REVIEWS

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Invasion Complexities: The Diverse Impacts of Nonnative Species on Amphibians

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Since the first documented declines of amphibian species, researchers have learned how nonnative species can depress amphibian populations and lead to local extinctions. Here, we explore the dimensions of invasions in the context of evolutionary history, anthropogenic disturbance, and climate change. Recent studies indicate that the nonnative groups that have most negatively affected amphibians are plants, fishes, and other amphibians. We review current work aimed at determining the direct and indirect effects of nonnative species on amphibian health, genotypes, and native ecosystem structure, as well as research examining invasions from a community level perspective. We also describe synergistic effects between abiotic, biotic, and nonnative factors. Recent studies have documented the intricacies of invasions and how numerous aspects of invasions can interact additively and complementarily to the detriment of the native ecosystem. Understanding the complexity of invasions means considering if and how biological, environmental, and ecological processes within ecosystems are being reshaped as a result of introduced species. Assessing the ecology and ecosystem dynamics of invasions at multiple levels, from the genome to the ecosystem, is paramount to the conservation, restoration, and future research of invaded amphibian ecosystems.

AQUATIC species tend to be susceptible to abrupt changes in biological community dynamics and composition (Fisher and Shaffer, 1996; Gamradt and Kats, 1996; Riley et al., 2005; Hamer and Parris, 2013; Pease and Wayne, 2014). Thus, amphibians are known to be particularly sensitive to community changes that occur when nonnative species become established (Kats and Ferrer, 2003; Blaustein et al., 2011). Numerous studies have documented the decline of amphibian populations that occur with the introduction of a nonnative species. Moreover, studies have noted the displacement and extinction of local native species after the introduction and establishment of a nonnative species (Gilpin and Soulé, 1986; Huxel, 1999; Pimm and Raven, 2000; Sax and Gaines, 2008). As the frequency and duration of nonnative species invasions escalates, novel negative effects on amphibians are being documented. Increasingly, studies are delineating the mechanisms that determine whether amphibians will be eliminated with the appearance of nonnative species or whether they will maintain some level of coexistence. What effect nonnative species may have on amphibians can depend heavily on evolutionary histories of both the amphibians and the invasive species (Keller and Taylor, 2008). As such, predicting the rate and future spread of prominent nonnative species and subsequent impacts on amphibians will be critical for management and conservation.

Understanding how nonnative species impact amphibians is especially important because it is one of the factors contributing to amphibian population declines and extinctions (Collins and Storfer, 2003; Kats and Ferrer, 2003; Collins, 2010). One estimate suggests that the extinction rate of amphibians is more than 200 times the background extinction rate (McCallum, 2007). A higher percentage of amphibians are threatened than birds or mammals (Stuart et al., 2004), with many amphibians on the brink of extinction. Nonnative species can be directly responsible for the negative impacts on native amphibian populations via predation and competition, or their effect can be indirect, by introducing a pathogen or altering habitat. Synergistic effects between abiotic, biotic, and nonnative species may also occur. In this review we discuss the numerous ways amphibians are impacted by introduced species (see Fig. 1) through direct threats, such as predation and displacement, as well as indirectly by affecting the genotypes of community members and structure of native ecosystems. We also provide insight into the intricacies of nonnative–native interactions from a community level perspective and how numerous aspects of the process can interact additively and complementarily to the detriment of native amphibians and their ecosystems.

The role of evolutionary history in the complexity of nonnative invasions in amphibian systems.—Some amphibians species may lack the evolutionary history to respond to pressures from nonnative species in ecological time, and in many cases populations decline. Invaders can harm amphibians 1) by predation (Salo et al., 2007), 2) through competition (e.g., Pearson and Goater, 2009), 3) by spreading disease (e.g., Kiesecker et al., 2001a; Blaustein and Kiesecker, 2002),

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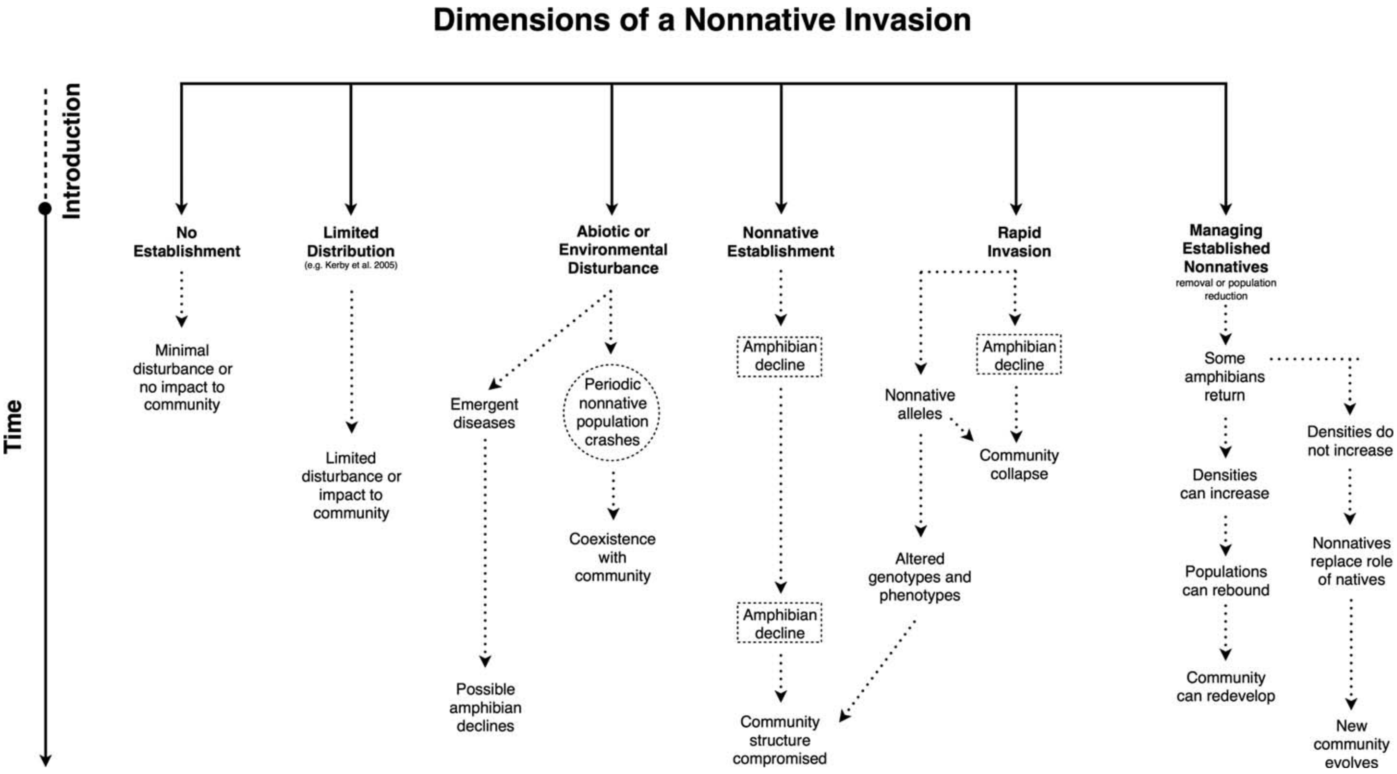

Fig. 1. The potential consequences of a nonnative species being introduced into an ecosystem that includes native amphibian species. Known invasion outcomes are presented across the top of the figure. The long term effects of a nonnative invasion are played out through time under each outcome.

4) by compromising the immune system of native amphibian within communities (Hayes et al., 2010), or 5) by hybridizing with them (e.g., Riley et al., 2003; Storfer et al., 2004; Ryan et al., 2009). Nonnative animal and plant species can also indirectly alter the habitat in ways that affect native amphibians (see Table 1 for an overview).

In many instances, even when amphibians have evolved with a functionally similar predator, they fail to avoid it. Gall and Mathis (2010) found that larval salamanders behaviorally responded to chemical cues from native predatory fish, but showed minimal or no response to chemical cues from ecologically similar, nonnative predatory fish. However, in a recent laboratory study, Davis et al. (2012) found that San Marcos Salamanders (*Eurycea nana*) exposed to chemical cues from a sympatric native sunfish, sympatric introduced sunfish, allopatric sunfish, and sympatric nonnative, non-centrarchid fish all elicited similar behavioral responses. Activity of salamanders was reduced, with no differences in the antipredator behavioral response between cue treatments. The authors reason that adult San Marcos Salamanders generalize fish predator cues within a genus and across a family, likely because they are similar to recognized sympatric predators.

Amphibians are generally more naïve toward introduced predators due to the heterogeneity of predation regimes in freshwater systems compared to the more homogenous predation regimes of terrestrial and marine systems (Cox and Lima, 2006). Terrestrial predators or their ecologically similar equivalents are often widespread across continents. However, in freshwater systems it is not uncommon that prey organisms have evolved without fish predators. For example, Foothill Yellow-Legged Frog (*Rana boylii*) tadpoles have evolved with newt predators and nonpredatory fishes (Paoletti et al., 2011). As a result of this shared evolutionary history with nonpredatory fishes, they show virtually no response to cues from introduced Smallmouth Bass (*Micropterus dolomieu*). In the few examples where amphibians have survived the introduction of a nonnative species, it appears that those species benefitted due to a genetic propensity for induced defenses (Moore et al., 2004).

