 0.22$) (Fig. 3).

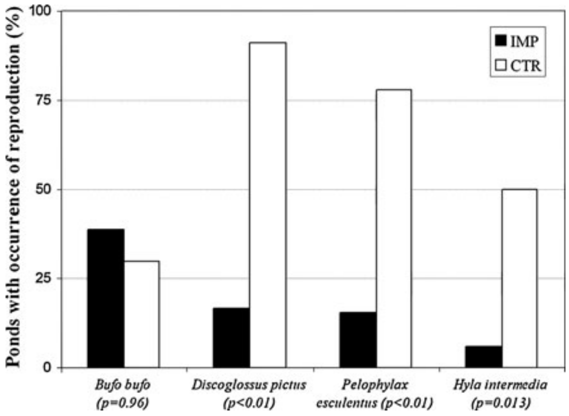

Fig. 3 Percentage of ponds with *Xenopus laevis* (IMP) and without *X. laevis* (CTR) that showed occurrence of reproduction of native amphibians during 2007

Table 2 Relative abundance of native and alien tadpoles in the focal pond during the colonization process by *Xenopus laevis* (2005 and 2008)

	I Year	II Year	III Year	IV Year
Bufo bufo	A	A	A	A
Discoglossus pictus	A	A	A	NP
Hyla intermedia	LP	LP	LP	NP
Pelophylax esculentus	A	A	A	NP
Xenopus laevis	NP	NP*	A	A

A abundant, *LP* low presence, *NP* not present, *NP** tadpoles absent but adults present. See “materials and methods” for details

Table 2 summarizes the yearly variation of reproductive occurrence in the focal pond for all amphibian species. During the observations conducted in 2005, we did not find African clawed frogs in the focal pond nor in the neighbouring ponds. In the same year the larvae of native amphibians were abundant (green frog, painted frog, common toad) or low (Italian tree frog) in the pond. In 2006 we observed few surfacing activities of African clawed frogs in the focal pond, but the repeated use of the dredge did not produce any capture because of their low density. Similarly, no tadpoles or postmetamorphs of African clawed frogs were observed and the relative abundance of native amphibian tadpoles was the same of the previous year. In 2007 the dredge captured eight adult and 164 tadpoles or postmetamorphs of African clawed frogs (ratio 0.05:1 adult: (tadpoles + postmetamorphs)). The occurrence of reproduction of native amphibians was again the same of the previous years. Finally, in 2008 the dredge captured 313 adult and 14 tadpoles or postmetamorphs of African clawed frog (ratio 22.4:1 adult: (tadpoles + postmetamorphs)), but no occurrence of reproduction was recorded for native amphibians in this year, except for the common toad. During these years the same pattern of colonization was observed in another eight ponds close to the focal pond and colonized by the alien species. On the contrary, four ponds where African clawed frog has not colonized during the years of observation, the occurrence of reproduction of all native amphibians has not changed.

For the diet analysis we examined the stomach contents of 21 specimens of adult green frog and 42 specimens of adult African clawed frog. We found a total of 16 Orders, three of which (Hemiptera, Hymenoptera and Diptera) are present both in green frogs and in African clawed frogs (Table 3). In the green frogs we found mostly non-aquatic prey (83.3%) belonging to six Orders of arthropods, while in the African clawed frogs we found mostly aquatic prey (95%) belonging to 12 orders of arthropods, and tadpoles of one amphibian species (African clawed frog). The Pianka Index showed a value of 0.01 indicating the almost total absence of overlap of trophic niches. Amongst the aquatic prey present in both amphibians (Hemiptera and Diptera), a clear difference is apparent: the prey found in the green frog stomachs belong mainly to Families of organisms living on the water surface, while prey present in the African clawed frogs stomachs belonged to Families of organisms living within the water column. Amongst the terrestrial prey, only the Order Hymenoptera occurs in both amphibians and with only one Family (Formicidae). Eggs, tadpoles and postmetamorphs of native amphibians were not present in the stomachs of the African clawed frog examined. Nevertheless, although the samplings were conducted during the reproductive period of green frog and Italian tree frog, spawning and tadpoles were not observed in the pond.

Discussion

Our results indicate different occurrence of reproduction of green frog, painted frog and Italian tree frog between ponds with and without African clawed

Table 3 Systematic list of the percentage of prey types in stomach contents of *Pelophylax* synklepton *esculentus* and *Xenopus laevis*

Order	Family	Ecological category	*Pelophylax esculentus* (%) n = 21	*Xenopus laevis* (%) n = 42
Acarina		A	–	1.2
Cladocera		A	–	6.4
Calanoida		A	–	0.1
Ciclopoida		A	–	29.6
Isopoda		NA	12.8	–
Collembola		A	–	0.3
Odonata		NA	8.5	–
Ephemeroptera (nymphs)		A	–	17.9
Odonata (nymphs)		A	–	21.4
Hemiptera	Naucoridae	A	2.1	–
	Micronectidae	A	–	0.3
	Notonectidae	A	–	1.6
	Pleidae	A	–	4.2
	Gerridae	**A**	**2.1**	**0.2**
	Hebridae	NA	2.1	–
	Mesoveliidae	NA	14.9	–
	Coreidae	NA	4.3	
Tricoptera (larvae)		A	–	0.3
Lepidoptera (larvae)		A	–	0.1
Coleoptera		NA	4.3	–
Hymenoptera	**Formicidae**	**NA**	**4.3**	**0.2**
	Vespidae	NA	25.4	–
	Apidae	NA	4.3	–
Diptera		NA	8.5	–
Diptera (pupae)		A	–	1.5
Diptera (larvae)	Chaoboridae	A	–	0.6
	Culicidae	**A**	**6.4**	**2.0**
	Ceratopogonidae	A	–	2.8
	Chironomidae	A	–	8.6
Anura		A	–	0.7

