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Invasive Species and Amphibian Conservation

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Abstract: The recognition that invasive alien species (IAS) are among the greatest threats to biodiversity has stimulated a growing interest in their impacts on native amphibians. Here we describe the multifaceted consequences of biological invasions on native amphibians and identify potential mechanisms and strategies that could better enable the long-term persistence of native species. IAS can influence amphibian fitness, population size, and community structure via multiple pathways and can exert major, direct impacts through predation, competition, and hybridization. The consequences of indirect impacts, too, such as habitat alteration and the spread of emerging diseases, can be particularly severe in native populations. Native amphibians may respond to IAS by modulating aspects of their behavior, morphology, or life history. Nevertheless, it is still unclear the extent to which phenotypic plasticity and rapid evolution may help native species withstand the impacts of IAS in invaded communities. Practical management strategies focused on prevention, monitoring, and early control are the most effective approaches to allay the impacts of IAS and should be prioritized in proactive conservation plans. Eradications of IAS and mitigation approaches, should IAS become established, are feasible and can greatly improve the status of native populations.

Key words: Amphibian decline; Biological invasions; Contemporary evolution; Fitness; Horizon scanning; Impacts; Invasive fish; Management strategies; Phenotypic plasticity

Invasive alien species (IAS) are a major threat to biodiversity. Of about 800 animal extinctions that have been recorded since 1500, IAS have been implicated in 33% of them (Blackburn et al. 2019). For amphibians, IAS have been the cause of about one-third of extinctions, and approximately 16% of extant species currently are threatened by IAS (Stuart et al. 2008; Blackburn et al. 2019). Nevertheless, biological invasions are a complex process (see Box 1 for definitions and conceptual framework), and the impact of IAS on biodiversity is highly heterogeneous both among habitats and geographic areas. Amphibians living on islands and in freshwater are disproportionately affected by invasive species (Stuart et al. 2008; Strayer 2010; Spatz et al. 2017).

Two decades ago, Kats and Ferrer (2003) summarized the negative impacts of IAS on amphibians. Since then, research in IAS has not progressed as quickly as research focusing on habitat loss and diseases; lately, however, interest has grown dramatically (Fig. 1). It is increasingly evident that IAS can have a broad range of impacts on amphibians, affecting species and communities through multiple processes. Yet the impact of IAS can be complex and multifaceted, and often interacts with other global stressors, such as disease (Blaustein and Kiesecker 2002) and habitat change (Didham et al. 2007). The growing awareness of the impacts of IAS has also stimulated research on potential conservation strategies in order to identify management practices that could halt or limit the impact of IAS.

Here we review the recent literature to understand the impact of IAS on native amphibians and evaluate potential mechanisms and strategies that could allow the long-term persistence of native species. First, we show that invasive species have a broad range of effects on native amphibians, both direct and indirect. Second, we describe the limited range of options that can allow amphibians to persist in invaded environments, such as plasticity and rapid adaptation. Finally, we show how the threat of invasive species can be limited through prevention, diligent monitoring, and early intervention. Our study highlights the complexity of the impact of IAS on amphibians, and identifies multiple questions for both research and practical conservation.

Impact of Invasive Alien Species on Amphibians

IAS can affect amphibians through a broad range of pathways (Fig. 2; Bucciarelli et al. 2014; Nunes et al. 2019) including predation (Kats and Ferrer 2003), competition (Richter-Boix et al. 2013), hybridization (Dufresnes et al. 2016), habitat alteration (Matsuzaki et al. 2009), and the spread of disease (Miaud et al. 2016).

Predation

Amphibians with aquatic life-history stages are particularly sensitive to the introduction of alien predators. This is because many amphibians breed in freshwater ecosystems such as isolated ponds or headwater streams where large predators normally are scarce (Cox and Lima 2006). Even though several amphibian species have evolved mechanisms to co-exist with some predacious fishes (Van Buskirk 2003), invasive predators can drive local populations to decline, or even extinction, because they directly reduce the abundance of eggs, larvae, or adults (Kats and Ferrer 2003; Bucciarelli et al. 2014; Nunes et al. 2019). Fish are probably the most frequently introduced large predators in freshwaters and have caused massive loss of amphibian breeding sites in all the continents (e.g., Knapp and Matthews 2000; Knapp 2005; Tiberti and von Hardenberg 2012). Large fishes such as trout, as well as small-sized fishes, are efficient amphibian predators (Remon et al. 2016; Miró et al. 2018). Besides fishes, many other taxa can exert heavy predation pressure. For instance, carnivorous tadpoles of Indian Bullfrogs, *Hoplobatrachus tigerinus,* rapidly prey upon native tadpoles,