Pinpointing mechanisms that allow nonnative species to successfully become established and integrated within novel habitat has been challenging. Though it is quite clear that the dispersal and proliferation of nonnative species is significantly influenced by human-mediated changes to hydroperiod (Herwig et al., 2013), waterways (Maret et al., 2006; Johnson et al., 2008; Ficetola et al., 2011; Davies et al., 2013) and urbanization (Riley et al., 2005), researchers have found ecological factors that largely affect the growth of nonnative species populations. As an example, nonnative amphibian success increases in the presence of congeneric species, and appears to be greater on islands than on the mainland (Tingley et al., 2011). Tingley et al. also found that the probability of a nonnative species succeeding in a novel habitat increases when abiotic conditions of the invaded habitat are similar to a nonnative species original habitat. Larger brain size relative to body size has also been suggested to be a successful trait of invaders (Amiel et al., 2011), and has also been considered for the invasion success of birds and mammals (Sol et al., 2005, 2008). Employing molecular genetics tools can also be useful to infer source population and invasion routes, effects of nonnative species upon native species, amounts of genetic diversity throughout nonnative species, and the role of adaptation and admixture. However, there are limitations to the application of molecular genetics tools when applied to biological inva-

Table 1. An overview of the effects that nonnative species have on native amphibian species based on experimental and theoretical research reviewed. Effects on native amphibian species can be negative or positive, and may occur directly (i.e., predation, competition, hybridization, coexistence) or indirectly (i.e., habitat alteration, facilitation, disease vector). Ultimate outcomes may include reduced or increased survival, delayed development, population declines, loss of habitat, modified behavior, increased abundances, decreased diversity, decreased breeding and recruitment, coexistence, decreased densities and distributions, limitations on gene flow, and altered genotypes and phenotypes.

Invasive species	Native species	Effects on native species	Reference
Invasive plants			
Triadica sebifera	*Pseudacris fouquettei*, *Lithobates sphenocephalus, Hyla versicolor*	Reduced survival (*P. fouquettei* and *L. sphenocephalus*) and negatively affected development (*H. versicolor*)	Cotten et al., 2012
	L. sphenocephalus	Negatively affected hatching success	Adams and Saenz, 2012
Phragmites australis	*Rana sylvatica*	Habitat alteration and increased developmental time	Perez et al., 2013
	Bufo fowleri	Population decline, loss of habitat	Greenberg and Green, 2013
	Ambystoma maculatum and *Lithobates palustris*	Negatively affected development and survival	Martin and Blossey, 2013
Rhamnus cathartica	*Pseudacris triseriata*	Negatively affected development and survival	Sacerdote and King, 2013
Lonicera maackii	*Anaxyrus americanus*	Habitat alteration, mortality, and modified behavior	Watling et al., 2011a, 2011b
	Lithobates palustris and *A. americanus*	Habitat alteration (microclimate) and decreased diversity	Watling et al., 2011c
	Lithobates clamitans	Increased abundance	Watling et al., 2011c
Microstegium vimineum	*R. sylvatica, L. palustris,* and *A. americanus*	Additional habitat	Nagy et al., 2011
Elaeis sp.	*Hyla labialis* and *Hyla glandulosa*	Decreased diversity	Faruk et al., 2013
Lythrum salicaria	*B. americanus*	Decreased survival and increased developmental time	Maerz et al., 2005; Brown et al., 2006
Phalaris arundinacea	*R. pretiosa*	Degraded ovipositing habitat	Kapust et al., 2012
	A. americanus, Hyla crysoscelis, L. pilustris, and *L. sylvatica*	Negatively affected survival	Rittenhouse, 2011
P. arundinacea, Phragmites australis, and *Rhamnus frangula*	*L. sylvaticus*	Increased survival and decreased developmental time	Stephens et al., 2013
Invasive invertebrates			
Lumbricus terrestris	*Plethodon cinereus*	Increased survival	Ransom, 2011, 2012a
Amynthas sp.	*P. cinereus*	Habitat alteration and decreased diversity	Maerz et al., 2009
Solenopsis invicta	*Ambystoma opacum* and *A. talpoideum*	Predation	Todd et al., 2008
	Gastrophryne caroleninsis	Coexistence	Deyrup et al., 2013
Procambarus clarkii	*P. regilla, Pseudacris cadaverina, Taricha torosa,* and *Bufo boreas*	Population declines	Riley et al., 2005
	P. regilla	Predation	Pease and Wayne, 2014
	Pleurodeles waltl, Triturus marmoratus, Rana perezi, Hyla arborea, and *Pelodytes punctatus*	Predation	Cruz et al., 2008
	Pelophylax perezi	Predation	Nunes, 2011
	Alytes sisternasii, *Discoglossus galganoi*, *Pelobates cultripes*, *Pelodytes ibericus*, *Bufo calamita*, *Hyla arborea*, *Hyla meridionalis*, *R. perezi*, *P. waltl*, *Salamandra salamandra*, *Triturus boscai*, *T. marmoratus*	Predation	Cruz and Rebelo, 2005
	Bufo calamita	Predation and deterred breeding	Cruz et al., 2006a

Table 1. Continued.

Invasive species	Native species	Effects on native species	Reference
	Alytes cisternasii, *Discoglossus galganoi*, *Pelobates cultripes*, *Pelodytes ibericus*, *Bufo bufo*, *B. calamita*, *Hyla arborea*, *H. meridionalis*, *Rana perezi*, *Pleurodeles waltl*, *Salamandra salamandra*, *Triturus boscai*, *T. marmoratus*	Predation and decreased diversity	Cruz et al., 2006b
	Alytes cisternasii, *Discoglossus galganoi*, *Pelobates cultripes*, *Pelodytes ibericus*, *Bufo bufo*, *B. calamita*, *Hyla arborea*, *H. meridionalis*, *Pelophylax perezi*	Predation, altered life histories and morphological changes	Nunes et al., 2014
	Pelobates cultripes	Predation	Polo-Cavia and Gomez-Mestre, 2013
Invasive amphibians			
Xenopus laevis	*Discoglossus pictus*, *Hyla intermedia*, and *Pelophylax synklepton esculentus*	Decreased breeding	Lillo et al., 2011
Lithobates catesbeianus	*Rana draytonii*	Predation	D'Amore et al., 2009
	L. sylvaticus	Disease vector for *Batrachochytrium dendrobatidis*	Greenspan et al., 2012
	Ambystoma tigrinum stebbinsi	Predation	Maret et al., 2006
	Eight unnamed frog and toad species	Decreased density and diversity	Li et al., 2011
	P. regilla	Competition	Preston et al., 2012
	Hypsiboas albomarginatus	Competition	Both and Grant, 2012
Ambystoma tigrinum mavortium	*A. tigrinum stebbinsi*	Hybridization	Storfer et al., 2004
	Ambystoma californiense	Hybridization	Riley et al., 2003; Ryan et al., 2009
Osteopilus septentrionalis	*Hyla cinerea* and *Hyla squirella*	Associated with reduced survival and abundance	Rice et al., 2011
Discoglossus pictus	*S. salamandra*, *T. marmoratus*, *Lissotriton helviticus*, *Alytes obstetricans*, *Pelodytes punctatus*, *Pelobates cultripes*, *Bufo calamita*, *B. bufo*, *Hyla meridionalis*, and *P. perezi*	Competition and decreased diversity	Richter-Boix et al., 2013
	B. calamito and *P. punctatus*	Competition	Richter-Boix et al., 2013
Invasive fishes			
Lepomis macrochirus, *L. cyanellus*, and *Ameiurus melas*	*Ambystoma texanum*	Predation	Walston and Mullin, 2007
Salvelinus fontinalis	*Ambystoma gracile*	Associated with decreased recruitment	Hoffman et al., 2004
S. fontinalis and *Oncorhynchus mykiss x O. m. aquabonita* hybrids	*Rana muscosa*	Associated with population declines	Knapp et al., 2007
Salmo trutta	*Salamandrina perspicillata*	Associated with decreased recruitment	Piazzini et al., 2011
Cyprinus carpio, *Perca fluviatilis*, and *Gambusia holbrooki*	*Litoria booroolongensis*	Predation	Hunter et al., 2011
Gambusia affinis, *Lepomis cyanellus*, *Lepomis macrochirus*, *Poloxis annularis*, *Ameiurus melas*, and *Micropterus salmoides*	*A. tigrinum stebbinsi*	Predation	Maret et al., 2006
Carassius auratus	*Ambystoma macrodactylum columbianum*	Predation	Monello and Wright, 2001

Table 1. Continued.

