7-13-2014

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Abstract.—Ecosystems provide essential services for human society, which include provisioning, regulating, cultural, and supporting services. Amphibians provide provisioning services by serving as a food source for some human societies, especially in Southeast Asia. They also serve as models in medical research and provide potential for new pharmaceuticals such as analgesics and anti-viral drugs derived from skin secretions. Amphibians contribute to regulating services by reducing mosquito recruitment from ephemeral wetlands, potentially controlling other pest species, and indirectly through predation of insect pollinators. Often neglected, ecosystems also provide cultural services to human societies that increase the quality of human life through recreation, religion, spirituality, and aesthetics. As an abundant and diverse class of vertebrates, amphibians also play prominent roles in the culture of human societies through pathways such as mythology, literature, and art. Most research on the role of amphibians in ecosystems has been on their contribution to supporting services. This is also the area where amphibians are likely to have the largest contribution to ecosystem services. Supporting services have structural (e.g., habitat) and functional (e.g., ecosystem functions and processes) components. Amphibians can affect ecosystem structure through soil burrowing and aquatic bioturbation and ecosystem functions such as decomposition and nutrient cycling through waste excretion and indirectly through predatory changes in the food web. They also can control primary production in aquatic ecosystems through direct consumption and nutrient cycling. Unfortunately, amphibians are experiencing major declines and humans may be losing associated ecosystem services. It is important to understand how declines affect ecosystem services for human societies, but these declines can also serve as natural experiments to understand the role of amphibians in ecosystems.

Key Words.—amphibians; culture; ecosystem functions; food; medicine; regulating services

WHAT WE ARE LOSING

Numerous scientists contend that we are currently witnessing the 6th global mass extinction of species (Wilson 1992; Myers 1993; Wake and Vredenburg 2008; Barnosky et al. 2011). Even given the challenges of comparing historic and modern extinctions, it is clear from the fossil record that the current rate of extinction far exceeds baseline extinction (McCallum 2007; Roelants et al. 2007; Barnosky et al. 2011). Among vertebrates, amphibians are currently the most imperiled class, with approximately 41% of the more than 7,000 amphibian species on the planet threatened with extinction (Stuart et al. 2004; Collins and Crump 2009; Hoffmann et al. 2010). An additional 22.5% are classified as Data Deficient by the IUCN, which likely contributes to an underestimation of the number of threatened amphibian species (Stuart et al. 2004; Hoffmann et al. 2010; Li et al. 2013).

Amphibians are suffering from numerous pressures, but disease, habitat loss and alteration, along with fertilizer and pesticide stressors have caused the greatest declines (e.g., Lips et al. 2005; Wake and Vredenburg 2008; Hayes et al. 2010). Looming over all other factors is the threat of extinction due to climate change (e.g., Pounds and Crump 1994; Wake and Vredenburg 2008;

Rovito et al. 2009; Milanovich et al. 2010). Amphibian declines are a cause for concern in their own right, but also might be indicative of larger environmental problems with potentially systemic implications. Amphibian declines may be an early indicator of the impending loss of freshwater aquatic ecosystem services throughout the world (Lannoo 2008; Collins and Crump 2009). The decline of amphibians may also cause the loss of broader ecosystem services, a concern that has received scant attention. While it is critical to confront the global amphibian crisis, we should also examine what we are losing in terms of associated ecosystem services. Understanding the contribution of amphibians to ecosystems can help prioritize and garner support for conservation measures, and predict the biotic and abiotic changes associated with the potential loss of species (Sekercioglu et al. 2004).

ECOSYSTEM SERVICES

In the Millennium Ecosystem Assessment (2005), ecosystem services are divided into four categories: provisioning, regulating, cultural, and supporting services. These services are the components of ecosystems that influence human well-being. Provisioning services involve the production of useable

products including food, fresh water, fiber, genetic resources, and medicine. Regulating services include water purification, erosion control, climate regulation, disease control, pest species regulation, pollination, and control and dampening of natural disasters. Frequently underappreciated in economic analyses, cultural services increase the quality of human life through recreation, religion, spirituality, and aesthetics (Millennium Ecosystem Assessment 2005). These services improve human psychological well-being and social cohesion (Millennium Ecosystem Assessment 2005). Finally, supporting services are essential for maintaining the three other services. Supporting services generally consist of ecosystem physical structure and ecosystem functions including nutrient cycling, soil formation, and primary production (Millennium Ecosystem Assessment 2005).

Recently, there has been increased recognition of the importance of ecosystem services for human well-being (e.g., Daily et al. 1997; Millennium Ecosystem Assessment 2005; Schmitz et al. 2008). However, social capacity to use this knowledge is limited because our understanding of how various species interact to contribute to ecosystem services is still in its infancy. Numerous studies have attempted to determine how biodiversity (or species richness) contributes to the regulation of ecosystem functions and services (e.g., Bengtsson 1998; Balvanera et al. 2006; Cardinale et al. 2006). Other studies have started to examine the contribution of individual species or taxa (e.g., Terborgh et al. 2001; Ovadia and Schmitz 2002; Frank 2008; Schmitz 2008). Though amphibians play direct and indirect roles in provisioning, regulating, cultural, and supporting services, a comprehensive review of amphibian contributions to ecosystem services is lacking. We address this gap by synthesizing existing research on, and highlighting research needs that would greatly advance the field of amphibian contributions to ecosystem services.

AMPHIBIAN PROVISIONING SERVICES

Amphibians contribute to provisioning services through food and medicine. Frog legs are consumed throughout much of the world, with both the primary supply and consumption coming from Southeast Asia (Semlitsch 2003; Kusrini and Alford 2006; Warkentin et al. 2009), although more than 10 million frogs may be shipped illegally from India each year (Jensen and Camp 2003). Similarly, the indigenous Chorti people of Honduras consume a variety of *Lithobates* spp. in addition to other native bushmeat (Valencia-Aguilar et al. 2013). In the West Indies, the large frog *Leptodactylus fallax* is known as the Mountain Chicken, owing to the taste of its meat, which results in annual harvests of 8,000–36,000 individuals (Valencia-Aguilar

et al. 2013). The United Nations Food and Agriculture Organization estimated human consumption of 4,716 metric tons of frog legs annually (Kusrini and Alford 2006; Parker 2011). This is a minor portion of global food consumption, but may be a locally important protein source in some regions. The book "The Culinary Herpetologist" includes 26 salamander and 193 frog recipes (Liner 2005; Paulwels 2009). Who could resist succulent *Roasted Poison Dart Frog: Campa Indian style* or delectable *Amphiuma a la Poulette* (Liner 2005)? Although tangential to the primary topic of ecosystem services, we find it salient to point out that the harvesting and trade associated with amphibian consumption can be extremely detrimental to amphibian populations. Most amphibians sold for consumption are wild caught with minimal regulation or oversight, leading to declines of local populations (Jensen and Camp 2003; Kusrini and Alford 2006; Warkentin et al. 2009). Amphibians raised in ponds for the culinary market often have problems with disease, water quality, and ethical treatment of the animals (Weng et al. 2002; Mazzoni et al. 2003). Finally, transfer and incidental release of amphibians intended for consumption, or the pet trade, results in the spread of disease and invasive species and declines of populations (Jensen and Camp 2003; Gratwicke et al. 2009; Schloegel et al. 2009). Some amphibians could possibly become a sustainable protein source for certain regional populations, but current practices are detrimental to amphibian populations.

In addition to serving as a food resource, researchers have developed numerous medical advances using amphibians. Though largely discontinued, frogs from various families, most commonly *Xenopus laevis*, were used to test for human pregnancy during the 20th century (Jensen and Camp 2003). Amphibians are also used in traditional medicines throughout the world to treat a variety of ailments, from warts to heart disease (Jensen and Camp 2003). In the neotropics, more than 60 species of amphibians and reptiles are used in traditional medicine, with the skin and fat of *Rhinella jimi, Leptodactylus labyrinthicus,* and *Leptodactylus vastus* sold to treat everything from asthma, to skin ailments and tumors (Valencia-Aguilar et al. 2013).

In Western culture, approximately half of all drugs are derived from natural sources (Clark 1996). Amphibians use chemicals for a number of purposes including mating activity, territorial marking, predator defense, and combating microbial infections (e.g., Duellman and Trueb 1994; Stebbins and Cohen 1997; Petranka 1998) and these chemicals provide potential starting points for new drugs. Antimicrobial peptides from frog skin secretions have shown the potential to inhibit infection and transfer of the human immunodeficiency virus (HIV; Lorin et al. 2005; VanCompernolle et al. 2005). Given the challenge of combating HIV-related deaths in much

of Africa, the potential benefits of these amphibian-derived peptides could be significant.

The epibatidine molecule is another potential medical breakthrough derived from amphibians. It is a toxin isolated from the Ecuadoran poison dart frog *Epipedobates tricolor* that works as a painkiller in mice and rats (Bradley 1993; Changgeng et al. 1993; Myers and Daly 1993; Fisher et al. 1994). The natural product is 200 times more effective in pain suppression than opium (but see Bannon et al. 1995; Boyce et al. 2000). Scientists are optimistic that nontoxic, synthetic variants of this molecule can be developed as an alternative to opiates, which have side effects including drowsiness, addiction, and potential digestive and respiratory distress (Boyce et al. 2000; Wilson 2002). The potential pharmacological benefits derived from amphibians likely extend beyond neotropical dendrobatid frogs, especially as frogs from other parts of the world have adapted to produce a variety of similar chemicals through convergent evolution (Clark et al. 2005). As only a small percentage of amphibian-derived molecules from a very small number of species have been examined for prospective medical benefits, the potential importance of amphibians for human society is difficult to overestimate (Cury and Picolo 2006).