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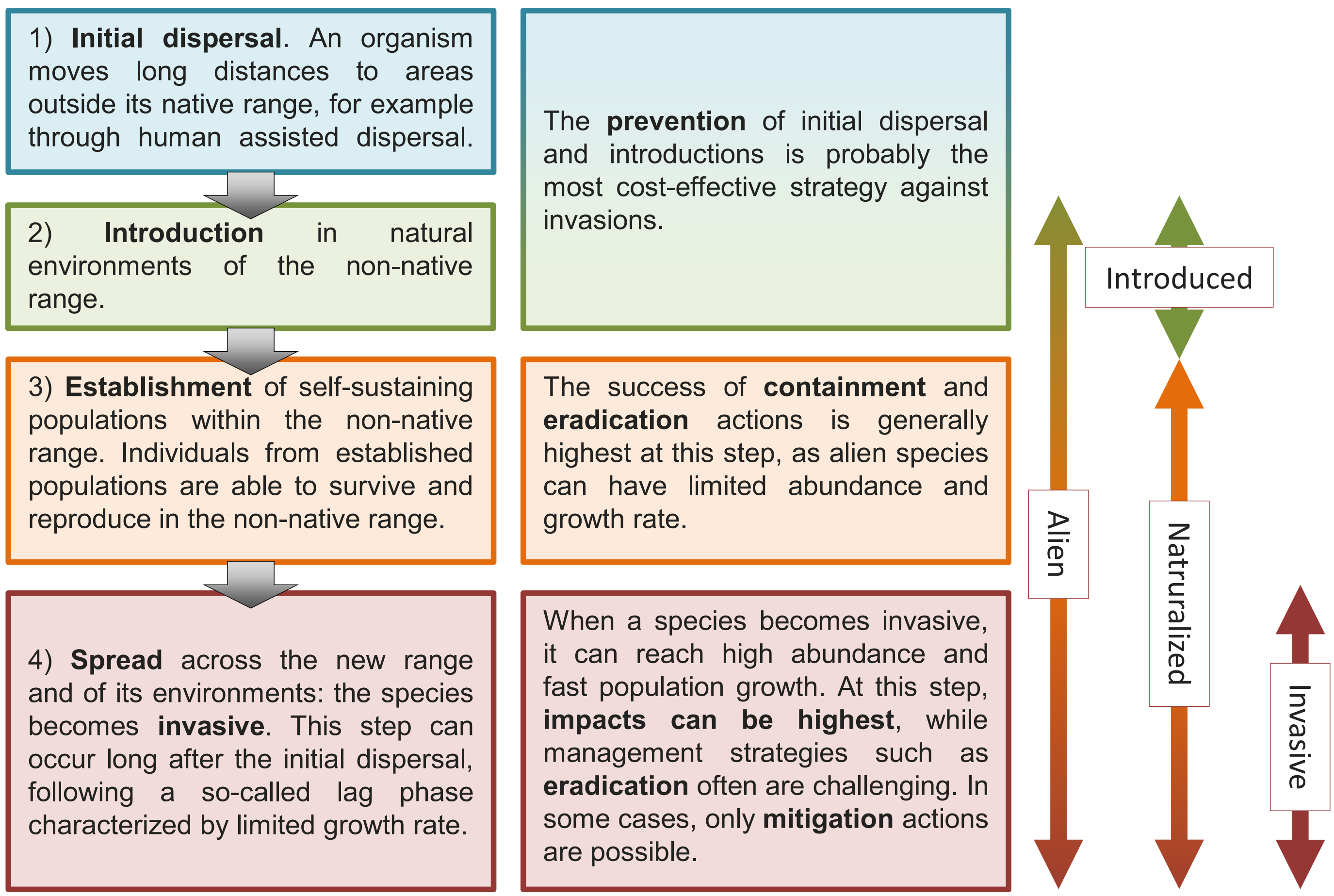

BOX. 1.—From introduced to invasive species: How to define a multistep process. Describing invasions as a multistep process, comprising four major phases, allows a better understanding of invasions, provides a unified terminology, and helps management given that different approaches can have different efficiency and feasibility across stages (modified after Blackburn et al. 2011). In this review, we generally focus on invasive species (i.e., the category causing the strongest impacts on biodiversity). Nevertheless, when discussing conservation strategies, we also consider the early stages because of the efficiency of management actions against them (Puth and Post 2005). A color version of this figure is available online.

hampering the survival of larvae of frogs endemic to the Andaman archipelago (Mohanty and Measey 2019).

The effects of alien predators can go well beyond simple declines in abundance at invaded sites. When predators invade a large number of sites, they can cause declines over broad regional or national scales. For example, many amphibians live in networks of spatially structured subpopulations (e.g., metapopulations) and invasive predators often may cause a loss of fitness at the invaded sites (Ficetola et al. 2011). This can lead to local declines but also to reductions in the number of juvenile amphibians that may disperse to nearby populations. This will result in negative effects on the long-term dynamics of the whole metapopulation network, and a negative impact at a regional scale even in noninvaded wetlands (Manenti et al. 2020). Furthermore, alien predators do not affect just species occurrence and abundance, they can also influence intraspecific variation. Paedomorphosis is an example of intraspecific variation, in which metamorphosing individuals coexist with fully aquatic, paedomorphic conspecifics that do not metamorphose, which has important consequences for adaptation and evolution of the species (Denoël et al. 2005). Fish introductions were the main determinant of extirpation of paedomorphs of two newt

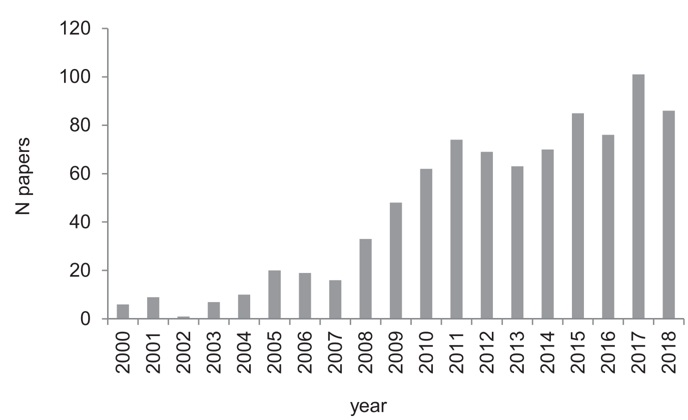

FIG. 1.—Increase in the number of papers on invasive alien species and amphibians since 2000. The number of papers was obtained from the ISI Web of Science on 8 July 2019, considering the "article" category only and using the following search terms: "invasive species" or "alien species" or "nonnative" AND amphibian* or frog* or salamander* or toad* or newt* or caecilian* or "anura" or "urodela" or "caudata" or "gymnophiona."