Invasive species	Native species	Effects on native species	Reference
Percichthys colhuapiensis	*Atelognathus patagonicus*	Associated with population declines	Cuello et al., 2009
Gambusia affinis	*Salamandra infraimmaculata*	Predation	Segev et al., 2009
	P. regilla	Disease vector for *Ribeiroia ondatrae*	Orlofske et al., 2012
	P. regilla and *T. torosa*	Predation	Preston et al., 2012
Gambusia holbrooki and *Perca fluviatilis*	*Geocrinia victoriana*, *Limnodynastes dumerilii*, *Limnodynaste peronnii*, *Crinia signifera*	Associated with decreased abundances	Hamer and Parris, 2013
O. mykiss, *salvelinus alpinus*, *S. fontinalis*, *Carassius auratus*, *G. affinis*, *Lepomis gibbosus*, and *Phoxinus phoxinus*	*Triturus alpestris* and *Triturus helveticus*	Associated with population declines	Denoël et al., 2005
O. mykiss, *S. fontinalis*, *Tinca tinca*, *C. carpio*, *Phoxinus phoxinus*, and *Chondrostoma arcasii*	*T. alpestris*, *T. helveticus*, *T. marmoratus*	Associated with limited distribution	Orizaola and Braña, 2006
Lepomis gibbosus and *Pseudorasbora parva*	*Triturus cristatus*, *Triturus vulgaris*, *Hyla arborea*, and *Rana temporaria*	Decreased diversity	Hartel et al., 2007
O. mykiss	*Anaxyrus boreas*	Disease vector for *Saprolegnia ferax*	Kiesecker et al., 2001a
O. mykiss and *S. fontinalis*	*Rana cascadae*	Population declines	Pope, 2008
	Rana cascadae	Competition	Joseph et al., 2011
	R. muscosa	Predation	Vredenburg, 2004
O. mykiss and *S. trutta*	*Hadromorphryne natalensis*	Decreased abundances	Karssing et al., 2012
O. mykiss and *P. promelas* Rafinesque	*A. macrodactylum*	Predation, competition	Pearson and Goater, 2009
O. mykiss and *O. m. aquabonita*	*R. muscosa*	Competition	Finlay and Vredenburg, 2007
O. mykiss and *S. trutta*	*Cryptobranchus alleganiensis alleganiensis* and *Cryptobranchus a. bishopi*	Predation	Welsh et al., 2006
O. mykiss, *S. trutta*, and *S. fontinalis*	*L. sylvaticus*	Coexistence	Schank et al., 2011
Lepomis auritus	*Eurysea nana*	Predation	Davis et al., 2012
Micropterus dolomieu	*Rana boylii*	Predation	Paoletti et al., 2011
Leucaspius delineatus	*Rana temporaria*	Predation	Leu et al., 2009
Gasterosteus aculeatus	*T. alpestris*, *T. helveticus*, *T. vulgaris*	Associated with limited distribution	Denoël and Ficetola, 2008
Invasive mammals			
Neovision vison	*R. temporaria*	Decreased densities and distribution	Ahola et al., 2006; Salo et al., 2010
N. vison and *Rattus rattus*	*Salamandra salamandra gallaica*	Predation	Velo-Anton and Cordero-Rivera, 2011
R. rattus	*Leiopelma hochstetteri*	Coexistence	Nájera-Hillman et al., 2009
Herpestes javanicus	*Babina subaspera*	Associated with limited distribution and gene flow	Iwai and Shoda-Kagaya, 2012
Dasypus novemcinctus	*Plethodon angusticlavius*	Predation	Crane et al., 2011

sions, which typically occur at rapid timescales. Fitzpatrick et al. (2012) suggest that population genetics can really only effectively be used to test hypotheses regarding the geographic origin of invasions, bottlenecks, and hybridization events given the assumptions of neutral theory inherent in population genetics analyses.

Interactions between native amphibians and nonnative plants.—The potential consequences of introduced flora upon amphibians is perhaps the least studied of the nonnative–native amphibian interactions currently recognized, although a body of research is beginning to develop (Martin and Murray, 2011). Maerz et al. (2005) first reported that native tadpoles (*Bufo americanus*) appeared to have reduced performance when raised in habitats that contained Purple Loosestrife (*Lythrum salicaria*). They hypothesized that high tannin levels from the leaves of the plant produce potentially toxic environments for developing tadpoles. In a follow up experiment, Brown et al. (2006) showed that native tadpoles had slower development and decreased survivorship when reared in experimental venues with Purple Loosestrife extracts, and the addition of leaf litter of *L. salicaria* exacerbated the effects. The authors found that algal communities differed between Purple Loosestrife venues and other venues, leading them to conclude that food quality and quantity were responsible for reduced tadpole performance. More recently, Maerz et al. (2010) have suggested that nonnative plants can ultimately change the nutrient quality of the detritus that tadpoles feed upon.

Other introduced plants have also shown marked effects on amphibians. Watling et al. (2011a, 2011b) have suggested that toad tadpoles (*Anaxyrus americanus*) reared in extracts from a nonnative shrub (*Lonicera maackii*) were more likely to die than tadpoles in native plant extracts. However, experimental studies showed that *L. maackii* is not fatal to three amphibian species tested: *Ambystoma maculatum, Hyla* sp., and *Lithobates blairi*. A behavioral study looking at the same species of larvae grown in extracts of *L. maackii* noted that larvae made frequent trips to the water surface, suggesting that the extracts may interfere with the respiratory physiology of the tadpoles. Other research by Watling et al. (2011c) demonstrated that amphibian species richness and evenness were lower in plots invaded by *L. maackii*. This also resulted in shifts in species composition. The authors suggest that nonnative plants may change microclimate when they become well established and ultimately negatively affect entire native communities. It also appears that invasions of *L. maackii* can indirectly affect native herpetofauna by shortening the hydroperiod of ephemeral ponds and streams. Boyce et al. (2012) found that transpiration of *L. maackii* was a significant source of habitat water loss, accounting for roughly 10% of stream flow draining in the wetland study area. The authors indicate that this estimate may be at the lower end since basal areas in the study sites were not as large as those in other invaded habitat.

The introduced deciduous tree Chinese tallow (*Triadica sebifera*) has also been found to affect anurans. Cotten et al. (2012) tested extracts from *T. sebifera* and two native tree species on survival and development of larval *Pseudacris fouquettei*, *Lithobates sphenocephalus*, *Hyla versicolor*, and *Incilius nebulifer* from eastern Texas. Early breeding amphibians (*P. fouquettei* and *L. sphenocephalus*) had lower survival and exhibited different growth patterns than later breeding amphibian species when exposed to *T. sebifera*. *Hyla versicolor* showed significant morphological and developmental differences between treatments. Adams and Saenz (2012) demonstrated similar effects of Chinese Tallow on eggs of *Lithobates sphenocephalus*. All eggs exposed to Chinese Tallow leaf litter died, regardless of concentration. The authors observed that greater amounts of Chinese Tallow leaf litter resulted in lower dissolved oxygen and pH levels.

Common Reed (*Phragmites australis*) is another plant nonnative to North America that researchers have determined affects tadpole development and food availability. Perez et al. (2013) used field enclosures with varied densities of the reed and found that survival did not differ between treatments, but tadpoles in medium and high reed density enclosures developed more slowly. Due to this delayed growth, the authors suggest larvae in ponds invaded by Common Reed could be exposed to threats for greater periods of time, including natal pools drying out and predation. Other researchers have found that the spread of Common Reed has contributed to an ongoing loss of amphibian breeding habitat and population declines for Fowler's Toads, *Bufo fowleri* (Greenberg and Green, 2013). Other nonnative reed grasses like the Reed Canary Grass (*Phalaris arundinacea*) appear to disrupt Oregon Spotted Frog (*Rana petiosa*) ovipositing habitat (Kapust et al., 2012). Rittenhouse (2011) had previously found no direct toxic effects of Reed Canary Grass on tadpoles, but did find that the reed reduced survival in native amphibian species and suggests it was due to decomposing reed grass that led to anoxic larval environments.

A recent study of the direct effects of European Buckthorn (*Rhamnus cathartica*) metabolites on amphibians was conducted by Sacerdote and King (2013). European Buckthorn is an aggressive nonnative that produces a secondary metabolite, emodin, which leaches into soil and water. They quantified amounts of emodin at amphibian breeding sites and exposed native Western Chorus Frog (*Pseudacris triseriata*) and African Clawed Frog embryos to an ecologically realistic gradient of emodin concentrations. Both frog species responded negatively to emodin; embryo mortality and malformation occurred, although the effect of the compound was more pronounced in Western Chorus Frog embryos.

Nonnative plants may not always pose immediate negative threats to amphibians (Hayes and Holzmueller, 2012). Nagy et al. (2011) found that a nonnative grass, Japanese Stilt Grass (*Microstegium vimineum*), can offer cover and nesting habitat for native frogs, especially in degraded habitat. Their research shows that in landscapes where White-Tailed Deer (*Odocolileus virginianus*) have overgrazed native flora, which has typically served as cover for native amphibians, *M. vimineum* has been able to provide suitable habitat. The authors later raise an interesting point, which is to consider how removal of a nonnative species may affect native species, especially if a native species has been able to exploit a nonnative species when there is little to no native habitat left. This seems particularly relevant when native habitat has been compromised as a result of land alteration, climate change, or the integration of nonnative species into native ecosystems. Similar questions are bound to arise as native forest plant communities become more disturbed and likely experience drastic changes in species composition.

Stephens et al. (2013) have explored how changes to tree forest composition have resulted in altered leaf litter input. Consequently, it appears that nonnative leaf litter affects the fitness of larval amphibians. They found that litter from native trees caused frogs to grow larger, develop faster, and survive better than larvae that were exposed to nonnative leaf litter treatments. Similar results have also been observed when Wood Frogs (*Lithobates sylvaticus*) were exposed to an array of native and nonnative species specific leaf litter (Stoler and Relyea, 2013). Compounds from chemically distinct tree species affected growth and developmental rate, and produced drastic morphological responses in intestines length and tail muscle depth.

The connection between terrestrial nonnative plants and terrestrial salamanders has not been as clear (Maerz et al., 2009). No significant decrease in woodland salamander species was found with increasing densities of nonnative plants. However, there were subtle interactions occurring between plants, nonnative earthworms, and amount of leaf litter that impacted salamanders. Maerz et al. (2009) concluded that rather than Eastern Red-Backed Salamander (*Plethodon cinereus*) abundance declining in response to the establishment and spread of nonnative plants, abundances were more strongly tied to nonnative earthworms due to shared leaf litter resource base.

Martin and Blossey (2013) present results that suggest there is intraspecific variation in plant compounds between plant populations and that such variation can significantly affect amphibians. In laboratory experiments, they exposed Spotted Salamanders (*Ambystoma maculatum*) to leaf litter extracts from 14 different populations of native and nonnative *Phragmites australis* and observed varied larval survival among plant populations. These results suggest that there is likely considerable intraspecific variation of secondary compound chemistry between plant populations, which managers and scientists may need to consider when preserving habitat and determining the direct and indirect effects of nonnative plants.