Another medically-relevant provisioning service comes from a group of Australian frogs. The Gastric-Brooding Frogs (*Rheobatrachus* spp.) had the unique ability to turn off the production of stomach acid for the purpose of raising offspring in the stomach. The mechanisms controlling this developmental oddity provide medical insights to help people suffering from severe acid reflux and stomach ulceration (Calvet and Gomollón 2005). Unfortunately, much like the more famous Golden Toad (*Incilius periglenes*) of Costa Rica, the gastric-brooding frogs went extinct from unknown causes shortly after its discovery (Tyler 1991; Collins and Crump 2009). With so many species at risk of extinction and so few studies regarding their potential benefits for humans, providing a reliable estimate of the provisioning services we may lose is currently not feasible.

Amphibians may offer additional insights into medically-relevant physiology, especially given their ability to regenerate limbs and tails. A recent study found that sodium ion transport to damaged cells is critical for tadpole tail regeneration (Tseng et al. 2010). Scientists hope that knowledge of this mechanism and associated ion channels can be applied to human medical advances (Tseng et al. 2010).

REGULATING SERVICES

Amphibians can influence regulating services by altering disease transmission and pest outbreaks. Predatory amphibians can help reduce the spread of mosquito-borne illness through predation and competition with mosquitoes. DuRant and Hopkins (2008) demonstrated the ability of newts (genus *Notophthalmus*) and mole salamanders (genus *Ambystoma*) to reduce mosquito larvae abundance in aquatic mesocosms. Rubbo et al. (2003) found these predatory effects to occur under natural conditions in ephemeral ponds. Although some fish may consume more mosquitoes than do salamanders, salamanders can play an important role controlling mosquitoes in ephemeral wetlands, which cannot support fish (Brodman and Dorton 2006; DuRant and Hopkins 2008; Rubbo et al. 2011). Tadpoles of the Cuban Treefrog (*Osteopilus septentrionalis*) also reduce populations of mosquito populations in laboratory and field experiments (Valencia-Aguilar et al. 2013). Similarly, the frog *Lysapsus limellus* feeds on flies of the family Ephydridae, which carry human diseases in the neotropics (Valencia-Aguilar et al. 2013). In addition to direct predation, predatory salamander larvae limit mosquito populations by deterring oviposition by female mosquitoes in aquatic habitats (Blaustein et al. 2004; Rubbo et al. 2011). Interactions between amphibians and mosquitoes are not always unidirectional, however. Just as tadpoles can prey upon mosquitoes (Petranka and Kennedy 1999), mosquitoes can also prey upon and compete with tadpoles (Blaustein and Margalit 1994, 1996). The exact effects of competition and intraguild predation between mosquitoes and amphibians may vary depending on conditions and species composition. How amphibian effects on mosquitoes translate to the spread of human diseases such as eastern and western equine encephalitis, West Nile virus, yellow fever, dengue fever, and malaria remains to be examined.

Beyond control of disease-vectors in invertebrate populations, amphibians can contribute to regulating services through invertebrate pest control and possibly through altered pollination dynamics. The role of amphibians in these services has received little scientific attention. The Cane Toad (*Rhinella marina*) derives this common name because it was brought to Australia to combat the Cane Beetle (*Dermolepida albohirtum*) and protect sugar cane crops. Like most capricious introductions of non-native species, the control was ineffective. The Cane Toad is now itself a major pest species in Australia (Turvey 2013). However, the idea behind the Cane Toad introduction was born with the knowledge that toads are major invertebrate predators. Although the decision to introduce the Cane Toad was ill conceived, it highlights a potentially important role of amphibians as invertebrate predators. In Argentina, *Rhinella arenarum, Leptodactylus latinasus, Leptodactylus chaquensis*, and *Physalaemus albonotatus* consume arthropods known to damage soybean crops (Valencia-Aguilar et al. 2013), but the extent of natural biological control in these agricultural systems remains

untested. Research should be undertaken to test whether species do provide valuable control of invertebrate pest species within their native ranges.

Amphibians also have the potential to affect pollination and seed dispersal. Most adult amphibians prey on a variety of arthropods including flies, butterflies, moths (mostly larvae), and beetles (e.g., Duellman and Trueb 1994; Petranka 1998; Lannoo 2005), which can be important pollinators for many plants including some agricultural crops (reviewed in Abrol 2012). Although rare among amphibians, some frogs are also known to consume fruit and disperse the seeds. For example, the treefrog, *Xenohyla truncata*, consumes whole fruits and defecates viable seeds in Brazilian forests (Silva et al. 1989; Silva and Britto-Pereira 2006). It is likely that seeds dispersed by these frogs have higher germination rates because of moist microhabitat selection by the frogs (Fialho 1990). It largely remains to be tested where and when amphibians can influence seed dispersal and pollination sufficiently to affect plants on an ecosystem scale.

CULTURAL SERVICES

As one of the major groups of vertebrates, amphibians find a place in the culture and awareness of many human societies. This is particularly evident with frogs, which can be very brightly colored and conspicuous and are often more vocal than salamanders or caecilians. For example, the Coqui (*Eleutherodactylus coqui*) is celebrated in its native Puerto Rico, although it is considered a noisy, invasive nuisance in Hawaii (Steinberg, J. 2001. Hawaiians lose sleep over tiny frog with big voice. New York Times, 1 October. Available from http://www.nytimes.com/2001/10/01/us/hawaiians-lose-sleep-over-tiny-frog-with-big-voice.html [Accessed 19 February 2014]). In Puerto Rico and beyond, amphibians provide cultural services through use in children's books (e.g., Lobel 1979; Horstman 1997; Grahame 2012), advertising (e.g., Super Bowl Budweiser frogs; Concha, J. 2004. Top five Superbowl commercials: from Bud Bowl to Apple, here's the best ads. NBC Sports, 30 January. Available from http://archive.is/HxOE [Accessed 19 February 2014]), television (Kermit the Frog, http://en.wikipedia.org/wiki/Kermit_the_Frog [Accessed 31 March 2014]), and even video games such as *Frogger* (Konami Corporation, Tokyo, Japan), the classic arcade game featured in Seinfeld (http://www.imdb.com/title/tt0697701 [Accessed 31 March 2014]), and contemporary iPhone games such as *Ancient Frog* (http://www.ancient-workshop.com [Accessed 31 March 2014]), *Slyde the Frog*[TM] (Skyworks Interactive, Inc., Glen Head, New York, USA), and *Pocket Frog* (http://www.nimblebit.com [Accessed 31 March 2014]). The visually appealing

Red-Eyed Treefrog (*Agalychnis callidryas*) and numerous poison-dart (family Dendrobatidae) frogs frequently find their way into calendars and nature magazines (Gibbons 2003). It is not difficult to find examples of amphibians in literature, music, art, jewelry, and in decorations (Gibbons 2003). Even Shakespeare's witches famously add, "eye of newt, and toe of frog" to their cauldron of "hell-broth" (Macbeth IV. I. 14; Shakespeare 1994). With more levity, amphibians serve as stuffed animals for children, and most batrachologists accumulate a collection of frog toys, carvings, and pewter figurines, whether desired or not.

Frogs and salamanders from around the globe find their way into our lives through zoos and museums and into homes through the television and the pet trade (Jensen and Camp 2003; Schlaepfer et al. 2005). Amphibians make popular pets because many species are relatively easy to care for and maintain. Although the number of amphibians in the pet trade is difficult to quantify and separate from live animals destined for human consumption, it is clear that millions of amphibians are sold annually to serve as pets (Jensen and Camp 2003; Garner et al. 2009; Nijman and Shepherd 2011). Beyond our homes, amphibians also serve an educational purpose through classroom dissections (especially large *Rana* spp. and *Necturus maculosus*) for biology, anatomy, and physiology courses in schools (Jensen and Camp 2003). Through these experiences, amphibians become ingrained in our psyche and our culture.

Not surprisingly, as an abundant transglobal vertebrate, amphibians have been part of human culture since long before plush frog toys reached American box stores. Toads play a prominent role in Meso-American art. The toad appears in Aztec art of central Mexico representing a form of Mother Earth, both birthing and consuming life. This toad, Tlaltecuhtli, was believed to be torn apart to become the heavens and the earth (DeGraaf 1991). Mythologies led to folklore and artistic renderings of frogs and toads from nearly every culture from Mexico, Central America, and northern South America over the past 3,000 years (DeGraaf 1991). This art was often associated with rain gods and fertility. This includes green jadeite carved frogs, ceramic toads, and even true golden toad pendants from Costa Rica from the Disquis culture (ca. 1000–1550 A.D.; DeGraaf 1991). Mythology surrounding toads has not been restricted to North America. In both Chinese and Japanese cultures, toads have historically been associated with magic, wisdom, and eternal life (DeGraaf 1991). It was medieval Europe that brought us the notion of the evil toad and likely led to its use in the hell broth of the Shakespearian witches. However, medieval Europeans may have been strongly influenced by the second biblical plague in which Moses overran the Egyptian Pharaohs with frogs upon the command of

God. In Medieval Europe, frogs and toads became associated with magic, wizardry, witchcraft, and reviled diseases such as tumors and skin ailments. The least negative association known from this time period was the use of a toadstone from the head of a mature toad which would supposedly indicate poison or otherwise protect the wearer from poison (DeGraaf 1991).