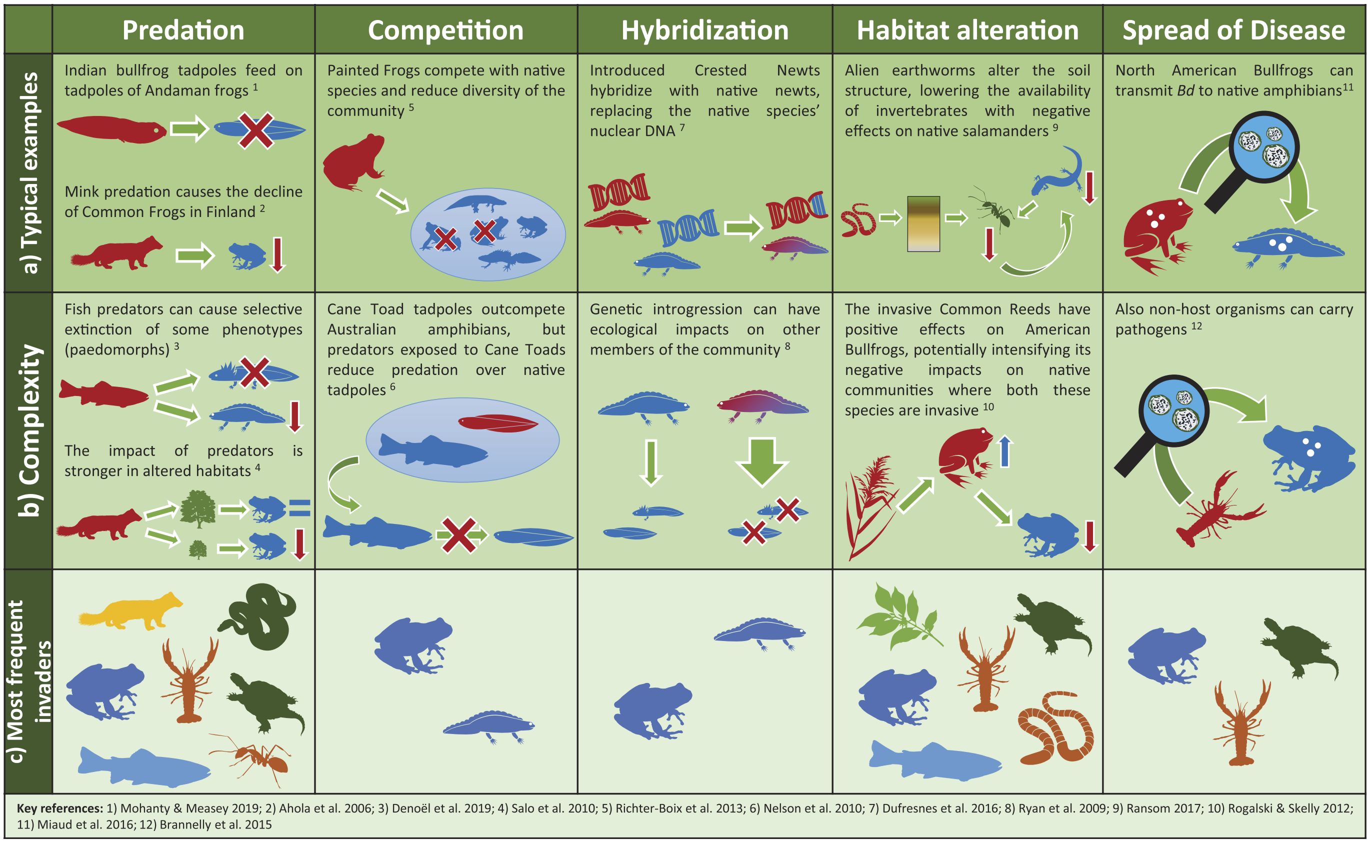

FIG. 2.—The main processes through which invasive species affect amphibians. (a) Examples of direct impacts. (b) Examples of complex impacts, often mediated via interactive effects. (c) Examples of the most frequent taxonomic groups involved in each process. Native species are depicted in blue. Invasive species are depicted in red. Drawings by MF, GFF, B. Comix, and N. Sinegina and obtained from http://www.supercoloring.com/ under a Creative Commons 4.0 License. A color version of this figure is available online.

species (*Ichthyosaura alpestris* and *Lissotriton graecus*) in Montenegro (Denoël et al. 2019). The abundance declined at a much faster rate among paedomorphic populations than among metamorphic populations. The paedomorphic populations have declined by >80% in <70 years, whereas metamorphic newts have lost approximately 50% of populations during the same period.

Competition

When an invader's ecological niche overlaps that of a native species, the resulting competition can lead to the native species' decline or even extirpation (Mooney and Cleland 2001). Many studies on interspecific competition have focused on interaction between native and alien amphibians. For example, Painted Frogs, *Discoglossus pictus,* are invasive in Spain, where they have the potential to reduce fitness in native Spanish toads and modify the composition of native anuran communities because its larvae can out-compete larvae of the native species (Richter-Boix et al. 2013). Native toads now avoid laying eggs in ponds where Painted Frog larvae are present, producing a complex pattern of species co-occurrence at the landscape scale due to the interaction between competition and breeding preferences (Richter-Boix et al. 2013; Pujol-Buxó et al. 2019).

The broader the ecological niche of an invasive species, the more likely it will compete with native species. American Bullfrogs, *Lithobates* (*Aquarana*) *catesbeiana,* are typical of IAS with broad ecological niches and are among the most problematic of invasive amphibians. American Bullfrogs, which are generalist predators and have a broad climatic tolerance, strongly affect many native amphibians where they have been introduced (Ficetola et al. 2007; D'Amore 2012; Bissattini et al. 2019). American Bullfrog tadpoles and adults often become the dominant amphibian competitors in freshwater communities because of their large size and voracious behavior (D'Amore 2012). They may also be vectors of diseases, so American Bullfrogs may alter environmental processes in complex ways (D'Amore 2012; Measey et al. 2016).

Hybridization

Hybridization of native species with alien species can lead to loss of fitness in the native taxa and, in some cases, to extirpation (Mooney and Cleland 2001). For example, Italian Crested Newts, *Triturus carnifex,* which were introduced in Switzerland at the beginning of the 20th century, hybridize with native Great Crested Newts, *T. cristatus*. In places where *T. carnifex* was introduced, newt populations showed a high rate of genetic introgression, sometimes leading to the complete elimination of pure *T. cristatus* (Dufresnes et al. 2016). Via hybridization, natural selection may favor the rapid spread of some genes of an invasive lineage across the range of native species, resulting in genetic pollution that may accelerate the replacement of native lineages (Fitzpatrick et al. 2010). This form of genetic introgression may thus have indirect effects on other components of the invaded ecological community. Compared with native Tiger Salamanders, introgressed Tiger Salamanders will drastically decrease recruitment of native amphibians as a result of their higher predation rates (Ryan et al. 2009).