Nonnative plants may also have indirect effects upon amphibians, which appear to be remarkably different from native flora. Smith (2013) discussed how leaf phenology of nonnative trees is an important invasion mechanism. Compared to native tree species, the leaves of nonnative trees often emerge earlier in the spring and abscise later in the fall. Amphibians may indirectly be harmed in a number of ways. Cooler water temperatures due to increased shading could affect rates of metamorphosis, and synergistic effects of secondary metabolites or other organic compounds could be deleterious to tadpoles (e.g., Martin and Blossey, 2013). At a much larger scale, variation of native tree communities in forested ecosystems could have even greater consequences, since they often can control forest structure and ecosystem dynamics (Ellison et al., 2005). Amphibian genotypes and phenotypes could ultimately be affected too, with the relative fitness of community members, species composition, and abundances all being influenced by interspecific variation in native ecosystems (e.g., Whitham et al., 2008).

The effects of nonnative terrestrial invertebrates upon native amphibians.—While many current studies focus on the spread of aquatic nonnative species and their impacts upon amphibians, Todd et al. (2008) have noted that human-mediated effects upon the landscape are facilitating the spread of nonnative Fire Ants (*Solenopsis invicta*) to the detriment of terrestrial salamanders. They compared Fire Ant densities in non-harvested woodlands to partially thinned stands and clear-cut stands. They found that more disturbed habitats had higher numbers of Fire Ants and that terrestrial salamanders at these locations (*Ambystoma* spp.) suffered higher predation from Fire Ants. Conversely, Deyrup et al. (2013) found that native Eastern Narrow-Mouthed Toad (*Gastrophyrne carolinensis*) in Florida consumed ants from numerous genera, including ants known to possess toxins or other toxic substances. The authors conclude that *G. carolinensis* could possibly subsist on exotic species of ants such as Fire Ants. Studies in Indonesia show similar results. On the island of Sulawesi, an endemic toad (*Ingerophrynus celebensis*) preys on a nonnative ant species (*Anoplolepis gracilipes*), which ultimately promotes native ant diversity (Wanger et al., 2011).

Introduced earthworms also directly and indirectly affect amphibian ecology (Ransom, 2011, 2012a). As ecosystem engineers, their establishment has altered nutrient regimes, leaf-litter decomposition rates, and soil structure. Greiner et al. (2012) demonstrated that nonnative Asian (*Amynthas hilgendorfi*) and European (*Lumbricus rubellus*) earthworms increased leaf litter decomposition rates and increased concentrations of mineral forms of phosphorous and nitrogen. Research performed by Ransom (2011) shows that the Common Earthworm (*Lumbricus terrestris)* decreases amounts of leaf litter and macroinvertebrates. However, earthworm burrows provided effective refuge for *Plethodon cinereus* during encounters with predators and overwintering habitat. In follow up studies, Ransom (2012b) showed that recent or historical co-occurrence of *P. cinereus* with North American native (*Eisenoides carolinensis* or *Diplocardi* sp.) or nonnative (*L. terrestris*) earthworms affected burrowing time and time to first burrow. *Plethodon cinereus* that evolved with native earthworms (~7,000 years ago) and without did not differentiate between earthworm species as prey, nor did *P. cinereus* demonstrate any preference for species-specific earthworm burrows. However, if populations of *P. cinereus* co-occurred with native earthworms, they attacked worms more quickly, had shorter handling times, and were more likely to consume earthworms. Ransom demonstrates the importance of understanding the various ways in which nonnative species interact with native species and communities. It is thought that coexisting species of earthworms can perhaps facilitate invasional meltdown (Simberloff and Von Holle, 1999), which takes place when a nonnative species acts as a catalyst and increases the possibility of greater numbers of nonnative species invading an ecosystem, thus amplifying the effects of those invaders (Cameron and Bayne, 2011; Cameron et al., 2012). This may result in strong negative impacts upon local native species, especially at the species level and potentially throughout the entire community.

The effect of nonnative aquatic invertebrates.—Often nonnative species reshape communities and ecological associations, in which case the behaviors and antipredatory responses of natives become unfit. Diamond and Case (1986) have suggested that amphibians often cannot coexist with introduced species due to a lack of shared evolutionary history and inexperience with a functionally equivalent native predator. Thus, native amphibian populations are more likely to decline if an introduced species is from a novel functional group. Ricciardi and Atkinson (2004) used a meta-analysis and found that high impact invaders are usually species that belong to a genus not currently found within an ecosystem. As an example, amphibian populations in North America and Europe have been dramatically reduced by the introduction of the Red Swamp Crayfish (*Procambarus clarkii*). Amphibian populations that suddenly must cope with *P. clarkii* do poorly, in part, because these same amphibian species have not encountered voracious aquatic omnivores like *P. clarkii* in their native habitat (Cruz et al., 2008). Native crayfishes have very small geographic ranges (Lodge et al., 2000), and as a result many amphibians have no evolutionary history with them.

Nunes (2011) investigated how coexistence time with *P. clarkii* affected Iberian Waterfrog (*Pelophylax perezi*) antipredatory behavior. In laboratory experiments, tadpoles of *P. perezi* from populations that did not co-occur with *P. clarkii* reduced behavior in the presence of crayfish. However, populations with long-term exposure to *P. clarkii* did not show a similar response, but did exhibit morphological defenses, such as a deeper tail and shorter head-body length. Although the invasion of *P. clarkii* occurred roughly 30 years ago, the authors believe that these predators imposed such strong selection pressure that it has led to a rapid evolution of morphological defenses.

Similar experiments conducted by Gomez-Mestre and Diaz-Paniagua (2011) showed that chemical cues from *P. clarkii* failed to activate morphological defenses in *P. perezi*, even though chemical cues from native predatory dragonfly nymphs did. The authors argue that responding to crayfish chemical cues would be adaptive, but that the observed lack of morphological defenses in *P. perezi* could be due to cue recognition failure and too recent of an invasion for defenses to evolve. It is also possible that the opposing results are due to inherent variation within and between populations, as observed by Nunes (2011) and Nunes et al. (2014), and may be attributable to differences in exposure and thus, selection intensity.

Recent experiments by Nunes et al. (2013, 2014) show that anurans may not respond to chemical cues from *P. clarkii,* but will respond defensively to chemical cues from native predatory macroinvertebrates. In the presence of adult crayfish, a subset of anurans exhibited behavioral defenses, which appear to have been facilitated by chemical cues from injured conspecifics that *P. clarkii* preyed upon (Nunes et al., 2013). Nunes et al. (2014) also tested how larval morphology, growth, and development may differ between nine tadpole species from southern Portugal reared in the presence of *P. clarkii* and native predatory odonate nymphs (*Aeshna* sp.). They found that more species of tadpoles responded with morphological or life history changes when grown with native odonate predators than when grown with predators of *P. clarkii*. The authors suggest that intra- and inter-specific variation in response to *P. clarkii* could lead to a greater risk of those individuals and species becoming extirpated, ultimately reducing local biodiversity throughout invaded communities. Divergence in morphology and behavior has also been observed in North America between naïve Pacific Tree Frog tadpoles (*Pseudacris regilla*) exposed to *P. clarkii* chemical cues and tadpoles from streams with crayfish (Pease and Wayne, 2014).

In other systems, naïve tadpoles of the Western Spadefoot Toad (*Pelobates cultripes*) were not capable of responding to water-borne chemical stimuli from *P. clarkii* unless the stimuli was a combination of *P. clarkii* and injured conspecific chemical compounds (Polo-Cavia and Ivan Gomez-Mestre, 2013). Experimental results showed that conditioned tadpoles experienced greater survivorship than unconditioned tadpoles. Ultimately, the ability of native amphibians to detect, respond to, and learn from introduced species, especially through association with alarm cues, may very well improve recruitment and decrease the vulnerability of native amphibian species to novel predators.

Compromised recruitment and impaired reproduction have also been documented as a direct result of *P. clarkii* expanding into novel habitat. The presence of *Bufo calamita* throughout breeding habitat in the southwest Iberian Peninsula was negatively associated with presence of *P. clarkii* (Cruz et al., 2006a). Surveys indicated that coexistence between *B. calamita* and *P. clarkii* was limited to only one of 31 ponds. Experimental evidence showed that the survivorship of embryos was significantly reduced in the presence of *P. clarkii*. Furthermore, breeding sites disturbed by *P. clarkii* in the southwest Iberian Peninsula also appear to negatively affect breeding activity of urodeles, too. Cruz et al. (2006b) indicate that the probability for all local urodeles to breed is deterred in the presence of *P. clarkii*, regardless of predatory fish. These results imply that communities within which amphibians reside may be permanently altered by the introduction of *P. clarkii* and that overall amphibian species richness may be lowered in these areas, too.

Invasion complexity in amphibian systems promoted by indirect and direct ecological effects of introduced fishes.—One of the greatest threats to native amphibians continues to be introduced fishes (Denoël and Ficetola, 2008; Cuello et al., 2009; Gall and Mathis, 2010; Hunter et al., 2011; Reshetnikov and Ficetola, 2011). Fish introductions can be accidental or intentional when released for game fishing (e.g., Welsh et al., 2006; Barrionuevo and Ponssa, 2008) or as pest control agents (Leu et al., 2009; Segev et al., 2009). While both frogs and salamanders are susceptible to nonnative fish, salamanders appear particularly vulnerable (Denoël et al., 2005; Orizaola and Braña, 2006; Piazzini et al., 2011). Piazzini et al. (2011) found that the presence of introduced trout and crayfish reduced the probability of Spectacled Salamander (*Salamandrina perspicillata)* egg occurrence from a mean probability of 0.90 to 0.12. Interestingly, native crayfish (*Austropotamobius fulcisianus*) had no detectable effect. These studies underscore the importance of disentangling the complexities of native and nonnative pressures on amphibian populations.