Salamanders have a less prominent place in human culture than frogs but do appear in art, literature, and music. They occur on children's clothes and in children's stories such as *The Great Smoky Mountain Salamander Ball* (Horstman 1997) and *The Salamander Room* (Mazer 1994). Salamanders also have an older tradition, usually associated with fire. In the 1st century CE Pliny the Elder noted that salamanders only emerge during heavy rain and went on to suggest that they are so cold as to extinguish fire and that milky secretions from the mouth cause a person's hair to fall out with the appearance of leprosy (Pliny the Elder 1855). Although lacking in factual accuracy, the cultural association of salamanders and fire remains. For example, in Ray Bradbury's novel *Fahrenheit 451*, the firemen wear a patch emblazoned with a salamander (Bradbury 1953). The examples of amphibians, especially anurans, from human culture span the globe and the centuries. Whether revered or reviled, amphibians play an important and continuing role in the culture of human societies.

SUPPORTING SERVICES

The role of amphibians in supporting services has received more research emphasis than their role in the other ecosystem services. Supporting services can be divided into structural components (e.g., trees serve as physical homes for other organisms, beavers create lentic habitats) and ecosystem functions (e.g., nutrient cycling, primary production, etc.). Amphibians primarily contribute to ecosystem supporting services through direct and indirect alteration of ecosystem functions, but may alter physical habitats in some ecosystems.

Aquatic ecosystems.—The role of larval amphibians in aquatic ecosystems is a function of altered nutrient dynamics, bioturbation, and their effects on the food web. Unfortunately, we still lack detailed information on the food web dynamics affected by larval amphibians or even what many species eat. Larval salamanders are primarily predators, but tadpoles are known to act as primary consumers, detritivores, predators, and even cannibals (e.g., Alford 1999; Petranka and Kennedy 1999; Altig et al. 2007). Some species confine themselves to consumption at a single trophic level and may even feed as specialists, whereas other species are omnivores with seasonal, ontogenetic, or opportunistic shifts in diet (e.g., Petranka and Kennedy 1999; Babbitt and Meshaka 2000; Altig et al. 2007; Whiles et al. 2010).

Despite some uncertainty in diet, tadpoles can occur in incredibly high densities in some ecosystems (McDiarmid and Altig 1999; Lannoo 2005) and are likely to have significant effects on ecosystem functions, including primary productivity, through changes in the food web. Furthermore, amphibian species have phenologies adapted to reduce competition and predation, while maximizing the availability of their food sources (Morin 1987; Alford 1999; McDiarmid and Altig 1999; Hocking and Semlitsch 2007, 2008). Therefore, even when extreme larval densities are not found at any given point in time, larvae may significantly influence ecosystem functions periodically or throughout the year through accumulated effects.

In lentic systems, tadpoles are known to significantly affect algal and periphyton community structure and biomass (Alford and Wilbur 1985; Morin 1987, 1999; Altig et al. 2007). However, depending on the nutrient dynamics of the system, time of year, solar exposure, algal community structure, and feeding dynamics of the herbivorous community, the effects on primary production may vary (Kupferberg 1997a). Most studies of larval amphibian effects on aquatic primary productivity measure algal standing crop, whereas fewer studies have directly measured primary productivity. In her seminal work, Seale (1980) measured primary production employing both diurnal oxygen flux and isotopic carbon techniques. She found tadpoles in Missouri ponds reduced primary production and appeared to stabilize fluctuations in primary production. The effects on production varied seasonally with reduced production being greatest during spring and early summer when tadpole biomass was highest. These seasonal depressions in production did not appear to be compensated for when tadpole biomass declined; therefore, tadpoles likely reduced total annual primary production (Seale 1980). Experimental research using cattle tank mesocosms revealed that reduced primary productivity associated with shading can also alter the effect of amphibians in lentic habitats (Luhring 2013). Additionally, top-down effects of predators reduced the effects of tadpoles on phytoplankton biomass (Luhring 2013).

In tropical streams, Ranvestel et al. (2004) also found that tadpoles decreased algal abundance and biomass, altered algal community structure, and reduced sediment accumulation. While not tested explicitly, the authors hypothesized that declines in neotropical frogs and tadpoles would reverberate through the food web resulting in predator declines, particularly frog-eating snakes (Ranvestel et al. 2004). They also observed possible shifts in stream invertebrate feeding in response to tadpoles (Ranvestel et al. 2004). Connelly et al.

(2008) confirmed that, in both small-scale exclusions and at the reach-scale, tadpoles reduced primary productivity and sedimentation in tropical streams. Similarly, near complete extirpation of tadpoles in a tropical stream resulted in increased algal biomass and sedimentation of fine detritus. Additionally, there was a reduction in whole stream respiration and in nitrogen uptake rates, resulting in a slowing of stream nitrogen cycling (Whiles et al. 2013).

Most studies have found general decreases in algae, phytoplankton, and periphyton in response to tadpole presence or abundance (Dickman 1968; Alford 1999; Morin 1999; Ranvestel et al. 2004; Altig et al. 2007). This reduction is often considered a result of direct grazing by herbaceous tadpoles (Dickman 1968; McDiarmid and Altig 1999; Ranvestel et al. 2004; Connelly et al. 2008). However, there is evidence that tadpoles can increase primary producer biomass (Osborne and McLachlan 1985; Kupferberg 1997a, b). In the case of increased primary production, there are numerous hypothesized mechanisms. In some circumstances, there is evidence that relatively inedible algae and macrophytes increase when released from competition with edible species and as epiphytes are removed (Kupferberg 1997a). Additionally, epiphyte removal in combination with nitrogen mineralization from tadpole excretion may enhance macrophyte growth (Osborne and McLachlan 1985; Kupferberg 1997a). Furthermore, changes in the invertebrate community may result in indirect effects on primary producers that counteract the direct effect of tadpole grazing (Kupferberg 1997a). Because the effects of tadpoles are not consistent across species and interspecific interactions often have non-additive effects (Morin 1999), the overall effects of tadpoles on primary production remain difficult to predict for specific communities and habitats. Furthermore, caution is required when comparing various metrics of primary production in aquatic ecosystems. Studies variously report area-specific, biomass-specific, and ash-free dry mass (AFDM) specific measures of net primary production (NPP) and chlorophyll a. It is possible to have differences in a measure of NPP in one metric and not another (Connelly et al. 2008). In terms of ecosystem functions and supporting services, it is also important to consider the whole-ecosystem effects on NPP. The results of small-scale studies do not always predict the effects at larger scales (Skelly and Kiesecker 2001; Skelly 2002).

Tadpoles also affect nitrogen cycling by serving as sinks of organic nitrogen, at least temporarily. The total organic nitrogen in the tadpoles is inversely related to, and can seasonally exceed, the total suspended organic nitrogen in ponds (Seale 1980). Tadpoles also appear to decrease the total suspended particles (Seale 1980). Further investigation regarding the relationship between amphibian communities in ponds and inorganic nitrogen levels is needed to understand the full effects of amphibians on aquatic nitrogen cycling. In small-scale enclosures, tadpoles convert particulate organic nitrogen into dissolved organic and inorganic forms of nitrogen plus fecal matter, which settle to the bottom, further reducing suspended organic nitrogen in the water column (Seale 1980).

Additionally, eggs, larvae, and even adults contribute significantly to particular energy pathways including as prey for predators and carcasses for decomposers in aquatic ecosystems (Regester et al. 2006). While these energy sources are small compared with total allochthonous inputs and primary production derived through solar radiation (Seale 1980), they can provide readily available energy and nutrient sources for specific consumer groups (Regester et al. 2006; Regester et al. 2008). Many amphibians serve as important prey for invertebrates (e.g., Skelly and Werner 1990; Petranka and Hayes 1998; Tarr and Babbitt 2002), other amphibians (Petranka and Thomas 1995; Petranka and Kennedy 1999; Babbitt and Meshaka 2000), reptiles (Petranka 1998; Lannoo 2005; Lips et al. 2005), and birds (Lannoo 2005; Fitzpatrick et al. 2009). Eggs, larvae, and decomposing carcasses provide seasonally-abundant energy and nutrient sources to support the aquatic food web. This can be important because allochthonous litter and detritus are the primary nutrient source in many aquatic ecosystems but decompose slowly, whereas decomposing egg masses and amphibian carcasses provide highly labile resources for heterotrophs (Regester et al. 2006, 2008). Specific ecosystem-level effects of these inputs warrant further study.

Beyond the effects of eggs and carcasses to the detrital system, the effect of aquatic salamanders (including larvae) on ecosystem functions has received little attention. As with tadpoles and terrestrial amphibians, aquatic salamanders may influence ecosystem functions through altered nutrient and food web dynamics. Aquatic salamanders are predators and significantly affect macroinvertebrates and tadpole abundance as well as tadpole feeding behavior (e.g., Morin 1983; Lawler 1989; Babbitt 2001). Additionally, larval salamanders represent a significant standing stock of nitrogen and phosphorus and provide 19–33% of stream phosphorus demand through excreta in Appalachian headwater streams (Milanovich 2010). In some stream habitats, metamorphosed individuals remain in the stream and occur with high abundance and biomass (Peterman et al. 2008), further contributing to the standing stock of nutrients and providing additional phosphorus through waste excretion.

Our understanding of the role of amphibians in aquatic ecosystems would benefit from future studies explicitly examining the influence of tadpoles and amphibian

communities on primary production rather than just changes in algal communities and standing crop. Additionally, studies examining the effects of aquatic predatory amphibians should go beyond predator-prey relationships to examine both top-down and bottom-up effects on ecosystem functions including primary production, nutrient cycling, and decomposition.