Hybridization with invasive species is particularly problematic among the hybridogenetic European water frogs of the genus *Pelophylax*. In several areas of Central and Western Europe, native Pool Frogs, *P. lessonae,* and Edible Frogs, *P. esculentus,* naturally form an L–E hybridogenetic system. *Pelophylax esculentus* is a klepton between Marsh Frogs, *P. ridibundus,* and Pool Frogs, *P. lessonae,* that eliminates the *lessonae* genome during gametogenesis and clonally transmits the *ridibundus* genome (Vorburger and Reyer 2003; Holsbeek and Jooris 2010). *Pelophlyax ridibundus* frogs native to Eastern Europe, however, are commonly traded for human consumption throughout Europe. In Eastern Europe, *P. ridibundus,* and *P. esculentus* form an R–E hybridogenetic system whereby the *ridibundus* genome in *P. esculentus* is eliminated during gametogenesis and the *lessonae* genome is clonally transmitted. When introduced to an L–E system, R–E *P. ridibundus* mate with both native frogs, producing *P. esculentus* offspring with *P. lessonae,* and *P. ridibundus* offspring with *P. esculentus*. Thus, in several areas of Europe, invasive *P. ridibundus* are rapidly spreading at the expense of both native taxa (Vorburger and Reyer 2003; Holsbeek and Jooris 2010). The situation is further complicated because multiple *Pelophylax* species are actually traded throughout Europe. The hybridization with *P. ridibundus* can produce sterile or fertile hybrids depending on geographic origin; therefore, morphological identification of species is very difficult (Vorburger and Reyer 2003; Holsbeek and Jooris 2010; Quilodrán et al. 2015). Management of this situation is a major challenge because of the risk of rapid elimination of the native species (Quilodrán et al. 2018).

Spread of Diseases

Hundreds of amphibian species are threatened by emerging infectious diseases, which are often spread by IAS (Stuart et al. 2008; Martel et al. 2014; Scheele et al. 2019). Worldwide, >500 amphibian species have declined because of chytridiomycosis, the disease caused by two chytrid fungi: *Batrachochytrium dendrobatidis* and *B. salamandrivorans* (Fisher et al. 2009; Scheele et al. 2019). Invasive amphibians have been implicated as vectors of the chytrid pathogens and some may even show resistance to the disease (Garner et al. 2006). American Bullfrogs and African Clawed Frogs, *Xenopus laevis,* which can be resistant to chytridiomycosis, are thought to be able to transmit the pathogens to native amphibians (Miaud et al. 2016), although crayfish (Brannelly et al. 2015) and mosquitoes (Gould et al. 2019) could also be vectors. Chytrids may have spread in Europe via infected amphibians in the commercial pet trade, possibly leading to dramatic declines in some populations of European salamanders (Martel et al. 2014; Fitzpatrick et al. 2018). Given the high impact that novel diseases may pose to amphibians, any efforts to prevent the spread of pathogens by the monitoring and control of trade, and the application of strict sanitary protocols, are worth considering (see also Bienentreu and Lesbarrères 2020).

Habitat Alteration

IAS that become keystone species and ecosystem engineers can cause major habitat alterations, with strong impacts on native amphibians. Changes in habitat structure that alter base levels of wind and solar radiation and thereby modify the thermal landscape can have particularly strong impacts on ectothermic vertebrates (Watling et al. 2011; Garcia and Clusella-Trullas 2019). Some invasive plants are capable of severely modifying both terrestrial and freshwater habitats. For example, Amur Honeysuckles, *Lonicera maackii,* form a dense shrub layer in invaded forests that results in a decrease of species richness and produces shifts in amphibian community composition (Watling et al. 2011). The invasive earthworm, *Octolasion tyrtaeum,* which modifies the soil by reducing the organic layer, reduces the abundance of Red-Backed Salamanders, *Plethodon cinereus* (Ransom 2017). The majority of amphibians spend their adult lifetimes in terrestrial environments, and many species, especially in tropical areas, are fully terrestrial; therefore, the impact of invasive terrestrial plants and other organisms on amphibians is probably underestimated (Nunes et al. 2019).

Indirect and Context-Dependent Impacts of Invasive Species

It is increasingly evident that multiple biotic and abiotic factors often act in concert, with synergistic effects between IAS with other stressors such as habitat loss and climate change. Such indirect effects can account for a large part of biodiversity changes (Menge 1995; Didham et al. 2007). Joint and indirect effects are evident at multiple scales. In several cases, the negative effect of alien species is magnified by habitat loss and landscape alteration (Salo et al. 2010). In South Carolina, for example, forest harvesting increased the local abundance of invasive Fire Ants, *Solenopsis invicta,* leading to higher predation pressure on native salamanders (Todd et al. 2008). At a broader scale, negative effects of IAS on population trends on European amphibians and reptiles are stronger in landscapes providing less suitable habitat to native species (Falaschi et al. 2019).

Indirect biotic interactions are also frequent, and can both amplify or limit the impact of IAS (White et al. 2006; Nelson et al. 2010; Rogalski and Skelly 2012). For example, invasive Japanese Stilt Grasses, *Microstegium vimineum,* led to an increased abundance of native lycopsid spiders in Georgia, which resulted in increased predation on small arthropods, leading to diminished food resources for native American Toads, *Anaxyrus americanus,* and a decline in their abundance (DeVore and Maerz 2014). Such connections and chains of causality are important components of overall the impact of IAS on native populations (Brook et al. 2008; Bucciarelli et al. 2014).

Amphibian Responses to Invasive Species

Although IAS are a major driver of amphibian decline, amphibians have developed a range of ecological, behavioral, and evolutionary responses that can improve their fitness and mediate the impact of IAS in complex ways.

How Do You Recognize an Alien Predator?

During biotic invasions, native populations face species with which they do not share a co-evolutionary history, which can hinder the expression of effective responses (Sih et al. 2010; Carthey and Banks 2014). Failing to recognize a predator can be fatal, but several mechanisms allow native species to identify IAS as predators and activate adequate responses. First, predator recognition can occur when the IAS shows similar traits or is phylogenetically close to native predators (Fig. 3A). This is the Predator Generalization Hypothesis (Ferrari et al. 2007). Predator generalization can be observed in the San Marcos Salamanders, *Eurycea nana,* which coexist with native Largemouth Bass (*Micropterus salmoides*) and will demonstrate the same behavioral response (activity reduction) when exposed to chemical cues of nonnative perciform fish (Davis et al. 2012). Second, amphibians in freshwater environments often detect predators via chemical signals, or kairomones (Ferrari et al. 2010; Manenti et al. 2016), and can identify nonnative predators when their kairomones are associated with alarm cues released by preyed-upon conspecifics or with predator dietary cues (Fig. 3B). Association with alarm cues can be surprisingly effective. For instance, the repeated exposure to a combination of conspecific alarm cues and chemical cues of otherwise innocuous Zebrafish, *Danio rerio* elicited a remarkable antipredator response (activity reduction) in tadpoles of the Iberian Green Frog, *Pelophylax perezi,* even when subsequently exposed to Zebrafish cues only (Gonzalo et al. 2007). Finally, antipredator response toward IAS might be mediated by neophobia (i.e., the generalized avoidance response to novel stimuli; Brown et al. 2013), or simply through generic risk cues such as avoiding large-sized moving shapes (Wilson et al. 2018).