Though most studies demonstrate that introduced game fishes reduce native amphibian populations by directly consuming adult or larval amphibians (Pope, 2008), recent studies indicate that even fishes not traditionally thought of as predators will consume native amphibian larvae, hence reducing frog and salamander populations (Monello and Wright, 2001; Leu et al., 2009). Furthermore, introduced fishes have numerous indirect effects on native amphibians too, affecting organisms at numerous scales ranging from the genome to the ecosystem (Cucherousset and Olden, 2011). Joseph et al. (2011) found that when adult Cascades Frog (*Rana cascadae*) co-occurred with introduced trout they had a smaller proportion of adult aquatic insects in their diet relative to those not found with trout. Fish gut content analyses showed that trout were feeding heavily on the aquatic stages of numerous insects. Frogs co-occurring with trout fed more heavily on terrestrial insects such as grasshoppers. The authors concluded that introduced trout affect native amphibians directly through predation and indirectly through resource competition (Finlay and Vredenburg, 2007), and it appears that these indirect effects in freshwater systems often have far reaching ecological consequences (Strayer, 2010).

Introduced fishes have can significantly alter trophic webs and resource partitioning by disrupting reciprocal prey subsidies. Benjamin et al. (2013) found indirect effects of nonnative Brook Trout (*Salvelinus fontinalis*) that have replaced native Cutthroat Trout (*Oncorhynchus clarkii*). The nonnative Brook Trout reduced the flux of emerging insects by greater than 50%, which they predicted would reduce spider abundance by 20% and the birds that prey on them. The consequences of these introductions may not only have negative biological effects on native amphibians in these communities, but also negative effects at the ecosystem level as well (Dunham et al., 2004).

The global spread of nonnative amphibians.—The topic of nonnative species has become one of great concern in the scientific community and has increasingly gained the attention of policy makers and the general public. There is no sign that the spread of nonnative species to new habitats is slowing, and it is often amphibians as a taxonomic group that are most vulnerable to invaders. However, nonnative amphibian species have successfully invaded native amphibian ecosystems, too. The American Bullfrog (*Lithobates catesbeianus*) is an example of a nonnative species that has had profound effects on native amphibians where it has been introduced (Adams and Pearl, 2007). This species, native to eastern North America, is now globally widespread and continues to establish new populations outside of its native range (Ficetola et al., 2007a; Akmentins and Cardozo, 2010), including South America, where it is predicted to invade biodiversity hotspots (Nori et al., 2011), and in the peninsula region of Baja California (USA), where the number of invaded sites doubled over an eight-year period (Luja and Rodríguez-Estrella, 2010a).

Lithobates catesbeianus is known to reduce native amphibian populations by preying upon natives and competing for resources (Adams and Pearl, 2007; D'amore et al., 2009). Although there are patterns where native amphibians and the presence of bullfrogs are negatively correlated, the underlying mechanisms of displacement of native amphibian species remains complex (Blaustein and Kiesecker, 2002; Kiesecker et al., 2001a; Pearl et al., 2004). For example, in the Willamette Valley of Oregon (USA), the impact of *L. catesbeianus* on native Red-Legged Frogs (*Rana aurora*) appears to be a mixture of direct and indirect effects compounded by habitat modifications, which intensify interactions. The presence of larval and adult bullfrogs results in alterations of microhabitat used by Red-Legged Frogs that make them more susceptible to predation by fishes (Kiesecker and Blaustein, 1998). Laboratory experiments have shown that tadpoles that were syntopic with bullfrogs display antipredator behavior when presented with chemical cues of larval or adult bullfrogs, but tadpoles from populations that were allotopic to bullfrogs did not (Kiesecker and Blaustein, 1997). In the field and in the laboratory, these behaviors resulted in higher rates of predation in tadpoles from allotopic populations (Kiesecker and Blaustein, 1997). However, further complexity was illustrated in this system because in field experiments, Red-Legged Frog tadpoles that altered their microhabitat use in the presence of bullfrogs had decreased growth and increased predation by fishes (Kiesecker and Blaustein, 1998). Thus, modified use of habitat appear to play a major role in the interactions of bullfrogs with native amphibians (Kiesecker, 2003 and references therein).

Understanding habitat conditions that allow *L. catesbeianus* to thrive in nonnative ecosystems is also being explored, as are patterns of native species distributions when ecosystems are invaded (Fuller et al., 2010). Others have tested the limits of the capacity of *L. catesbeianus* to adapt to local environmental conditions. Cook et al. (2013) determined that larvae of *L. catesbeianus* in the Willamette Valley, Oregon (USA) cannot survive changing hydroperiods because they seem to lack developmental plasticity. The authors suggest that artificially manipulating hydroperiod as a means to control nonnative American Bullfrogs could successfully help manage bullfrog invasions since it will not induce rapid metamorphosis.

In some cases, climate and land-use models can predict where American Bullfrogs might spread next (Ficetola et al., 2007b), and environmental DNA (eDNA) is also being used to detect *L. catesbeianus*, as well as other nonnative species, before they become established (Dejean et al., 2012). In field studies, the sensitivity of eDNA was compared to traditional field methods of call and visual surveys. Using eDNA, *L. catesbeianus* was detected in 38 sites while it was detected in only seven sites using survey methods. The results of this study imply that traditional survey methods have probably underestimated the presence of nonnative species, but it also shows great promise for detecting nonnative species early, when densities are low and manageable, and across all life stages. eDNA can also be used to detect threatened or cryptic species, or species whose numbers have been diminished due to the detriment of a nonnative species.

Another amphibian that has now spread to several continents and continues to show signs of invading new geographic regions is the African Clawed Frog, *Xenopus laevis* (e.g., Faraone et al., 2008; Measey et al., 2012). According to Lillo et al. (2011) African Clawed Frogs reduce the occurrence of native amphibian species from breeding sites in certain Italian populations. Like bullfrogs, African Clawed Frogs can potentially transmit the emerging infectious disease agent Bd (*Batrachochytrium dendrobatidis*) to native amphibians (Solís et al., 2010). Researchers are attempting to predict the spread of this nonnative amphibian to mediate further impacts on native species and their habitat (Fouquet and Measey, 2006; Rebelo et al., 2010; Lobos et al., 2013).

One area of research in invasion biology that remains truly understudied is how vocalizing nonnative species may potentially displace native vocalizing species. Strauss et al. (2006) asked if the deafening mating chorus of introduced Coqui Frogs affects the acoustic landscape of calling native species. Though much research has been conducted on the response of birds increasing song pitch to compete with noise due to urbanization (Slabbekoorn and Peet, 2003; Nemeth and Brumm, 2009), little has focused on how introduced bird species, as well as introduced frog species, affect calling. Frogs demonstrate higher pitched calls in urban settings (Parris et al., 2009), and to compensate for the extremely broad range of acoustic space that waterfalls occupy, some frogs have evolved calls that contain ultrasonic harmonics (Narins et al., 2004). But do the calls of frogs change in response to a vocalizing nonnative species? A particularly interesting study conducted by Both and Grant (2012) demonstrates how nonnative amphibians can displace native amphibians from their acoustic niche. In their experiments, native male White-Banded Tree Frogs (*Hypsiboas albomarinatus*) shifted their calls to significantly higher frequencies when researchers played back recordings of nonnative American Bullfrogs (*L. catesbeianus*) vocalizing. The tree frogs continued to use higher frequencies even after the bullfrog calls were terminated; however, tree frog call duration did decrease. Rate of call or inter-call interval did not change. Because the American Bullfrog call occupies a broad frequency band, the researchers expect the effects of bullfrog vocalization to be especially severe to communities of vocalizing species by disrupting numerous acoustic niches.

Hybridization between native and nonnative amphibians.—Community wide consequences have been observed when native genotypes are replaced by nonnative genotypes. When such evolutionary events occur, communities and ecosystems can become statistically distinct. Nonnative species that introgress through hybridization with native species not only change native species genotypes, but can also alter phenotypes and have the potential to largely affect ecological processes (e.g., Ryan et al., 2009). Ryan et al. (2009) found that hybridization between native, federally endangered California Tiger Salamanders (*Ambystoma californiense*) and introduced Barred Tiger Salamanders (*A. tigrinum mavortium*) produces offspring that significantly reduce survival of native amphibian community members. Furthermore, hybrid larvae reduced the size at metamorphosis of native larvae and prolonged the time to metamorphosis. These researchers also observed Mendelian dominance on size, time of metamorphosis, and predation rate of hybrids. Their results demonstrate how the displacement of native genotypes can potentially compromise ecosystems by generating novel genotypes and phenotypes.

Ryan et al. (2013) also found that salamanders with hybrid genotypes were able to survive major environmental stress while native genotypes could not. All native genotype salamanders died off unless they had already metamorphosed prior to die-off events. Throughout the range of native California Tiger Salamanders, human-mediated landscape modification, pesticide use, and climate change continue to pose a threat. These results imply that native genotype salamanders could be rapidly displaced by nonnative genotypes as a result of these anthropogenically induced environmental stressors.

The genetics of native amphibian species may also be disrupted indirectly by nonnative species impeding gene flow. On the Amami Islands of Japan, an introduced mongoose has created a large habitat gap between a native population of Otton Frog (*Babina subaspera*). Researchers have tested for genetic structure, gene flow, and genetic diversity and discovered very little gene flow between the disjunct population (Iwai and Shoda-Kagaya, 2012). The researchers also found that the disruption of gene flow potentially caused by mongoose has additionally led to relatively recent genetic differentiation.