Terrestrial ecosystems.—As predators, terrestrial and terrestrial-stage amphibians may support ecosystem services through their role in regulating invertebrate populations, altering physical habitats, and cycling nutrients. Thus far, Red-backed Salamanders (*Plethodon cinereus*), Bankor Toads (*Bufo bankorensis*), and Coqui are the only terrestrial amphibian species studied specifically for their roles in ecosystem functions. Wyman (1998) used mesocosm enclosures to manipulate salamander abundance and found that Red-backed Salamanders indirectly reduce decomposition rates by 11–17% through predation of leaf-fragmenting invertebrates. He suggested that Red-backed Salamanders exert top-down control on the detrital food web and therefore reduce decomposition rates. Salamanders reduced the abundance and average size of invertebrates, including millipedes, fly larvae, beetle larvae, mollusks, and spiders. However, Wyman (1998) did not examine whether salamander abundance affected nutrient cycling, primary production, or any other ecosystem function.

In contrast, Walton and Steckler (2005) found that Red-backed Salamanders had no effect on litter decomposition rates in a microcosm study, despite changes in the invertebrate community. Red-backed Salamanders are also known to differentially affect invertebrate detrital communities seasonally, possibly depending on leaf litter mass and moisture (Walton 2005; Walton et al. 2006). The effects of salamanders on ecosystem functions may be context-dependent and may actually depend on the scale of the experimental manipulation (Skelly and Kiesecker 2001; Skelly 2002; Beard et al. 2003). Salamanders are euryphagic predators of invertebrates (Petranka 1998; Casper 2005; Homyack et al. 2010) and forest-floor food webs are extremely complex with potential functional redundancy (Heneghan and Bolger 1998; Chalcraft and Resetarits 2003; Bengtsson and Berg 2005; Wardle et al. 2005). Food web dynamics may strongly influence the effect of salamanders on ecosystem functions. Additionally, most researchers have focused on litter decomposition but salamanders have the potential to affect other ecosystem functions. Although only a minor portion of the energy from forest primary production flows through Red-backed Salamanders, they may provide important energy and nutrient sources for specific trophic pathways (Burton and Likens 1975a). Red-backed Salamanders and other plethodontid salamanders often occur in high abundance throughout mesic forests of North America, making their effects potentially quite large in aggregate (Burton and Likens 1975b; Hairston 1987; Petranka 1998; Rovito et al. 2009). However, Hocking and Babbitt (2014) did not observe any effects of Red-backed Salamanders on plant growth, plant survival, wood or litter decomposition, or soil nitrogen cycling in American Beech (*Fagus grandifolia*) dominated forest stands. Research on the role of amphibians in terrestrial ecosystem functioning would benefit from explicit comparison of different forest types, soil characteristics, and nutrient pools to better understand environment-conditional effects.

In addition to the research on Red-backed Salamanders, there have been a few studies examining the role of anurans in terrestrial ecosystem functions. Huang et al. (2007) found that toads (*B. bankorensis*) alter litter chemistry by increasing phosphorous concentration. However, they found no effect of toads on litter C, N, K, Na, Ca, or Mg concentrations, or any effect on litter decomposition or invertebrate abundances (Huang et al. 2007). In contrast, the Coqui is known to decrease the C:N ratio, and increase K and P in leaf litter (Beard et al. 2002). Additionally, at high densities Coqui can increase foliage production and litter decomposition in both Hawaii and its native Puerto Rico (Beard et al. 2003; Sin et al. 2008). They also can reduce invertebrate abundances and plant herbivory (Beard et al. 2003). Although these effects were not observed in all locations and at all scales, it is clear that abundant frogs can affect a variety of ecosystem functions across different habitats (Beard et al. 2003; Sin et al. 2008).

Changes in decomposition and plant growth were suggested to be a function of available nutrients from Coqui excrement and carcasses. Beard et al. (2002) hypothesized that Coqui could influence microbial activity and plant growth through increasing the pool of limiting nutrients. They suggest that nitrogen in frog waste is in a more soluble form than in invertebrate waste; therefore, although Coqui decrease the invertebrate biomass, they increase nutrient cycling (Beard et al. 2002, 2003). Beard et al. (2002) hypothesized that highly abundant predators are not functionally replaced when removed and that the nutrients made available and the limiting nutrients in the system dictate what species are important to nutrient dynamics. These hypotheses are still in need of testing in virtually all systems for nearly all amphibian species. The implications of these hypotheses for ecosystem functions are also in need of further examination. Testing of the second hypothesis is likely to help elucidate differing results among studies of Red-backed Salamanders (Wyman 1998; Walton 2005; Walton et al. 2006; Homyack et al. 2010).

In addition to explicit studies of amphibian roles in terrestrial ecosystem functions, there is reason to expect that other species will affect various processes through predatory changes in the food web. In terrestrial ecosystems, virtually all amphibians are primarily invertebrate predators. Ants are known to play important roles in ecosystem functions including nutrient cycling, plant protection, seed dispersal, and even more complex roles such as harvesting plants for farming fungi (e.g., Brown and Davidson 1977; Folgarait 1998; Sanford et al. 2009). Many terrestrial amphibians prey on ants and some species such as the Eastern Narrow-mouthed Toad (*Gastrophryne carolinensis*) specialize on ants (Deyrup et al. 2013), thereby creating potential indirect effects on ecosystem functions. Similarly, collembola play a significant role in decomposition through consumption of saprotrophic fungi, and many amphibians prey heavily on collembola, which could indirectly affect decomposition. Additionally, as ectotherms with high efficiency in converting food into biomass, amphibians are likely to act as sinks that slow nutrient flow through the ecosystem. This may be particularly true for long-lived, abundant species with stable populations such as plethodontid salamanders (Hairston 1987). In at least one case, Red-backed Salamander populations have been shown to contain a significant amount of the sodium in a forest ecosystem (Burton and Likens 1975a). Much work remains to determine what species and in which terrestrial ecosystems amphibians affect ecosystem functions and how much of their influence is through direct or indirect pathways. The role of amphibians in ecosystem functions is likely a function of population density, the community structure, and form of the limiting nutrient pools in the ecosystem.

Flux between ecosystems.—As the etymology of the word amphibian implies (Greek: life on both sides; Jaeger 1955), many species move between aquatic and terrestrial habitats for various stages of their life cycle. The net exchange of energy and nutrients between terrestrial and aquatic habitats through amphibians depends on the species present and rates of survival from oviposition to metamorphosis for species with complex life cycles (Wilbur 1980). Data from a single pond in Missouri suggest a net export of nitrogen through the amphibian community (Seale 1980), whereas data from five ponds in Illinois reveal a net import of carbon and energy (ash-free dry mass) through mole salamanders (genus *Ambystoma*; Regester et al. 2008). Other studies have also found a net import of carbon and energy due to the low rates of survival from egg to metamorphosis, which are not sufficiently compensated for by the growth of the individuals leaving ponds (Reinhardt et al. 2013; Schriever et al. 2013).

The balance of nutrient and energy inputs and outputs depends on the breeding effort (egg deposition), adult in-pond survival, and survival from egg to metamorphosis. Given the tremendous annual variability in reproductive effort and larval survival to metamorphosis (Pechmann et al. 1989; Semlitsch et al. 1996; Babbitt et al. 2003), it is unlikely that the net output found by Seale (1980) is a general result. Additionally, there is significant heterogeneity among ponds in the breeding effort and survival to metamorphosis (e.g., Marsh and Trenham 2001; Skidds et al. 2007; Hocking et al. 2008). This is especially prevalent in ephemeral ponds where early-summer drying can result in total reproductive failure in some years despite high reproductive effort (Semlitsch et al. 1996; Babbitt et al. 2003). In some years when environmental conditions are favorable, the number and biomass of amphibians exported from ponds can be extremely large (Gibbons et al. 2006). The magnitude of this export can vary with factors such as temperature (Greig et al. 2012), canopy cover (Earl et al. 2011), allochthonous inputs (Earl and Semlitsch 2012), hydroperiod (Schriever et al. 2013), and species composition (Greig et al. 2012; Luhring 2013; Schriever et al. 2013). The high spatial and temporal variability in these systems can maintain populations through source-sink dynamics (Gill 1978; Pope et al. 2000; Marsh and Trenham 2001). However, these dynamics are difficult to predict, making forecasting the net flow of nutrients and energy associated with pond-breeding amphibians between terrestrial and aquatic ecosystems even more challenging (Schriever et al. 2013). The nutrients transferred between aquatic and terrestrial ecosystems on a per gram basis is a function of the species composition, growth rates of larvae, and stoichiometric differences between life stages for each species. For example, salamanders deposit eggs in ponds with relatively low concentrations of sulfur but salamander metamorphs exit ponds with high concentrations of sulfur resulting in net export (Luhring 2013). There is less of a sulfur concentration discrepancy between frog eggs and metamorphs; therefore, ponds are likely to have higher net sulfur exports when dominated by salamanders compared to ponds producing larger numbers of frogs (Luhring 2013). Additionally, how dispersing metamorphs move across the landscape will affect the distribution of nutrient exports from aquatic to terrestrial ecosystems (McCoy et al. 2009; Pittman et al. 2014).