Often, though, no response of amphibians to IAS can be detected (Fig. 3E and 3F), bringing the effectiveness of potential mechanisms into question. Nonetheless, in nature, behavioral patterns can be complex. A lack of response to the kairomones of an invasive predator may be compensated by other chemical signals such as alarm or digestion cues. Moreover, some habitat conditions can increase a species' ability to respond to novelties such as invasive predators. For instance, tadpoles living in more risky environments can respond more promptly to novel predators and have enhanced survival (Ferrari et al. 2015).

Phenotypic Plasticity

Phenotypic plasticity (i.e., the capacity of a given genotype to express different phenotypic responses under diverging environmental conditions; Pigliucci 2001), is a key evolutionary mechanism that allows species to persist under unpredictable conditions. Thus plasticity represents a key defense against alien species (Peacor et al. 2006; Berthon 2015). Plasticity in amphibians is well-documented because these organisms are frequently subject to heterogeneous and variable ecological pressures (Wells 2007), and IAS often induce plastic responses in native amphibians (Fig. 3C–E). Invasive predators can trigger the activation of multiple inducible defenses (Fig. 3F). These may be behavioral, including, for example, reduced activity, avoidance, microhabitat shift (Gamradt et al. 1997; Nunes et al. 2013), morphological (Nunes et al. 2014), or ontogenetic, involving, for example, faster growth or development rate (Nunes et al. 2019; Smith and Harmon 2019). For instance, some populations of *Pelophylax perezi* develop deeper tail muscles when reared in the presence of invasive crayfish, a trait that can favor faster swimming and escape from predators (Dayton et al. 2005; Nunes et al. 2014). Similarly, exposure to an invasive fish will elicit faster development in tadpoles of Gray Treefrogs, *Dryophytes versicolor,* which then metamorphose more quickly and leave riskier environments sooner (Smith and Harmon 2019). Thus phenotypic plasticity can offer advantages to native amphibian species facing both invasive predators and competitors, and can help to overcome mating disruptions or habitat modifications, thus broadening the range of conditions under which they can survive (Peacor et al. 2006; Caut et al. 2013; Polo-Cavia and Gomez-Mestre 2014; Hossie et al. 2017). Finally, plasticity can offer natural selection a pool of variability that can favor the emergence and fixation of new adaptive phenotypes through genetic assimilation and canalization (Levis et al. 2018), which could help the long-term persistence of amphibians facing biotic invasions (Peacor et al. 2006; Berthon 2015).

Behavioral Responses

Behavioral responses to IAS are often rapid because they are modulated by plasticity and influenced by experience (Sih et al. 2010; Weis and Sol 2016). It is no surprise that a large amount of research has focused on behavioral response of native species toward invasive predators (Fig. 3D). In amphibians, common antipredator behaviors include changes in activity to limit predator exposure, space use modification to enhance predator avoidance, shifts in microhabitat to reduce niche overlap, and aggregation to dilute risk (Wells 2007). Several studies have demonstrated these behavioral responses in amphibian larvae exposed to alien predators (Caut et al. 2013; Nunes et al. 2014; Polo-Cavia and Gomez-Mestre 2014). For instance, toad tadpoles that recognize invasive predators reduce activity levels, which increases their survival (Polo-Cavia and Gomez-Mestre 2014). Nevertheless, behavioral responses against invasive predators can be weaker than the ones to native predators (Nunes et al. 2019).

There is less information on antipredator responses in adult amphibians (Winandy and Denoël 2013; Winandy et al. 2016). Alpine Newts, *Ichthyosaura alpestris,* exposed to goldfish spend more time in refuges to reduce predation risk, but consequently decrease their courtship activity, which affects breeding dynamics (Winandy and Denoël 2013). Amphibians can also adjust their behavior in response to other interactions with IAS apart from predation, including disturbance, habitat modification, competition, or reproductive interference. For example, males of Australian Marble Frogs, *Limnodynastes convexiusculus,* adjust their calls in the presence of invasive Cane Toads, *Rhinella marina,* by reducing frequency and matching Cane Toad calling pauses in order to reduce overlap with the calls of the toads (Bleach et al. 2015).

Strong Selective Pressure Can Foster Rapid Adaptation

In a sense, biotic invasions are a global, unintended experiment in unraveling the mechanisms of natural selection (Strauss et al. 2006). Rapid adaptation is possible