Invasions complicated by the spread of pathogens.—Nonnative species may also be a major carrier of pathogens that infect native amphibians. The globally distributed water mold *Saprolegnia* (Wood and Willoughby, 1986; Blaustein et al., 1994; Kiesecker and Blaustein, 1997) has become widespread due to movement of hatchery-raised fishes (Blaustein et al., 1994) and has shown to negatively affect Western Toad (*Bufo boreas*). In laboratory experiments, mortality induced by *Saprolegnia* was greater in Western Toad embryos exposed directly to hatchery-reared Rainbow Trout (*Oncorhynchus mykiss*) experimentally infected with *Saprolegnia* than in control embryos (Kiesecker et al., 2001a). Embryos also developed significant *Saprolegnia* infections when raised on soil that was experimentally exposed to trout infected with *Saprolegnia* (Kiesecker et al., 2001a). It also appears that different strains of *Saprolegnia* may have different virulence (Kiesecker et al., 2001a), and as a result, introduced fishes may transmit strains of *Saprolegnia* that are more virulent to native amphibians. Furthermore, variation in susceptibility to *Saprolegnia* may contribute to pathogen-induced changes in species interactions and community structure. Kiesecker and Blaustein (1999) observed that the differential effects of *Saprolegnia* on larval recruitment of Pacific Tree Frog (*Hyla regilla*) and Cascades Frog (*Rana cascadae*) reversed the outcome of competitive interactions between the two species (Kiesecker and Blaustein, 1999). Larvae are potentially affected by *Saprolegnia* if the mold infects eggs, which may cause early hatching and increase larval susceptibility to predation (Gomez-Mestre et al., 2006). Moreover, the effects of *Saprolegnia* infections on amphibian larval recruitment are moderated by the spatial distribution of egg masses and their exposure to sunlight (Kiesecker and Blaustein, 1995, 1997). Kiesecker et al. (2001b) and Kiesecker and Blaustein (1995) reported that periodic mass mortality of embryos of *B. boreas* in Oregon resulted from a synergism between ultraviolet-B (UV-B) radiation and infection with *Saprolegnia*. UV-B exposure was in large part determined by water depth at oviposition sites. Kiesecker et al. (2001b) linked El Niño/Southern Oscillation (ENSO) events with decreased winter precipitation in the Oregon Cascade Range and suggested that less winter snow pack resulted in lower water levels when toads breed in early spring. Toad embryos developing in shallower water exposed to higher levels of UV-B radiation experienced increased mortality from infection with *Saprolegnia*. In this example, global events and nonnative fish species combine in a complex series of interactions that clearly affect local amphibian populations. Given the widespread practice of introducing hatchery-reared fishes and climate-induced changes in snow pack levels, we suggest that fishes used in stocking programs could be an important vector for diseases responsible for amphibian losses.

Lithobates catesbeianus may also be a carrier of the chytrid fungus (*Batrachochytrium dendrobatidis*, Bd), that causes chytridiomycosis, a disease that negatively affects amphibian populations and is associated with global amphibian declines (Daszak et al., 2004; Briggs et al., 2010; Duffus and Cunningham, 2010; Kilpatrick et al., 2010; Gervasi et al., 2013a; Olson et al., 2013). The chytrid fungus has a long evolutionary history, which predates its recent outbreak (Rosenblum et al., 2013). It is hypervirulent to some species (Blaustein et al., 2005; Searle et al., 2011) and has emerged across at least five continents (Farrer et al., 2011). American Bullfrogs are widely reported to be a tolerant host and a carrier of Bd, and can often spread the pathogen to less tolerant hosts (Greenspan et al., 2012). As an example of how bullfrogs may spread the chytrid fungus, recent South American studies have noted the fungus in frog species where it had not previously been found, and this infection corresponds closely with the recent invasion of the American Bullfrog (e.g., Arellano et al., 2009; Barrasso et al., 2009).

Although *L. catesbeianus* may be carriers of Bd in some situations, they may be quite susceptible to Bd in others. It appears that susceptibility depends upon the strain of Bd in question and the ecological circumstances (Gervasi et al., 2013b). Moreover, since *L. catesbeianus* do not occupy all regions where Bd is found they cannot be responsible for transmitting the fungus to many native species, especially for example, amphibians that inhabit high elevation habitats. Gervasi et al. (2013b) showed that the dynamics of transmitting Bd from *L. catesbeianus* to native species may be more complex than previously thought. They exposed laboratory-reared metamorphs of *L. catesbeianus* to one Bd strain isolated from western toads and another strain isolated from *L. catesbeianus* to examine whether metamorphs were differentially susceptible. Bullfrogs were susceptible to the strain isolated from the western toads and not the other. In both experiments, infection load detected in the skin decreased over time, suggesting that bullfrog metamorphs from some populations may be inefficient long-term carriers of Bd. *Lithobates catesbeianus* also appears to be a carrier of a novel species of *Chlamydiales* bacteria, *Candidatus Amphibiichlamydia ranarum*, which causes diseases in amphibians and possibly harbors emerging amphibian pathogens such as ranavirosis (Fard et al., 2011; Martel et al., 2013).

The community level effects of nonnative species.—As concern grows regarding the effects nonnative species can have upon native species, there is an increasing emphasis to test whether their impacts upon amphibians reverberate throughout communities. Blaustein et al. (2011) argued the importance of researching amphibian declines at the community level and investigating synergistic effects of multiple stressors instead of focusing on single factors. In recent studies, Richter-Boix et al. (2013) compared invaded and non-invaded amphibian populations on the Iberian Peninsula to test whether the introduction of Painted Frog (*Discoglossus pictus*) altered communities. They found that the presence of *D. pictus* compromised species co-occurrence patterns at the regional scale. In non-invaded areas, the community was statistically structured, but in the invaded areas, community structure appeared to be random. Li et al. (2011) looked at frogs on island ponds off the coast of China and found that the higher the density of nonnative American Bullfrogs (*L. catesbeianus*) the lower the richness and density of native frog species. These negative impacts on the native frog community were proportional to the density of American Bullfrogs.

On Pacific islands, the Coqui Frog (*Eleutherodactylus coqui*) has demonstrated negative effects at the community level since its introduction in the late 1980s. This frog reaches high densities, feeds heavily on invertebrates, and appears to cause community-level changes by altering invertebrate communities (Choi and Beard, 2012). Coqui frogs were associated with a decrease in flying or foliage invertebrate communities, reduced the total number of leaf-litter invertebrates by 27%, and increased dipterans by 19%. These results demonstrate a significant effect on the macroinvertebrate community at the landscape level.

The African Clawed Frog (*Xenopus laevis*) has compromised communities as well. Lillo et al. (2011) looked at the impacts of African Clawed Frogs on native amphibian populations in Italy. Three species of the native frog community were extirpated quickly after the establishment of African Clawed Frogs. Only populations of *Bufo bufo* did not seem to be impacted by *X. laevis*. Lobos and Measey (2002) demonstrated that nonnative African Clawed Frogs in Chile prey heavily on zooplankton and aquatic invertebrates, implying that African Clawed Frogs can have widespread negative effects on aquatic systems.

Introduced fishes are also known to compromise aquatic systems. Hamer and Parris (2013) found that nonnative fishes negatively affect larval amphibian communities in urban wetlands. The authors suggest that draining wetlands throughout the year and preserving or restoring natural ephemeral wetland habitat is necessary to conserve amphibian assemblages in urban areas. Others have found that the diversity of pond breeding assemblages—that includes amphibians—increases after nonnative predatory fishes are removed from pond habitats (Knapp et al., 2007; Walston and Mullin, 2007).

Aquatic amphibian communities can also be affected simultaneously by multiple nonnative species. Preston et al. (2012) showed the ways in which multiple invaders can directly and indirectly affect such communities. Across 139 wetlands, they determined that introduced fishes and bullfrogs (*L. catesbeianus*) decrease the probability of occupancy of native Pacific Tree Frogs (*Pseudacris regilla*) using occupancy models and experimental venues. In the mesocosm experiments they found that introduced fish reduce zooplankton and palatable amphibian larvae, which increased nutrient load and phytoplankton. Because unpalatable bullfrog larvae had little competition, they were able to grow rapidly. Bullfrog larvae did not reduce the survival of native amphibian larvae, but did reduce native larvae growth rates. Apparently, the combined effects of these introduced species interact additively.

Nonnative species can also negatively affect native amphibians by altering host-parasite interactions. Orlofske et al. (2012) studied whether alternative hosts and predators of parasites effect trematode (*Ribeiroia ondatrae*) infection in a native frog (*Pseudacris regilla*). They found that native amphibians could remove up to 93% of infectious stages and thereby reduce the infection rate in *P. regilla* by half, but that introduced predatory fishes did not reduce transmission. Though other amphibians in this system had similar infection intensities as *P. regilla*, introduced fishes had much lower infection intensities. These results suggest that native amphibians can serve as alternative hosts, while nonnative species do not. Similarly, native Australian Green Tree Frog (*Litoria caerulea*) were shown to be unaffected by an introduced parasite, the lungworm *Rhabdias pseudosphaerocephala*, which arrived with introduced cane toads (*B. marinus*; Pizzatto and Shine, 2011). *Litoria caerulea* can harbor very high numbers of the parasite, but host-switching occurs between *L. caerulea* and an allied frog species, *Litoria splendida*. When infected, *L. splendida* survivorship is significantly reduced, yet the fitness of *L. caerulea* is not affected by the parasite.

Nonnative species may also affect communities by dampening diversity. Cruz and Rebelo (2005) studied the effect of nonnative crayfish on amphibian species native to the Iberian Peninsula. Using mesocosm experiments they examined the survival rates of embryos and larvae from 13 native amphibian species when exposed to *Procambarus clarkii*. Only survivorship of *Bufo bufo* was not reduced by crayfish. As a follow up study, Cruz et al. (2008) also used field surveys to demonstrate the same phenomenon. Most native amphibian populations were greatly reduced or extinct within eight years of the crayfish introduction. Crayfish invasions pose similar threats in areas of the Colorado River Basin. In conjunction with nonnative fishes, Martinez (2012) suggests that nonnative crayfish (*Orconectes virils*) invasions may have been overlooked and severely underestimated in the Upper Colorado River Basin, and as a result create a most challenging recovery and preservation of the native community.