Quantifying nutrient and energy input through egg deposition and in-pond adult mortality, plus output through metamorphosis at all ponds used by a metapopulation would be valuable for determining net flow across ecosystem boundaries. Further, it would be informative to evaluate how within-pond processes change depending on seasonal and net amphibian inputs. Finally, the net flow varies among species (Seale 1980) and amphibian competition and predation significantly

affect species composition, growth, and survival (Morin 1981; Werner 1986; Semlitsch et al. 1996). Therefore, the community structure, especially the density of predators, will affect both reproductive effort and success (Werner 1986; Skelly 2001; Baber and Babbitt 2003).

Tropical treefrogs also provide seasonally significant sources of nitrogen to epiphytic bromeliads (Romero et al. 2010). This is an important nutrient source for the epiphytes and increases primary production during the rainy season (Romero et al. 2010). Given the significant use of bromeliads by amphibians for reproduction, foraging, and humid refuge, frogs and salamanders are likely to contribute essential nutrients to bromeliads throughout much of the tropics. How this deposition varies spatially and annually remains to be tested.

Ecosystem engineering.—In addition to altering ecosystem functions, amphibians have the potential to contribute to supporting services through alteration of their physical environments. Although the effect of amphibians is certainly less dramatic than that of beavers (*Castor* spp.), amphibians may still significantly contribute to physical habitat modification. In aquatic ecosystems, tadpole-grazing activity can alter the physical structure of aquatic macrophytes and periphyton (Kupferberg 1997a; Wood and Richardson 2010). Additionally, the grazing behavior can influence sedimentation through bioturbation or through ingestion and excretion of particles (Ranvestel et al. 2004; Connelly et al. 2008; Wood and Richardson 2010). Although untested, burrowing amphibians or those that use and maintain the burrows of other organisms may alter soil bulk density and water infiltration. Even temporary habitat alteration, such as the breeding pools dug in mud along streams by gladiator frogs (*Hypsiboas* spp.) may serve as habitat for other species such as invertebrate larvae (Burger et al. 2002). Regardless of the ecosystem type, it is clear that amphibians have the potential to provide supporting services and this is a worthwhile direction of future research.

CONCLUSIONS AND FUTURE DIRECTIONS

Amphibians provide valuable services to human societies. They provide food and medicine, have the potential to affect the spread of disease, and find ways into our homes, hearts, and art, contributing to cultural services that are important for social, spiritual, and psychological wellbeing. Amphibians also support the other ecosystem services through changes in decomposition, primary production, and nutrient cycling. While it is clear that, as a large class of vertebrates, amphibians contribute to ecosystem services, much research remains to understand the extent of their roles. Most studies of these contributions are limited to a few species or habitats. Students of medicine, zoology, ecology, ecosystem science, human-environment relations, and other fields will find promising research careers studying the influences of amphibians on ecosystem services. The information gained on amphibian roles in ecosystems can help inform and prioritize conservation efforts.

Improved communication, tracking, and policy are also needed to quantify amphibian collection and farming for human consumption. This will be important for maintaining amphibian populations while providing a sustainable protein source for some societies.

Systematic studies on pest control, the reduction of disease-carrying invertebrates, and influence on human disease will likely find broad interest and appeal. More than 20 years ago, Hairston (1987) suggested that the role of salamanders in ecosystem functions had not been previously considered and would almost certainly provide a fruitful research program for future investigators. Unfortunately, this line of investigation still remains underappreciated for nearly all amphibians in terrestrial habitats, but has been gaining some interest recently (e.g., Wyman 1998; Beard et al. 2002; Walton et al. 2006). Our knowledge of the importance of amphibians in aquatic habitats is markedly better than in terrestrial habitats (e.g., Seale 1980; Morin 1999; Whiles et al. 2006; Altig et al. 2007), but it is still limited to a small number of species under limited conditions. Additionally, there is potential for species with complex life cycles to contribute to the flow of energy and nutrients between habitats (Regester et al. 2006, 2008; Romero et al. 2010), but the balance of these flows remains unclear for nearly all ecosystems.

Clearly, more explicit experiments are needed in all habitats with nearly all amphibian taxa to better understand the role of amphibians in ecosystem supporting services. The primary techniques for understanding predation, competition, and trophic cascades will also be of great use in furthering our understanding of amphibian services. These commonly incorporate experimental manipulations of density, including presence-absence, through depletions (Hairston 1987; Petranka and Murray 2001), enclosures or mesocosms (Morin et al. 1990; Harper et al. 2009; Earl et al. 2011) and other exclusion methods (Ranvestel et al. 2004; Whiles et al. 2006; Connelly et al. 2011) and can be further developed to include measurements of ecosystem functions. To maximize our understanding, amphibian ecologists must continue to expand our creative research methods beyond just these direct means of experimentation. We must borrow from chemists and biogeochemists to gain inference when direct manipulation is not feasible or insufficient. Some ecologists have already begun using stoichiometry and stable isotope approaches to understand energy and nutrient pathways affected by amphibians (e.g.,

Newsome et al. 2007; Milanovich 2010; Whiles et al. 2010). For generalist and omnivorous amphibians, fatty acid stable isotope analysis and mixing models may elucidate amphibian-altered energy pathways in the ecosystem (DeForest et al. 2004; Moore and Semmens 2008; Parnell et al. 2010; Ward et al. 2011). Additionally, the creative labeling of carbon in different tissues of the primary producers and various detritus sources can further our understanding of base energy sources for parts of the food web associated with amphibians (Pollierer et al. 2007).

Sadly, we must also take advantage of natural experiments including the decline and loss of amphibians due to disease and climate change. As the wave of death associated with the chytrid fungus, *Batrachochytrium dendrobatidis* (Bd), spreads into new areas, opportunities exist to examine the ecosystem functions before and after the declines (e.g., Ranvestel et al. 2004; Connelly et al. 2008; Whiles et al. 2010). If Bd can be combated or resistant amphibians found, bred, or engineered, we will benefit from examining changes in ecosystem supporting services as species are reintroduced and repopulated. Similarly, as changes in temperature and precipitation affect amphibian populations, natural experiments can be conducted to determine the associated changes in ecosystem services. Additionally, Bd is already widespread, but changes in temperature could influence associated mortality and amphibian populations leading to changes in ecosystem services.

For maintenance of future ecosystem services, it is important to understand which species or communities contribute the most and which of those are likely to be threatened by future disease and anthropogenic change. Unfortunately, it is unclear where amphibians contribute the most to ecosystem services or which species are likely to contribute most significantly. In terms of provisioning services, large-bodied frogs in Southeast Asia are the most important for food, but nearly any species could be potentially informative for medical advances. Maintaining taxonomic and genetic diversity is critical for ensuring the potential for future medical use. In this regard, the tropics support the greatest diversity and montane regions globally support high diversity due to low gene flow. However, different genetic lineages persist outside these areas so protecting tropical and montane regions is insufficient for ensuring maximal diversity. Amphibians contribute relatively little to regulating services, but future research quantifying amphibian control of disease and pest invertebrates would be beneficial, especially in tropical areas with disease concerns and agriculture that is interspersed with natural ecosystems. Large, loud, colorful, and diurnal species tend to contribute most to cultural services and should warrant conservation measures, but many less charismatic species also contribute to local cultural services.

Amphibians likely play the largest role in supporting services, but the number of species and habitats studies remains quite limited. Aquatic species or life stages tend to have significant effects on supporting services, whereas the effects in terrestrial systems are less consistent. Beard et al. (2003) suggest that the most abundant species are not functionally replaced when lost, so priority might be given to examination of species that reach the highest densities in particular habitats. However, even extremely abundant species do not always have clear effects on ecosystem supporting services (Hocking and Babbitt 2014).

Species declines have been most significant in the neotropics and Australasian-Oceanic regions, especially in montane streams (Stuart et al. 2004). These declines have been largely a result of Bd, especially in otherwise intact habitats (Lips et al. 2005, 2008). It is important to understand what associated ecosystem services have been lost in these systems, but in many cases it is too late unless reintroductions prove successful. Forest-associated amphibians have also declined globally due to deforestation, but it is impossible to separate the loss of ecosystem services due to amphibian decline and forest loss. Better models forecasting future amphibian declines related to climate change would be useful for directing research to predict future changes in ecosystem services.

LITERATURE CITED

Abrol, D.P. 2012. Pollination Biology: Biodiversity Conservation and Agricultural Production. Springer, New York, New York, USA.

Alford, R.A. 1999. Ecology: resource use, competition, and predation. Pp. 189–214 *In* Tadpoles: The Biology of Anuran Larvae. McDiarmid, R.W., and R. Altig (Eds). The University of Chicago Press, Chicago, Illinois, USA.

Alford, R.A., and H.M. Wilbur. 1985. Priority effects in experimental pond communities: competition between *Bufo* and *Rana*. Ecology 66:1097–1105.

Altig, R., M.R. Whiles, and C.L. Taylor. 2007. What do tadpoles really eat? Assessing the trophic status of an

understudied and imperiled group of consumers in freshwater habitats. Freshwater Biology 52:386–395.

Babbitt, K.J. 2001. Behaviour and growth of Southern Leopard Frog (*Rana sphenocephala*) tadpoles: effects of food and predation risk. Canadian Journal of Zoology 79:809–814.

Babbitt, K.J., and W.E. Meshaka. 2000. Benefits of eating conspecifics: effects of background diet on survival and metamorphosis in the Cuban Treefrog (*Osteopilus septentrionalis*). Copeia:469–474.

Babbitt, K.J., M.J. Baber, and T.L. Tarr. 2003. Patterns of larval amphibian distribution along a wetland hydroperiod gradient. Canadian Journal of Zoology 81:1539–1552.