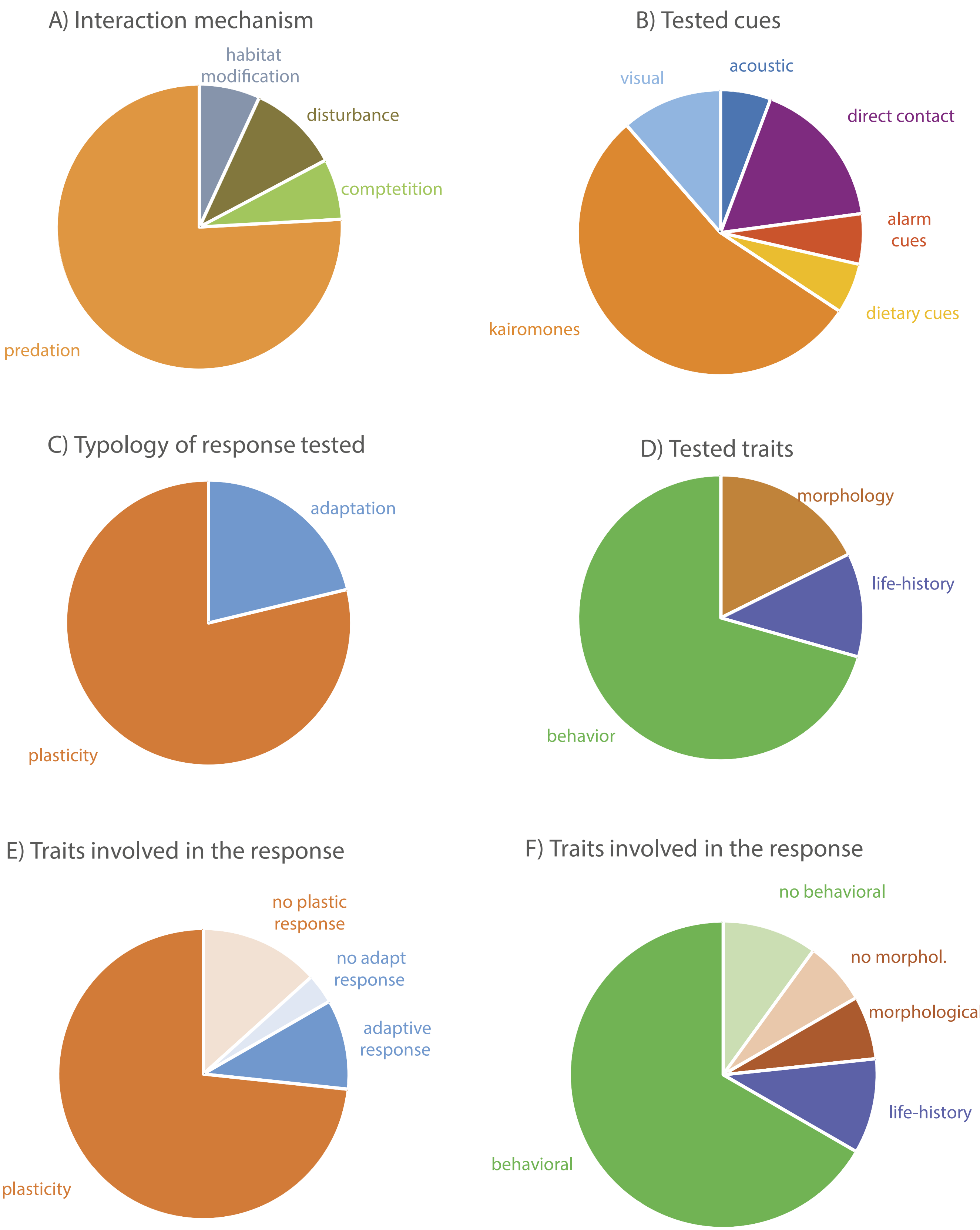

FIG. 3.—Amphibian responses to biological invasions. (A) Types of tested interactions between invasive alien species (IAS) and native amphibians. (B) Cues potentially involved in the response of amphibians to IAS. (C) Frequency of studies assessing phenotypic plasticity and local adaptations in native amphibians in presence of IAS. (D) Frequency of studies considering different types of traits in native amphibians. (E, F) Frequency of responses effectively detected in native amphibians. Results are based on the analysis of 99 papers obtained through the ISI Web of Science using the following search terms: "invasive species" or "alien species" or "nonnative" AND amphibian* or frog* or salamander* or toad* or newt* or caecilian* or "anura" or "urodela" or "caudata" or "gymnophiona" AND "response" or "defence*" AND "phenotypic plasticity" or "behavior" or "life history" or "rapid evolution" or "contemporary evolution" or "rapid adaptation" or "habitat shift." A color version of this figure is available online.

when a species is exposed to a strong novel selective force, and this has been documented in multiple taxa exposed to alien species. In amphibians, rapid adaptation in response to invasive predators (Fig. 3C) has occurred in multiple systems (Moore et al. 2004; Nunes et al. 2014). For instance, *Pelophylax perezi* tadpoles originating from populations where invasive Red Swamp Crayfish, *Procambarus clarkii,* has been resident for approximately 30 yr demonstrate consistently lower activity levels when exposed to the crayfish than did tadpoles from populations where the crayfish is not present (Nunes et al. 2014). They can also express an inducible morphological defense—deeper tails—not seen in tadpoles from uninvaded populations, further indicating that rapid adaptive evolution has occurred in the invaded populations. Rapid adaptation to invasive predators might be widespread among amphibians, but current information is limited and the genetic mechanisms involved in such adaptations remain poorly known.

Can Responses Improve Amphibian Persistence?

Although there is considerable evidence that amphibians respond to the presence of IAS, demonstrations that those responses increase survival and coexistence with invasive species remain rare (Polo-Cavia and Gomez-Mestre 2014). In some instances, selection has rapidly favored the fixation of advantageous traits that probably help populations withstand IAS for long periods (Nunes et al. 2014). On the other hand, declines observed in many invaded populations suggest that amphibian responses often are insufficient. Assessing the effectiveness of responses under natural conditions is particularly complex because multiple abiotic and biotic factors act together in a context-dependent fashion (Blaustein and Kiesecker 2002). Despite these difficulties, understanding whether responses to IAS can help long-term persistence of invaded populations is important information because it may enable prediction of the consequences of invasions and identify the conditions under which management actions are most likely to be successful.

Amphibian Conservation in the Face of Biological Invasions

Given the multiple impacts of alien species on amphibians, it is essential to adopt effective management strategies at all stages of invasions: prevention of the introduction of harmful species, early detection of introduced species, active containment and eradication of IAS, and mitigation of their impact.

An Ounce of Prevention or a Pound of Cure?

Some of the IAS exerting the strongest impact on amphibians have been introduced through trade of fish bait, pets, and live food for pets (Pethiyagoda and Manamendra-Arachchi 2012; Bellard et al. 2016; Gozlan et al. 2019). The pet trade is particularly problematic because it can also cause the introduction of nonnative genotypes and the spread of diseases (Bellard et al. 2016; O'Hanlon et al. 2018). The most economically developed regions, where most exotic animal pets are sold, also host a greater richness of invasive species (Fonseca et al. 2019). Major impacts are also caused by species sold as food for human consumption. These species, once released into freshwater systems, can prey upon native amphibian species, as European salmonids have done after their introduction into American streams (Knapp and Matthews 2000; Pope 2008).