Anthropogenic disturbance as a dimension of invasions.—Current studies of nonnative species and amphibians include how future disturbances and anthropogenic induced climate change may further negatively affect native amphibians and convolute nonnative–native amphibian interactions. Much of this literature links modified habitat to the loss of amphibian species or shows an overall negative trend in amphibian species abundances and distributions due to anthropogenic disturbance (Trombulak and Frissell, 2000; Ficetola and De Bernardi, 2004; Ernst et al., 2006; McKinney, 2008). Specifically, Herwig et al. (2013) showed that human-modified landscapes associated with the installation of drainage networks, wetland consolidation, and agricultural networks alter hydroperiod, which negatively affect amphibian assemblages, and depress amphibian breeding success in Minnesota (USA) by increasing distributions of native and nonnative fishes. In other studies, maintaining viable populations of salamanders (*Ambystoma tigrinum*) was dependent upon spatial connectivity of wetland habitat (Cosentino et al., 2011), and the preservation of waterfalls in other systems has allowed native amphibians to coexist with nonnative predatory trout species (Karssing et al., 2012). Ficetola et al. (2011) also found that land use affects distribution of *Salamandra salamandra*, which was related to landscape, hydrological, and water characteristics. Heavy sedimentation and siltation of streams from human-modified lands has affected populations of the critically endangered Chile Mountains False Toad (*Telmatobufo venustus*) and congeners, and *ex-situ* assurance colonies have been implemented to mitigate the effects of modified and lost habitat (Fenolio et al., 2011). Other studies show that human-modified tropical forests negatively affect anuran community composition and diversity (Faruk et al., 2013), and human intervention in freshwater ecosystems has been shown to fuel disease emergence (Peeler and Feist, 2011). Furthermore, Hof et al. (2011) have shown how land modification in conjunction with pathogens and climate change will negatively affect amphibian diversity. A recent experimental study has also documented negative synergistic effects between commonly applied insecticides and nonnative species. Kerby and Sih (unpubl. data) show that a carbamate compound, carbaryl, and nonnative aquatic predators can interact to greatly reduce survivorship of a federal species of concern, the Foothill Yellow Legged Frog (*Rana boylii*).

Human-modified landscapes can not only harm amphibian populations directly, but such altered environments are often ground zero for introduced species. Riley et al. (2005) noted that stream habitats that had considerable urbanization nearby also had higher water flows than nearby streams with less urbanization. The increased water flow allowed nonnative crayfishes and fishes to persist versus less urbanized streams where they appeared to have difficulty surviving low summer water flow. Subsequently, areas that contained nonnative species contained fewer native amphibians.

Although there are many ways in which nonnative introductions occur (e.g., Christy et al., 2007), Johnson et al. (2008) have suggested that human-altered bodies of water spur the establishment and proliferation of nonnative species. As they inhabit increasing numbers of water bodies, a stepping stone effect takes place whereby nonnative species gradually radiate from one habitat to a nearby habitat. Dams have been shown to promote this phenomenon (Davies et al., 2013) and commercial livestock facilities also seem to assist nonnative species dispersal (Gonzalez-Bernal et al., 2012). Similarly, where nonnative species previously could not survive the summer drought, cattle ponds have replaced seasonal marshes in Arizona (Maret et al., 2006), inadvertently enabling the survivorship of nonnative predators. Again, the persistence of nonnative species in this system has been harmful to local amphibians. Griffis-Kyle et al. (2011) observed that earthen livestock-watering tanks influence breeding populations of native amphibians in Chihuahuan Desert grasslands in New Mexico (USA) by significantly increasing their breeding range. Although tanks could expand breeding opportunities, the authors speculate that artificial bodies of water in this landscape could serve as sinks for populations and potentially lead to a loss of genetic diversity by eroding local adaptation. To understand the extent that man-made modifications have on the spread of nonnative species, Ficetola et al. (2010) used land-use change models to test their efficacy to predict the spread of the nonnative American Bullfrog (*R. catesbeianus*) from the 1950s to present day in northern Italy. Models that took into account changes in human land-use patterns accurately predicted the spread of the nonnative frog versus models that assumed constant land-use patterns.

In general, climate change is predicted to globally disrupt species distributions and abundances (Bellard et al., 2013). Climate change models indicate that nonnative species will gain greater advantages as a result of warmer water temperatures, shorter winters, less winter hypoxia, and for the most part, improved conditions to facilitate their spread (Brook et al., 2008; Hellman et al., 2008; Rahel and Olden, 2008). Loyola et al. (2012) estimated whether climate change could drive the invasion of American Bullfrogs (*L. catesbeianus*) into established reserves in the Atlantic Forest Biodiversity Hotspot. Employing distribution and climate models, they found that the American Bullfrogs will likely invade reserves as a result of climate change. These results obviously raise concerns, since the goal of establishing preserves is to protect species, diversity, and native habitat. Should climate change improve conditions for nonnative species to spread and become established, then preserves may be jeopardized.

How climate change will affect amphibians and invading species at the organismal level, as well as ecological and evolutionary processes (see Shine, 2012) may become an even greater concern in the future (Lawler et al., 2009). New invasion prevention and control strategies will need to be considered to protect and preserve native amphibian populations from further decline (Beachy et al., 2011; Snow and Witmer, 2011; Cabrera-Guzmán et al., 2013). Models may need to incorporate interspecific dispersal patterns and species interactions to more accurately determine species responses to climate change (Urban et al., 2013). It has also been suggested that fitting models with data from a species pooled range and not just mean dispersal range will assist in better predicting the extent of invasions and biotic responses to climate change (Broennimann and Guisan, 2008; Urban et al., 2013).

Amphibian–nonnative coexistence and ecosystem restoration.— More than two decades of studies have documented amphibian population declines, and many more studies are now attempting to understand the relationship between nonnative species and amphibian population status and conservation. The questions being asked are: Can nonnative species be removed and habitat restored to pre-invasion conditions? Will amphibian population numbers improve when nonnative species are removed? Are there situations where native amphibians can persist with nonnative predators? Rice et al. (2011) showed that an introduced frog species, *Osteopilus septentrionalis*, that had invaded natural protected areas in the Everglades, Florida (USA) and preys on larval and adult species of native tree frogs (*Hyla cinerea* and *Hyla squirella*), could have significant population level effects on native amphibians. After a 12-month effort to capture and remove *O. septentrionalis*, estimated abundances of native tree frog species increased. Within a similarly short time frame, Cascade Frog (*Rana cascadae*) densities, survival, and recruitment increased in the Klamath Mountains of California (USA) when introduced fishes were experimentally removed from lakes (Pope, 2008). Predatory introduced trout from mountain lakes have compromised amphibian assemblages in other systems too, but when removed, native frogs and salamanders were able to recover (Hoffman et al., 2004; Vredenburg, 2004; Knapp et al., 2007). Other studies have shown that when nonnative predatory mink are removed from islands, native amphibian populations begin to increase (Ahola et al., 2006; Salo et al., 2010). Velo-Anton and Cordero-Rivera (2011) documented an island population of nonnative mammals preying upon a native salamander (*Salamandra salamandra*). They suggest that eradication could positively affect the salamander population, but may be extremely difficult given the topography and dense vegetation of the island.

Armadillos (*Dasypus novemcinctus*), which have recently expanded their range in North America, pose similar threats to native salamanders (*Plethodon angusticlavius*; Crane et al., 2011), as do introduced feral swine that have invaded southern parts of the United States (Hartley et al., 2012). Research conducted by Crane et al. (2011) indicates that salamanders are able to detect armadillo chemical cues and that such cues cause *P. angusticlavius* to exhibit antipredator behavior. Removal of these mammals could also benefit native ecosystems, but will be extremely challenging given the lack of predators, high fecundity, and survival of these species.

In many systems, total removal of an alien species may not be possible, and Hartel et al. (2007) suggest that some amphibian populations might persist with nonnative predators where habitat complexity exists. Nájera-Hillman et al. (2009) and Salo et al. (2010) found that native frog species were able to persist with nonnative predatory mammals in sites with complex habitat. Habitats that had cover in the form of boulders and vegetation (shrubs and grasses) allowed native amphibians to persist better than habitats with less cover. Other studies have concluded that complexity provides benefits for urban herpetofauna (Banville and Bateman, 2012). Schank et al. (2011) also found that complexity of habitat positively affected coexistence of native frogs (*Lithobates sylvaticus)* in lakes with stocked trout. The presence of native fish, lake trophic status, and the length of larval period of *L. sylvaticus* also seem to promote amphibian persistence in this system.

Seasonal water conditions can also encourage coexistence between natives and introduced species. Pagnucco et al. (2011) hypothesized that the observed coexistence of introduced lake chub (*Couesius plumbeus*) and native salamanders (*A. macrodactylum)* in Linnet Lake, Alberta (Canada) may be due to winter hypoxic conditions that lead to major lake chub die offs, relaxing predation pressure on salamanders during breeding. Abiotic factors can also aid the persistence of the federally endangered California Tiger Salamander (*Ambystoma californiense*). Because of ongoing hybridization between an introduced congeneric, native populations of *A. tigrinum* have been genetically compromised. Johnson et al. (2013) demonstrate that native genotypes are better able to survive in rapidly drying mesocosms relative to other genotypes. They suggest that management of aquatic habitat could minimize the spread of nonnative genotypes.