Baber, M.J., and K.J. Babbitt. 2003. The relative impacts of native and introduced predatory fish on a temporary wetland tadpole assemblage. Oecologia 136:289–295.

Balvanera, P., A.B. Pfisterer, N. Buchmann, J.-S. He, T. Nakashizuka, D. Raffaelli, and B. Schmid. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters 9:1146–1156.

Bannon, A.W., K.L. Gunther, and M.W. Decker. 1995. Is epibatidine really analgesic? Dissociation of the activity, temperature, and analgesic effects of (±)-epibatidine. Pharmacology Biochemistry and Behavior 51:693–698.

Barnosky, A.D., N. Matzke, S. Tomiya, G.O.U. Wogan, B. Swartz, T.B. Quental, C. Marshall, J.L. McGuire, E.L. Lindsey, K.C. Maguire, et al. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

Beard, K.H., K.A. Vogt, and A. Kulmatiski. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. Oecologia 133:583–593.

Beard, K.H., A.K. Eschtruth, K.A. Vogt, D.J. Vogt, and F.N. Scatena. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. Journal of Tropical Ecology 19:607–617.

Bengtsson, J. 1998. Which species? What kind of diversity? Which ecosystem function? Some problems in studies of relations between biodiversity and ecosystem function. Applied Soil Ecology 10:191–199.

Bengtsson, J., and M.P. Berg. 2005. Variability in soil food web structure across time and space. Pp. 201–210 *In* Dynamic Food Webs: Multispecies Assemblages, Ecosystem Development, and Environmental Change. de Ruiter, P.C., V. Wolters, and J.C. Moore (Eds.). Academic Press, Boston, Massachusetts, USA.

Blaustein, L., and J. Margalit. 1994. Mosquito larvae (*Culiseta longiareolata*) prey upon and compete with toad tadpoles (*Bufo viridis*). Journal of Animal Ecology 63:841–850.

Blaustein, L., and J. Margalit. 1996. Priority effects in temporary pools: nature and outcome of mosquito larva-toad tadpole interactions depend on order of entrance. Journal of Animal Ecology 65:77–84.

Blaustein, L., M. Kiflawi, A. Eitam, M. Mangel, and J. Cohen. 2004. Oviposition habitat selection in response to risk of predation in temporary pools: mode of detection and consistency across experimental venue. Oecologia 138:300–305.

Boyce, S., J.K. Webb, S.L. Shepheard, M.G.N. Russell, R.G. Hill, and N.M.J. Rupniak. 2000. Analgesic and toxic effects of ABT-594 resemble epibatidine and nicotine in rats. Pain 85:443–450.

Bradbury, R. 1953. Fahrenheit 451. Ballantine Books, New York, New York, USA.

Bradley, D. 1993. Frog venom cocktail yields a one-handed painkiller. Science 261:1117.

Brodman, R., and R. Dorton. 2006. The effectiveness of pond-breeding salamanders as agents of larval mosquito control. Journal of Freshwater Ecology 21:467–474.

Brown, J.H., and D.W. Davidson. 1977. Competition between seed-eating rodents and ants in desert ecosystems. Science 196:880–882.

Burger, J., W. Arizabal, and M. Gochfeld. 2002. Nesting behavior of a Gladiator Frog *Hyla boans* in Peru. Journal of Herpetology 36:640–648.

Burton, T.M., and G.E. Likens. 1975a. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook experimental forest, New Hampshire. Ecology 56:1068–1080.

Burton, T.M., and G.E. Likens. 1975b. Salamander populations and biomass in the Hubbard Brook experimental forest, New Hampshire. Copeia 1975:541–546.

Calvet, X., and F. Gomollón. 2005. What is potent acid inhibition, and how can it be achieved? Drugs 65:13–23.

Cardinale, B.J., D.S. Srivastava, J. Emmett Duffy, J.P. Wright, A.L. Downing, M. Sankaran, and C. Jouseau. 2006. Effects of biodiversity on the functioning of trophic groups and ecosystems. Nature 443:989–992.

Casper, G.S. 2005. *Plethodon cinereus* (Green, 1818) Eastern Red-backed Salamander. Pp. 796–800 *In* Amphibian Declines: The Conservation Status of United States Species. Lannoo, M. (Ed.). University of California Press, Berkeley, California, USA.

Chalcraft, D.R., and W.J. Resetarits. 2003. Predator identity and ecological impacts: functional redundancy or functional diversity? Ecology 84:2407–2418.

Changgeng, Q., L. Tongchuan, T.Y. Shen, L. Libertine-Garahan, J. Eckman, T. Biftu, and S. Ip. 1993. Epibatidine is a nicotinic analgesic. European Journal of Pharmacology 250:R13–R14.

Clark, A.M. 1996. Natural products as a resource for new drugs. Pharmaceutical Research 13:1133–1141.

Clark, V.C., C.J. Raxworthy, V. Rakotomalala, P. Sierwald, B.L. Fisher, and J. Meinwald. 2005. Convergent evolution of chemical defense in poison frogs and arthropod prey between Madagascar and the neotropics. Proceedings of the National Academy of Sciences of the United States of America 102:11617–11622.

Collins, J.P., and M.L. Crump. 2009. Extinction in Our Times: Global Amphibian Decline. Oxford University Press, New York, New York, USA.

Connelly, S., C. Pringle, R. Bixby, R. Brenes, M. Whiles, K. Lips, S. Kilham, and A. Huryn. 2008. Changes in stream primary producer communities resulting from large-scale catastrophic amphibian declines: can small-scale experiments predict effects of tadpole loss? Ecosystems 11:1262–1276.

Connelly, S., C.M. Pringle, M.R. Whiles, K.R. Lips, S. Kilham, and R. Brenes. 2011. Do tadpoles affect leaf decomposition in neotropical streams? Freshwater Biology 56:1863–1875.

Cury, Y., and G. Picolo. 2006. Animal toxins as analgesics – an overview. Drug News and Perspectives 19:381.

Daily, G.C., S. Alexander, P.R. Ehrlich, L. Goulder, J. Lubchenco, P.A. Matson, H.A. Mooney, S. Postel, S.H. Schneider, D. Tilman, et al. 1997. Ecosystem services: benefits supplied to human societies by natural ecosystems. Issues in Ecology 2:1–16.

DeForest, J.L., D.R. Zak, K.S. Pregitzer, and A.J. Burton. 2004. Atmospheric nitrate deposition, microbial community composition, and enzyme activity in northern hardwood forests. Soil Science Society of America Journal 68:132–138.

DeGraaf, R.M. 1991. The Book of the Toad. Park Street Press, Rochester, Vermont, USA.

Deyrup, M., L. Deyrup, and J. Carrel. 2013. Ant species in the diet of a Florida population of Eastern Narrow-mouthed Toads, *Gastrophryne carolinensis*. Southeastern Naturalist 12:367–378.

Dickman, M. 1968. The effect of grazing by tadpoles on the structure of a periphyton community. Ecology 49:1188–1190.

Duellman, W.E., and L. Trueb. 1994. Biology of Amphibians. Johns Hopkins University Press, Baltimore, Maryland, USA.

DuRant, S.E., and W.A. Hopkins. 2008. Amphibian predation on larval mosquitoes. Canadian Journal of Zoology 86:1159–1164.

Earl, J.E., and R. Semlitsch. 2012. Reciprocal subsidies in ponds: does leaf input increase frog biomass export? Oecologia 170:1077–1087.

Earl, J.E., T.M. Luhring, B.K. Williams, and R.D. Semlitsch. 2011. Biomass export of salamanders and anurans from ponds is affected differentially by changes in canopy cover. Freshwater Biology 56:2473–2482.

Fialho, R.F. 1990. Seed dispersal by a lizard and a treefrog–effect of dispersal site on seed survivorship. Biotropica 22:423–424.

Fisher, M., D. Huangfu, T.Y. Shen, and P.G. Guyenet. 1994. Epibatidine, an alkaloid from the poison frog *Epipedobates tricolor*, is a powerful ganglionic depolarizing agent. Journal of Pharmacology and Experimental Therapeutics 270:702–707.

Fitzpatrick, B.M., K. Shook, and R.D.O. Izally. 2009. Frequency-dependent selection by wild birds promotes polymorphism in model salamanders. BMC Ecology 9:12.

Folgarait, P. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiversity and Conservation 7:1221–1244.

Frank, D.A. 2008. Evidence for top predator control of a grazing ecosystem. Oikos 117:1718–1724.

Garner, T., I. Stephen, E. Wombwell, and M. Fisher. 2009. The amphibian trade: bans or best practice? EcoHealth 6:148–151.

Gibbons, J.W. 2003. Societal values and attitudes: Their history and sociological influences on amphibian conservation problems. Pp. 214–227 *In* Amphibian Conservation. Semlitsch, R.D. (Ed.). Smithsonian Institute, Washington, D.C., USA.

Gibbons, J.W., C.T. Winne, D.E. Scott, J.D. Willson, X. Glaudas, K.M. Andrews, B.D. Todd, L.A. Fedewa, L. Wilkinson, R.N. Tsaliagos, et al. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conservation Biology 20:1457–1465.

Gill, D.E. 1978. The metapopulation ecology of the Red-spotted Newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs 48:145−166.

Grahame, K. 2012. The Wind in the Willows. 3rd Edition. Sterling Children's Books, New York, New York, USA.