The impacts of IAS on native amphibian populations are often heavy, complex, and poorly predictable; therefore, it is essential to establish effective protocols to prevent the introduction of species that can naturalize and become invasive. Complete bans of all trade activities involving live animals would be virtually impossible, so other means of control are required. Blacklists of problematic species are one way to help set up trade regulations and focus screening protocols. Several strategies exist to identify species that should be blacklisted. First, species that are already invasive in some areas or resemble known, problematic invasive species in terms of phylogenetic relatedness, life history, or ecological traits can be prioritized (Masin et al. 2014; Maceda-Veiga et al. 2019). This approach, though, may miss many potential new invaders. Integrated horizon-scanning procedures are valuable for identifying new IAS that have the potential to affect native species but are not yet established in a region. Horizon scanning is a structured consultation with experts of multiple taxonomic groups, associated with consensus-building procedures and, in some cases, modeling of invasion risks. In the United Kingdom, horizon scanning enabled the creation of a ranked list of species with highest risk of arrival, establishment, and impact, and was able to predict new IAS with some success (Aldridge et al. 2014; Roy et al. 2014). Horizon scanning can thus produce inclusive and dynamic lists of actual and potential IAS that can be made subject to regulations and restrictions on trade and propagation (e.g., European Regulation 1143/2014; Tollington et al. 2017).

Live organisms of all kinds are constantly being spread via international and intercontinental flights, ships, roads, and railways. Although detailed screening protocols have been established in several countries, especially for international flights, it is hard to find information on the effectiveness of such management schemes. New Zealand and Australia have very strict protocols to hamper the introduction of new alien species. In these countries, all livestock must satisfy a rigorous import health standard on the basis of frequently updated risk assessment procedures (Henderson et al. 2011). Setting up effective screening protocols also requires that all personnel staffing trading facilities are updated on emerging issues. Airport managers in a number of major commercial hubs regularly met with IAS specialists to stay up-to-date on current incoming problematic species (Bisi et al. 2018). Developing prevention protocols for intracontinental trade is more challenging because regulations at this level often allow free trade, making the control and tracking of living organisms transported for food or pets extremely difficult (Ficetola et al. 2008a; Kikillus et al. 2012).

Commercially traded animals that are maintained in captivity do not become alien species unless they escape or are released into natural environments (see Box 1). Restaurant managers or the owners of pets may decide to release excess animals into nearby habitats. More seriously, when aquaculture businesses fail, they may simply release their stocks of exotic organisms. This was most likely the pathway for the introduction of the Red Swamp Crayfish in

Europe and Africa (Gherardi 2006). Prevention of these releases is feasible but challenging, and the role of single companies, organizations, and even individuals in the unintended release of alien species should not be underestimated.

Horizon scanning procedures and outreach campaigns can help to prevent the release of imported captive animals. Species identified as invasion risks could be made to require specific procedures of containment, such as special enclosures for aquaculture (Liu and Li 2009), or their trade as pets could be forbidden. Nevertheless, even after the adoption of dedicated legislation in Spain that has prohibited many species from entering the pet market, such animals continue to be released into the wild by their owners (Maceda-Veiga et al. 2019). It is thus essential to combine regulations with dedicated education and outreach activities to ensure the actual implementation of best practices (Ficetola et al. 2012a, Maceda-Veiga et al. 2019).

Early Detection

Even after alien species have been introduced, early detection can still allow for effective eradication. The problem is that, immediately after introduction, nonnative species often are at very low abundance and remain elusive. This makes it essential to regularly monitor areas at highest risk of new introductions, such as suburban areas or the surroundings of major seaports and airports, using techniques that enable detection of a wide range of potentially invasive species (Murphy et al. 2013). The use of environmental DNA (eDNA) is emerging as a particularly effective strategy for early detection of invasive species, particularly in freshwater (Ficetola et al. 2019). eDNA can be extracted from water and soil, allowing the detection of IAS while population size is still small and unnoticed using normal surveys (Ficetola et al. 2019). In Europe, eDNA has been used to monitor American Bullfrogs and enabled detection of bullfrogs in more sites compared with traditional visual and audio surveys (Ficetola et al. 2008b; Dejean et al. 2012). Regular eDNA sampling and amplification with primers designed on the basis of national or regional risk assessments can allow prompt detection of IAS, which is essential for early and effective eradication plans (Bellard et al. 2016; Strand et al. 2019).

Mitigation and Management to Ensure Long-Term Persistence of Amphibians

In relatively small sites, removal campaigns performed consistently through time can successfully remove those invasive predators that most reduce amphibian breeding success (Ahola et al. 2006). For instance, the removal of invasive Brook Trout, *Salvelinus fontinalis,* from western Italian Alpine lakes allowed the prompt recovery of breeding activity by European Common Frogs, *Rana temporaria* (Tiberti et al. 2019). However, when invasive species have spread over entire regions, eradications become far more complex. Actions must occur simultaneously at multiple sites because invasive species may often exist in networks of interconnected subpopulations. Management actions will have limited effectiveness if such spatial connections among sites are overlooked (Nicol et al. 2017; Manenti et al. 2020). There have been successes in removing some IAS, but eradication of most IAS is challenging and may not even be feasible if they occur in multiple metapopulations or very large waterbodies (Day et al. 2018). In such cases, effective management strategies to ensure long-term survival of amphibians affected by IAS can focus on keeping IAS densities low and providing suitable amphibian breeding sites that cannot be accessed or effectively colonized by IAS. Artificial ponds surrounded by vertical stone banks (Fig. 4A, B), for example, can be built that will allow amphibians to reach the water but that cannot be climbed by invasive crayfish (Fig. 4A, B; Bruni 2010). Similarly, it is possible to build barriers in small streams that prevent upstream dispersal of invaders. As recently proposed in Switzerland, thin foils of stainless steel (Fig. 4C) may be used to coat the vertical and horizontal surface of small waterfalls in such streams (30 cm can be sufficient, Fig. 4C; Manfrin et al. 2019).

In some places, stopping new invasions by alien species is impossible. In some urban or high-use areas, local people may repeatedly release predatory fishes and aquatic reptiles. In complex hydrographical networks, IAS may continuously spread from source populations. In these cases, small artificial ponds that can regularly be dried after tadpoles reach metamorphosis can be refuges for pond-breeding amphibians (Werner et al. 2007; Ficetola et al. 2012b). Finally, it is essential that researchers and managers share information about successful versus unsuccessful management practices. Most of the time, only unpublished technical reports performed during specific projects are available, and long-term assessments of the effectiveness of mitigation actions are lacking. Studies comparing amphibian densities and distributions before and after the control or eradication of IAS are essential to ensure successful long-term persistence of native populations and develop effective conservation protocols for amphibians in relation to IAS at all levels, from preventing IAS introductions to eradicating IAS if established to mitigating IAS effects.