A aquatic, *N* non-aquatic. Rows in bold indicate prey common to both *Pelophylax* and *Xenopus*

frogs. The choice of ponds with similar biotic and abiotic characteristics decreases the probability of a different suitability between the two pond groups. Furthermore, declines in populations of native frogs after a few years since the first alien colonization and the persistence of the reproduction occurrence in *Xenopus*-free ponds suggest the negative effects of African clawed frog on the three native amphibians species. However, the occurrence of reproduction and the relative abundance of tadpoles of the common toad was not affected by presence of the African clawed frogs. The common toad is resistant against some other alien species including predatory fish (Cruz et al. 2006; Hartel et al. 2007; Orizaola and Braña 2006). Moreover, the reproductive activity of the common toad in the study area occurs during the coldest months (December/February), when the activity of African clawed frogs is low due to low temperatures (Casterlin and Reynolds 1980; Measey 2001). The predation on conspecific tadpoles confirms the significant cannibalistic behaviour of this species (Tinsley et al. 1996; Measey 1998; Faraone et al. 2008b).

The consequences of biological invasions are usually predicted as undesirable and detrimental. However, in many cases it is difficult to assess objectively the impact of an alien species. So, often the precautionary principle is the main subject of aversion against the introduction of alien species in a new area (Cooney 2004) or, at the worst, the knowledge of the effects of species with similar ecological features can suggest its undesirability. In other cases the consequences of biological invasions are concrete and well known (Holway et al. 2002; Courchamp et al. 2003).

Following Parker et al. (1999) to assess the impact of an invasive species it is not sufficient to know the effect on native species or ecosystems, but the impact must be considered as the product of three factors: the range size of the invader species, its average abundance per unit area across that range (in number of individuals, biomass, or other relevant measure) and the effect per individual or per biomass unit of the invader. So, if the three factors of the Parker equation have high values, the value of the impact is high. In this study we observed and increment of 17.6% of ponds colonized by African clawed frog in four years. Moreover, Faraone et al. (2008a) recorded the African clawed frog's Sicilian range of distribution measuring $\sim$225 km^2 in 2006, evaluated by using the Minimum Convex Polygon method. Our successive studies show an enlarging area of more of 300 km^2 in 2009 and an estimation of population in a focal pond by using capture-mark-recapture method of about 2100 adult African clawed frogs in a single pond (Lillo et al. unpublished data). These data, together with the results of the present study, represent the three factors of the Parker equation with high values. So seem appropriate to asses high the impact of the African clawed frog on the Sicilian amphibians.

African clawed frog has been so far considered an undesirable species more for potential effects on native species than for the knowledge of its effective consequences on host ecosystems (Ricciardi and Cohen 2007). Indeed studies on the biology and the ecology of African clawed frogs in their invasive environments conducted in Chile, USA, France, Portugal and Wales did not clarify the effects of interactions between the alien species and the native species, and in particular the impact on native amphibians (e.g., Fouquet and Measey 2006; Lobos and Jaksic 2005; Measey and Tisley 1998). Instead, our results for the first time, show an association between the presence of African clawed frog and a concrete decline of the reproduction occurrence of three native amphibians.

The diet comparison between African clawed frog and green frog, points out the strong preference of green frogs towards terrestrial prey, as already known (Lőw and Török 1998; Sas et al. 2007), and the almost absolute preference of African clawed frogs towards aquatic prey (see Faraone et al. 2008b; Measey 1998). The observed predation on Formicidae by African clawed frog probably depends mainly on occasional ingestions of organisms accidentally fallen in the water (see Measey 1998; Tinsley et al. 1996). These data, at the same time as the almost total absence of overlap of the trophic niche indicated by Pianka Index, suggest the lack of competition for trophic resources between the two species, and probably also between the alien species and the other two semi-terrestrial native amphibians that feed overground. At the same time our data does not permit to support or to discard an impact hypothesis due to direct predation on eggs or larvae of native amphibians. It is possible that the high density of African clawed frogs and the low density of native larvae could decrease the probability to detect these in the stomach contents. On the other hand the difficulty to record the direct predation was already presumed by Measey (1998). He describes that *Rana temporaria* spawned in a pond colonized by African clawed frog in Wales, and that numbers of larvae were monitored. Later no tadpoles or postmetamorphic could be found, but, at the same time, no larvae were found in the stomach contents of African clawed frogs.

So currently it is not possible to point out the conclusive mechanisms of impact of African clawed frog on native amphibians, and new studies will be necessary to clarify this aspect. In particular in the future it will be useful to test if the African clawed frog direct predation can be the main process of native amphibians decline that we observed in our study. Other studies are necessary, in Sicily or in other new colonized areas, to asses the ecological fall of African clawed frog introduction of freshwater ecosystems and in particular on invertebrate community

Despite the insular isolation of Sicily which can prevent the undesirable dispersal of the alien species in other geographic areas, insular communities and amphibian populations are considered particularly vulnerable to biological invasions (Collins and Storfer 2003; Savage 1987). So the effects of African clawed frog invasion reported in this study is cause for high concern. Efficacy control methods should be tested to allow quick and proportionate interventions of population control to avoid the detriment to the Sicilian amphibians populations.

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