Gratwicke, B., M.J. Evans, P.T. Jenkins, M.D. Kusrini, R.D. Moore, J. Sevin, and D.E. Wildt. 2009. Is the international frog legs trade a potential vector for deadly amphibian pathogens? Frontiers in Ecology and the Environment 8:438–442.

Greig, H.S., P. Kratina, P.L. Thompson, W.J. Palen, J.S. Richardson, and J.B. Shurin. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. Global Change Biology 18:504–514.

Hairston, N.G., Sr. 1987. Community Ecology and Salamander Guilds. Cambridge University Press, New York, New York, USA.

Harper, E.B., J.H.K. Pechmann, and J.W. Petranka. 2009. Chapter 12. Field enclosures and terrestrial cages. Pp. 203–226 *In* Ecology and Conservation of Amphibians: A Handbook of Techniques. Dodd, C.K. (Ed.). Oxford University Press, New York, New York, USA.

Hayes, T.B., P. Falso, S. Gallipeau, and M. Stice. 2010. The cause of global amphibian declines: a developmental endocrinologist's perspective. Journal of Experimental Biology 213:921–933.

Heneghan, L., and T. Bolger. 1998. Soil microarthropod contribution to forest ecosystem processes: the importance of observational scale. Plant and Soil 205:113–124.

Hocking, D.J., and K.J. Babbitt. 2014. The role of Red-backed Salamanders on ecosystem functions. PLoS ONE 9:e86854.

Hocking, D.J., and R.D. Semlitsch. 2007. Effects of timber harvest on breeding-site selection by Gray Treefrogs (*Hyla versicolor*). Biological Conservation 138:506–513.

Hocking, D.J., and R.D. Semlitsch. 2008. Effects of experimental clearcut logging on Gray Treefrog (*Hyla versicolor*) tadpole performance. Journal of Herpetology 42:689–698.

Hocking, D.J., T.A.G. Rittenhouse, B.B. Rothermel, J.R. Johnson, C.A. Conner, E.B. Harper, and R.D. Semlitsch. 2008. Breeding and recruitment phenology of amphibians in Missouri oak-hickory forests. American Midland Naturalist 160:41–60.

Hoffmann, M., C. Hilton-Taylor, A. Angulo, M. Böhm, T.M. Brooks, S.H.M. Butchart, K.E. Carpenter, J. Chanson, B. Collen, N.A. Cox, et al. 2010. The impact of conservation on the status of the world's vertebrates. Science 330:1503–1509.

Homyack, J.A., E.B. Sucre, C.A. Haas, and T.R. Fox. 2010. Does *Plethodon cinereus* affect leaf litter decomposition and invertebrate abundances in mixed oak forest? Journal of Herpetology 44:447–456.

Horstman, L. 1997. The Great Smoky Mountain Salamander Ball. 5th Edition. Great Smoky Mountains Association, Gatlinburg, Tennessee, USA.

Huang, C., C. Wang, and P. Hou. 2007. Toads (*Bufo bankorensis*) influence litter chemistry but not litter invertebrates and litter decomposition rates in a subtropical forest of Taiwan. Journal of Tropical Ecology 23:161–168.

Jaeger, E.C. 1955. A Source-book of Biological Names and Terms. 3rd Edition. Charles C. Thomas, Publisher, Springfield, Illinois, USA.

Jensen, J.B., and C.D. Camp. 2003. Human exploitation of amphibians: direct and indirect impacts. Pp. 199–213 *In* Amphibian Conservation. Semlitsch, R.D. (Ed.). Smithsonian Institution, Washington, D.C., USA.

Kupferberg, S.J. 1997a. Facilitation of periphyton production by tadpole grazing: functional differences between species. Freshwater Biology 37:427–439.

Kupferberg, S.J. 1997b. The role of larval diet in anuran metamorphosis. American Zoologist 37:146–159.

Kusrini, M.D., and R.A. Alford. 2006. Indonesia's exports of frogs' legs. Traffic Bulletin 21:13–24.

Lannoo, M.J. (Ed.). 2005. Amphibian Declines: The Conservation Status of Unites States Species. University of California Press, Berkeley, California, USA.

Lannoo, M.J. 2008. Malformed Frogs: The Collapse of Aquatic Ecosystems. University of California Press, Berkeley, California, USA.

Lawler, S.P. 1989. Behavioural responses to predators and predation risk in four species of larval anurans. Animal Behaviour 38:1039–1047.

Li, Y., J.M. Cohen, and J.R. Rohr. 2013. Review and synthesis of the effects of climate change on amphibians. Integrative Zoology 8:145–161.

Liner, E.A. 2005. The Culinary Herpetologist. Bibliomania!, Salt Lake City, Utah, USA.

Lips, K.R., P.A. Burrowes, J.R. Mendelson, and G. Parra-Olea. 2005. Amphibian population declines in Latin America: a synthesis. Biotropica 37:222–226.

Lips, K.R., J. Diffendorfer, J. Mendelson III, and M. Sears. 2008. Riding the wave: reconciling the roles of disease and climate change in amphibian declines. PloS Biology 6:441–454.

Lobel, A. 1979. Frog and Toad are Friends. Harper Collins, New York, New York, USA.

Lorin, C., H. Saidi, A. Belaid, A. Zairi, F. Baleux, H. Hocini, L. Bèlec, K. Hani, and F. Tangy. 2005. The antimicrobial peptide dermaseptin S4 inhibits HIV-1 infectivity in vitro. Virology 334:264–275.

Luhring, T.M. 2013. Complex life-histories and biogeochemical cycles; interactions between amphibian life-history strategies and elemental cycling. Ph.D. Dissertation. University of Missouri, Columbia, Missouri, USA. 123 p.

Marsh, D.M., and P.C. Trenham. 2001. Metapopulation dynamics and amphibian conservation. Conservation Biology 15:40–49.

Mazer, A. 1994. The Salamander Room. Dragonfly Books, Random House Children's Books, New York, New York, USA.

Mazzoni, R., A.A. Cunningham, P. Daszak, A. Apolo, E. Perdomo, and G. Speranza. 2003. Emerging pathogen in wild amphibians and frogs (*Rana catesbeiana*) farmed for international trade. Emerging Infectious Diseases 9:995–998.

McCallum, M.L. 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. Journal of Herpetology 41:483–491.

McCoy, M.W., M. Barfield, and R.D. Holt. 2009. Predator shadows: complex life histories as generators of spatially patterned indirect interactions across ecosystems. Oikos 118:87–100.

McDiarmid, R.W., and R. Altig. 1999. Tadpoles: The Biology of Anuran Larvae. University of Chicago Press, Chicago, Illinois, USA.

Milanovich, J.R. 2010. Modeling the current and future roles of stream salamanders in headwater streams.

Ph.D. Dissertation. University of Georgia, Athens, Georgia, USA. 156 p.

Milanovich, J.R., W.E. Peterman, N.P. Nibbelink, and J.C. Maerz. 2010. Projected loss of a salamander diversity hotspot as a consequence of projected global climate change. PLoS ONE 5:1–19.

Millennium Ecosystem Assessment. 2005. Ecosystems and Human Well-being: Synthesis. Island Press, Washington, D.C., USA.

Moore, J.W., and B.X. Semmens. 2008. Incorporating uncertainty and prior information into stable isotope mixing models. Ecology Letters 11:470–480.

Morin, P.J. 1981. Predatory salamanders reverse the outcome of competition among three species of anuran tadpoles. Science 212:1284–1286.

Morin, P.J. 1983. Predation, competition, and the composition of larval anuran guilds. Ecological Monographs 53:119–138.

Morin, P.J. 1987. Predation, breeding asynchrony, and the outcome of competition among treefrog tadpoles. Ecology 68:675–683.

Morin, P.J. 1999. Community Ecology. Blackwell Science, Inc., Malden, Massachusetts, USA.

Morin, P.J., S.P. Lawler, and E.A. Johnson. 1990. Ecology and breeding phenology of larval *Hyla andersonii*: the disadvantages of breeding late. Ecology 71:1590−1598.

Myers, C.W., and J.W. Daly. 1993. Tropical poison frogs. Science 262:1193.

Myers, N. 1993. Questions of mass extinction. Biodiversity and Conservation 2:2–17.

Newsome, S.D., C. Martinez del Rio, S. Bearhop, and D.L. Phillips. 2007. A niche for isotopic ecology. Frontiers in Ecology and the Environment 5:429–436.

Nijman, V., and C.R. Shepherd. 2011. The role of Thailand in the international trade in CITES-listed live reptiles and amphibians. PLoS ONE 6:e17825.

Osborne, P.L., and A.J. McLachlan. 1985. The effect of tadpoles on algal growth in temporary, rain-filled rock pools. Freshwater Biology 15:77–87.

Ovadia, O., and O.J. Schmitz. 2002. Linking individuals with ecosystems: Experimentally identifying the relevant organizational scale for predicting trophic abundances. Proceedings of the National Academy of Sciences of the United States of America 99:12927–12931.

Parker, P.M. 2011. The world market for frogs' legs: a 2011 global trade perspective. Icon Group International, Las Vegas, Nevada, USA. 14 p.

Parnell, A.C., R. Inger, S. Bearhop, and A.L. Jackson. 2010. Source partitioning using stable isotopes: coping with too much variation. PLoS ONE 5:e9672.

Paulwels, O.S.G. 2009. Book reviews: The culinary herpetologist. Herpetological Review 40:126–127.