CONCLUSIONS

Our understanding of the multifaceted impacts of IAS on native amphibian populations is increasingly deep, yet a disconnection remains between academic research on IAS and conservation efforts. Many studies have described the multiple impacts of IAS following invasions, while much less research has measured the benefits of alternative management strategies. Is the complete eradication of IAS necessary for maintaining native populations? Or, would habitat management and thinning actions aimed at limiting IAS abundance be enough? Answers to these questions will require a trial-and-error approach and the publication of management results to allow evidence-based conservation (Schmidt et al. 2020).

Although it has long been recognized that the impacts of IAS are context-dependent and heavily affected by environmental conditions (White et al. 2006; Didham et al. 2007), too many studies consider just one or a few factors. Multivariable analyses that take into account the complexity of parameters determining population dynamics at a range of spatial scales or that can evaluate what happens when we manage multiple stressors are sorely needed (Falaschi et al. 2019). It is also evident that native species can show some adaptive responses to IAS (Fig. 3C, E, F). Still, identifying,

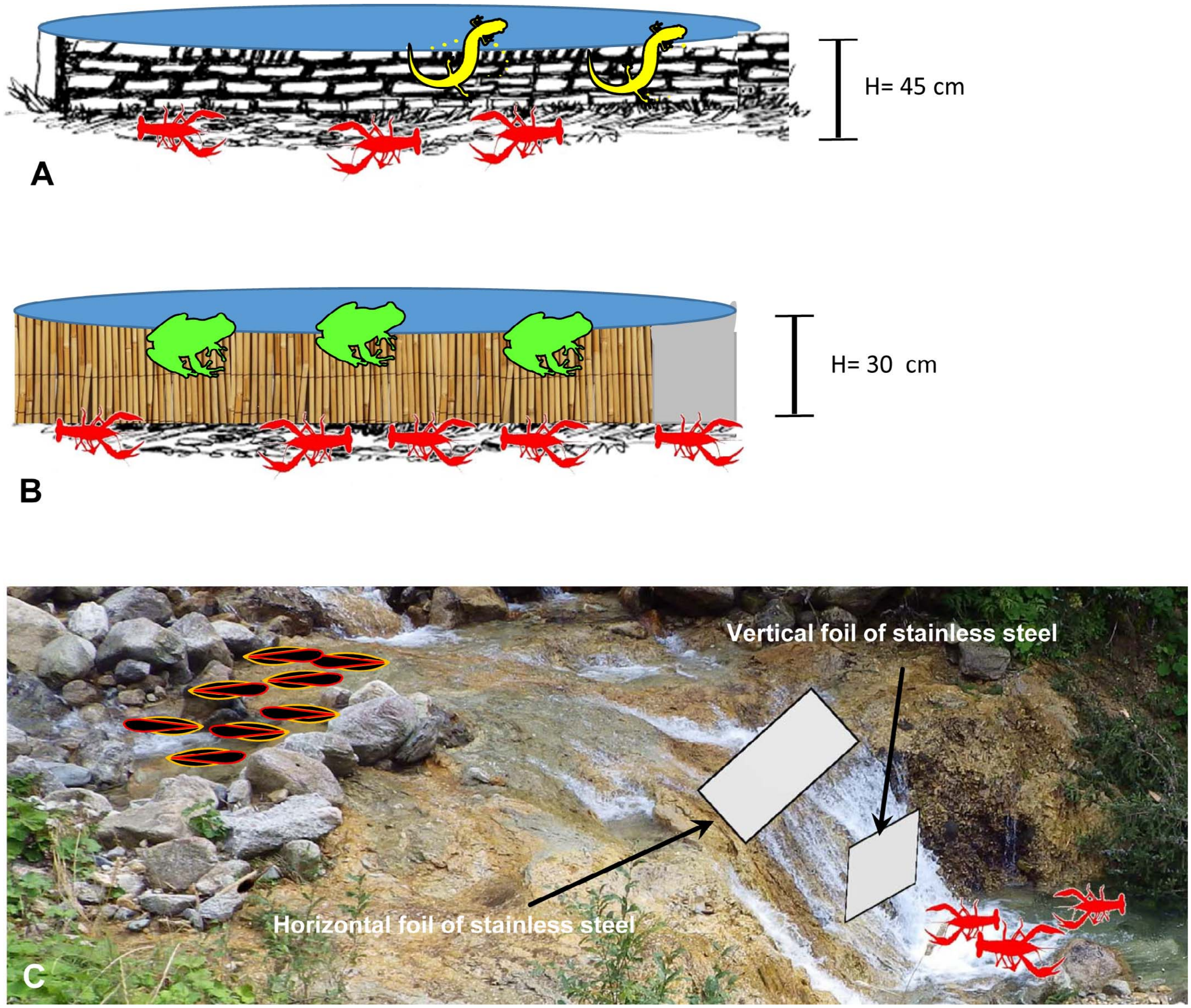

Fig. 4.—Examples of barriers designed to prevent invasive predatory crayfish from colonizing amphibian breeding sites. A color version of this figure is available online.

for example, a behavioral shift in presence of IAS does not mean that tadpoles will be better able to survive. Although measuring fitness in nature has long been a major challenge for evolutionary biology and ecology, we have now an increasingly complete analytical toolbox available (e.g., Dodd 2010) that can better enable quantitative fitness estimation. Producing quantitative measures of population responses in the field is pivotal for fine-tuning ongoing actions and guiding future mitigation efforts.

In some contexts, management of IAS has been extremely successful, allowing quick restoration of native species. For every five species of birds and mammals that have deteriorated in conservation status because of IAS, two have improved in status through mitigation efforts (Hoffmann et al. 2010). For amphibians, however, conservation actions have been rarer, and measures of their success have been limited (Hoffmann et al. 2010). It is imperative to transform our increasing knowledge of IAS and their effects on native amphibian populations into evidence-based conservation actions.

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