Kats et al. (2013) report that above average rainfall combined with the trapping of nonnative crayfishes during dry years promotes coexistence between native amphibians and invaders. Above average rainfall results in flooding events, and in streams with steep gradients, nonnative crayfishes that are more adapted to swamp habitats are washed away, allowing native amphibians bursts of successful breeding and recruitment. In years where rainfall is below average, traps are set to bring down crayfish populations and give native amphibians an opportunity to breed. Similarly, Luja and Rodríguez-Estrella (2010b) found that tropical cyclones produce heavy water flow that periodically washed out nonnative American Bullfrogs. Endemic Baja California Tree Frogs (*Pseudacris hypochondriaca curta*) have evolved with cyclonic conditions and their populations are not impacted in the same way as bullfrogs. These periodic tropical storms facilitate the coexistence of the native tree frogs and the nonnative bullfrogs. Walls et al. (2013) modeled the effect that extreme variation in precipitation can have on amphibians, and stressed the importance of considering how precipitation patterns, and not just total amounts of rainfall, will affect amphibians and ecological interactions with native and introduced species.

Coexistence between nonnative and native species may also be possible when native species are capable of regulating the abundances of a nonnative species. Competition by native Green Tree Frogs (*Litoria caerulea)* significantly reduced the growth rate of nonnative Cane Toads (*Bufo marinus)* and increased their larval period in natural Australian waterbodies (Cabrera-Guzmán et al., 2013), as well as significantly decreased the body length and mass of Cane Toad metamorphs. There was no significant negative effect on tree frog tadpoles from Cane Toad tadpoles. However, there was strong intraspecific competition between tree frogs, which led to an increased larval period and reduced survival, growth rate, or size at metamorphosis. The authors suggest that native tree frogs could be used as part of an integrated regime to control nonnative species and make coexistence possible, but at what cost to the native species remains unclear. Follow up studies in the same system indicate that *B. marinus* could also be controlled, and possibly eradicated, by using intraspecific chemical stimuli (Crossland et al., 2012).

Currently, the number of documented restoration projects that have eradicated nonnative species without having negative consequences to the native ecosystem remains low (however, see Hobbs and Cramer, 2008 for an overview). Nonnative removal experiments have demonstrated that the negative effects of nonnative species throughout communities can be reversed if nonnative species are removed (Hartman and McCarthy, 2004; Vredenburg, 2004; Gratton and Denno, 2006; Knapp et al., 2007; Bay and Sher, 2008; Marchante et al., 2009). Yet, there are few, if any, examples where nonnative species are successfully removed and amphibian populations return to pre-invasion population numbers, or where native amphibians can successfully coexist with nonnative predators (Kats and Ferrer, 2003). As has been detailed, the complexity of invasions has diverse impacts that resonate throughout the entire community. As a result, the task of conserving and preserving habitat to prevent the introduction and proliferation of nonnative species has been overwhelming.

A major question with regard to invasions is whether nonnative species are eliciting behavioral responses in native species that may affect communities, and as a result reshape biological, environmental, and ecological processes within ecosystems. Native species already show shifted behavioral responses in the presence of nonnative species, and as a result demonstrate remarkably different feeding ecology, breeding habits, communication systems, or use of resources. As we work to understand how amphibians are responding to nonnative species, it seems opportune to identify their responses to the removal or reduction of nonnative species. Furthermore, if a nonnative species has led to the displacement of native species and altered their ecology, we should perhaps begin to wonder how reintroduced native species will respond to one another, and to question whether the effect of nonnative species has been so extreme as to have reduced native species ability to coexist as they once did prior to the establishment and proliferation of an introduced species.

Given the multitude of challenges facing amphibian populations, ongoing projects aimed at restoring native populations of frogs and salmonids seem paradoxical. In the Santa Monica Mountains (Los Angeles, CA, USA), native amphibians have experienced population declines associated with the individual and synergistic effects of nonnative crayfish (*Procambarus clarkii*), predatory fish (*Gambusia affinis*), and siltation of streams due to land modification and altered fire regimes, which has resulted in remarkably less deep pools in many streams (Bucciarelli and Kats, unpubl. data). Consequently, suitable habitat for the reintroduction of the threatened Red-Legged Frog (*Rana boylii*) is limited to sites that are occupied by native amphibians such as the California Newt (*Taricha torosa*), a Species of Special Concern in the southern part of its range (Jennings and Hayes, 1994). Translocating egg masses of *R. boylii* to sites where *T. torosa* breed may be problematic for subsequent generations given that *T. torosa* prey on *R. boylii*. Coexistence of *R. boylii* and *T. torosa* occurs in more northerly localities where greater population numbers of *R. boylii* mitigate predation pressure by *Taricha*. However, in the Santa Monica Mountains, populations of *R. boylii* are nearly nonexistent and thus, predation by *Taricha* may overwhelm populations of *R. boylii*. In a system attenuated by predatory nonnative species, as well as abiotic stressors, how will the reintroduction of this native ranid into limited and sympatric habitat occupied by a native predatory amphibian pan out?

The challenges facing conservation and restoration programs is not limited to native amphibian populations, and programs focused on the restoration of other native taxa may further threaten amphibian populations. Also in the Santa Monica Mountains, restoring native trout habitat to facilitate their return to local streams is an even more complex restoration project. As mentioned, amphibian populations in the Santa Monica Mountains have declined over the last ten years. As a result, it is questionable if amphibian populations can persist in the presence of reintroduced native fish, while simultaneously experiencing continued habitat loss, increased fire frequency, drought, and land modification. Essentially, the ability of native species to coexist has been greatly compromised as a result of the direct and indirect effects of nonnative species. Effectively restoring the ecosystem by reintroducing native species is thus intricately entwined in the role and history of nonnative species in the system. Even after their removal, the long-term effects of invasions throughout ecosystems will likely linger. That is not to say the work should not occur, but instead to realize that ecosystems will likely be haunted by the ghosts of nonnative species and in effect, play a major part in recovery and restoration projects, possibly making it more complex and longer than expected, or impractical due to the interaction of multiple stressors that cannot be mitigated and limited logistical resources. Undoubtedly, similar nonnative–native restoration scenarios lie on the horizon and exploring the complexity of not only invasions, but restorations too, will surely provide many exciting projects.

Conclusion.—The negative effects that invasions may generate throughout ecosystems make it difficult to imagine a positive role for nonnative species in ecosystems. However, Schlaepfer et al. (2011) have speculated that nonnative species may contribute to conservation objectives. Where the effects of climate change and habitat modification are depleting native species abundances and biodiversity, they suggest nonnative species may persist, provide some beneficial ecosystem services, and may ultimately evolve into new, endemic taxa. The authors also propose that nonnative species may provide resources (food or habitat) for rare native species, functionally replace extinct taxa, and perform beneficial ecosystem functions. In contrast though, it seems that numerous native species and overall biodiversity have been compromised as a result of nonnative species (Simberloff et al., 2013), and that nonnative species will likely impair more than aid conservation efforts. As a result, when eradication is not opted for, land managers will need to revise conservation and restoration practices (Hobbs et al., 2009).

Given the relatively short period of time since widespread biological invasions have occurred in communities where amphibians reside, the long-term consequences are unclear (Crooks, 2011). It is apparent that not all nonnative species will have an immediate negative impact upon native species. However, long-term studies are necessary to assess the true effects of nonnative species on native species (Strayer et al., 2006). Time lags may obscure initially observed neutral or positive immediate effects of nonnative species (Crooks, 2011). Some nonnative species may take a much greater amount of time from the period of introduction to a point of integration within the native ecosystem before they produce a negative effect (Crooks and Soulé, 1999). Maintaining nonnative species at low densities could dampen, mitigate, or prevent the immediate negative effects of nonnative species and preclude potentially much greater negative effects associated with time lags.

Understanding and predicting when the population of a nonnative species will increase and cause major changes in an ecosystem is a critical component of conservation biology. Metrics used to ascertain the effects of nonnative species must be augmented, and be capable of providing quantitative evidence of the ways in which native communities are impacted by nonnative species (Vilà et al., 2009; Simberloff et al., 2013). Methods used to elucidate the effects of nonnative species should be able to measure both their direct and indirect effects upon an ecosystem. Developing some metric to quantify how integrated a nonnative species is within a native community may be a valuable gauge for scientists, land managers, and policy makers. Understanding how native species, communities, and ecosystem functioning are affected by nonnative species and sharing pertinent data with policy makers, land managers, and the public is crucial to achieving conservation goals.

As globalization continues, massive trade and travel will likely accelerate the frequency of introduced species to nonnative habitats (Vitule et al., 2012), and it appears that less developed countries with rapidly growing economies will be more prone to nonnative species introductions (Lin et al., 2007; Vitule et al., 2012). In the coming decades, invasion biologists may want to quantify how native communities throughout less developed countries respond to nonnative species and compare those initial responses to previously invaded communities throughout more developed countries. Doing so may provide a valuable framework for building predictions about biological invasions. Furthermore, results gleaned from nonnative founder populations may offer scientists and land managers insight into the ways ecosystem impacts develop. Researchers could work to determine how nonnative species affect nutrient regimes, test whether structural change due to nonnative species affects ecosystem processes, measure the strength of selection upon native species, or assess population growth of a nonnative species and the direct effect of such an expansion upon the ecology of native species.

Though most introductions of nonnative species do not have an impact at the level of the ecosystem (Simberloff, 2011), it is clear that interactions of nonnative and native species in many systems need to be further studied. It is difficult to estimate how ecosystems and native species have been, are, or will be, affected by the introduction, establishment, and integration of nonnative species as exemplified by the complex interactions discussed in this review. The rate of amphibian population declines coupled with the increased rate of introduced nonnative species into communities with amphibians should catalyze research efforts to reveal the role of nonnative species in community dynamics.

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