Pechmann, J.H.K., D.E. Scott, J.W. Gibbons, and R.D. Semlitsch. 1989. Influence of wetland hydroperiod on diversity and abundance of metamorphosing juvenile amphibians. Wetlands Ecology and Management 1:3–11.

Peterman, W.E., J.A. Crawford, and R.D. Semlitsch. 2008. Productivity and significance of headwater streams: population structure and biomass of the Black-bellied Salamander (*Desmognathus quadramaculatus*). Freshwater Biology 53:347–357.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, D.C., USA.

Petranka, J.W., and L. Hayes. 1998. Chemically mediated avoidance of a predatory odonate (*Anax junius*) by American Toad (*Bufo americanus*) and Wood Frog (*Rana sylvatica*) tadpoles. Behavioral Ecology and Sociobiology 42:263–271.

Petranka, J.W., and C.A. Kennedy. 1999. Pond tadpoles with generalized morphology: is it time to reconsider their functional roles in aquatic communities? Oecologia 120:621–631.

Petranka, J.W., and S. Murray. 2001. Effectiveness of removal sampling for determining salamander density and biomass: a case study in an Appalachian streamside community. Journal of Herpetology 35:36–44.

Petranka, J.W., and D.A.G. Thomas. 1995. Explosive breeding reduces egg and tadpole cannibalism in the Wood Frog, *Rana sylvatica*. Animal Behaviour 50:731–739.

Pliny the Elder. 1855. The Natural History. Translated by J. Bostock and H.T. Riley. Taylor and Francis, London, England.

Pittman, S.E., M.S. Osbourn, and R.D. Semlitsch. 2014. Movement ecology of amphibians: a missing component for understanding population declines. Biological Conservation 169:44–53.

Pollierer, M.M., R. Langel, C. Korner, M. Maraun, and S. Scheu. 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. Ecology Letters 10:729–736.

Pope, S.E., L. Fahrig, and H.G. Merriam. 2000. Landscape complementation and metapopulation effects on leopard frog populations. Ecology 81:2498–2508.

Pounds, J.A., and M.L. Crump. 1994. Amphibian declines and climate disturbance: the case of the Golden Toad and the Harlequin Frog. Conservation Biology 8:72–85.

Ranvestel, A.W., K.R. Lips, C.M. Pringle, M.R. Whiles, and R.J. Bixby. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshwater Biology 49:274–285.

Regester, K.J., K.R. Lips, and M.R. Whiles. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in

ponds and adjacent forest in southern Illinois. Oecologia 147:303–314.

Regester, K.J., M.R. Whiles, and K.R. Lips. 2008. Variation in the trophic basis of production and energy flow associated with emergence of larval salamander assemblages from forest ponds. Freshwater Biology 53:1754–1767.

Reinhardt, T., S. Steinfartz, A. Paetzold, and M. Weitere. 2013. Linking the evolution of habitat choice to ecosystem functioning: direct and indirect effects of pond-reproducing fire salamanders on aquatic-terrestrial subsidies. Oecologia 173:281–291.

Roelants, K., D.J. Gower, M. Wilkinson, S.P. Loader, S.D. Biju, K. Guillaume, L. Moriau, and F. Bossuyt. 2007. Global patterns of diversification in the history of modern amphibians. Proceedings of the National Academy of Sciences 104:887–92.

Romero, G.Q., F. Nomura, A.Z. Gonçalves, N.Y.N. Dias, H. Mercier, E.C. Conforto, and D.C. Rossa-Feres. 2010. Nitrogen fluxes from treefrogs to tank epiphytic bromeliads: an isotopic and physiological approach. Oecologia 162:941–949.

Rovito, S.M., G. Parra-Olea, C.R. Vásquez-Almazán, T.J. Papenfuss, and D.B. Wake. 2009. Dramatic declines in neotropical salamander populations are an important part of the global amphibian crisis. Proceedings of the National Academy of Sciences 106:3231–3236.

Rubbo, M., J. Lanterman, R. Falco, and T. Daniels. 2011. The influence of amphibians on mosquitoes in seasonal pools: can wetlands protection help to minimize disease risk? Wetlands 31:799–804.

Rubbo, M.J., V.R. Townsend, S.D. Smyers, and R.G. Jaeger. 2003. An experimental assessment of invertebrate/vertebrate predation: the interaction between wolf spiders (*Gladicosa pulchra*) and terrestrial salamanders (*Ambystoma maculatum*). Journal of Zoology 261:1–5.

Sanford, M.P., P.N. Manley, and D.D. Murphy. 2009. Effects of urban development on ant communities: implications for ecosystem services and management. Conservation Biology 23:131–141.

Schlaepfer, M.A., C. Hoover, and C.K. Dodd, Jr. 2005. Challenges in evaluating the impact of the trade in amphibians and reptiles on wild populations. Bioscience 55:256–264.

Schloegel, L.M., A.M. Picco, A.M. Kilpatrick, A.J. Davies, A.D. Hyatt, and P. Daszak. 2009. Magnitude of the US trade in amphibians and presence of *Batrachochytrium dendrobatidis* and ranavirus infection in imported North American Bullfrogs (*Rana catesbeiana*). Biological Conservation 142:1420–1426.

Schmitz, O.J. 2008. Effects of predator hunting mode on grassland ecosystem function. Science 319:952–954.

Schmitz, O.J., J.H. Grabowski, B.L. Peckarsky, E.L. Preisser, G.C. Trussell, and J.R. Vonesh. 2008. From individuals to ecosystem function: toward an integration of evolutionary and ecosystem ecology. Ecology 89:2436–2445.

Schriever, T., M.W. Cadotte, and D.D. Williams. 2013. How hydroperiod and species richness affect the balance of resource flows across aquatic-terrestrial habitats. Aquatic Sciences:1–13.

Seale, D.B. 1980. Influence of amphibian larvae on primary production, nutrient flux, and competition in a pond ecosystem. Ecology 61:1531–1550.

Sekercioglu, C.H., G.C. Dally, and P.R. Ehrlich. 2004. Ecosystem consequences of bird declines. Proceedings of the National Academy of Sciences 101:18042–18047.

Semlitsch, R.D. (Ed.). 2003. Amphibian Conservation. Smithsonian Institute Press, Washington D.C., USA.

Semlitsch, R.D., D.E. Scott, J.H.K. Pechmann, and J.W. Gibbons. 1996. Structure and dynamics of an amphibian community: evidence from a 16-year study of a natural pond. Pp. 217–248 *In* Long-Term Studies of Vertebrate Communities. Cody, M.L., and J.A. Smallwood (Eds.). Academic Press, San Diego, California, USA.

Shakespeare, W. 1994. Macbeth. William Shakespeare: The Complete Works. Barnes and Noble, Inc., New York, New York, USA.

Silva, H.R., and M.C. Britto-Pereira. 2006. How much fruit do fruit-eating frogs eat? An investigation on the diet of *Xenohyla truncata* (Lissamphibia: Anura: Hylidae). Journal of Zoology 270:692–698.

Silva, H.R., M.C. Britto-Pereira, and U. Caramaschi. 1989. Frugivory and seed dispersal by *Hyla truncata*, a neotropical treefrog. Copeia 1989:781–783.

Sin, H., K.H. Beard, and W.C. Pitt. 2008. An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. Biological Invasions 10:335–345.

Skelly, D.K. 2001. Distributions of pond-breeding anurans: an overview of mechanisms. Israel Journal of Zoology 47:313–332.

Skelly, D.K. 2002. Experimental venue and estimation of interaction strength. Ecology 83:2097–2101.

Skelly, D.K., and J.M. Kiesecker. 2001. Venue and outcome in ecological experiments: manipulations of larval anurans. Oikos 94:198–208.

Skelly, D.K., and E.E. Werner. 1990. Behavioral and life-historical responses of larval American Toads to an odonate predator. Ecology 71:2313–2322.

Skidds, D.E., F.C. Golet, P.W.C. Paton, and J.C. Mitchell. 2007. Habitat correlates of reproductive effort in Wood Frogs and Spotted Salamanders in an urbanizing watershed. Journal of Herpetology 41:439–450.

Stebbins, R.C., and N.W. Cohen. 1997. A Natural History of Amphibians. Princeton University Press, Princeton, New Jersey, USA.

Stuart, S.N., J.S. Chanson, N.A. Cox, B.E. Young, A.S.L. Rodrigues, D.L. Fischman, and R.W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306:1783–1786.

Tarr, T.L., and K.J. Babbitt. 2002. Effects of habitat complexity and predator identity on predation of *Rana clamitans* larvae. Amphibia–Reptilia 23:13–20.

Terborgh, J., L. Lopez, P. Nunez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G.H. Adler, T.D. Lambert, et al. 2001. Ecological meltdown in predator-free forest fragments. Science 294:1923–1926.

Tseng, A., W.S. Beane, J.M. Lemire, A. Masi, and M. Levin. 2010. Induction of vertebrate regeneration by a transient sodium current. The Journal of Neuroscience 30:13192–13200.

Turvey, N. 2013. Cane Toads: A Tale of Sugar, Politics and Flawed Science. Sydney University Press, Sydney, Australia.

Tyler, M.J. 1991. Declining amphibian populations: a global phenomenon? An Australian perspective. Alytes 9:43–50.

Valencia-Aguilar, A., A.M. Cortés-Gómez, and C.A. Ruiz-Agudelo. 2013. Ecosystem services provided by amphibians and reptiles in neotropical ecosystems. International Journal of Biodiversity Science, Ecosystem Services and Management 9:257–272.

VanCompernolle, S.E., R.J. Taylor, K. Oswald-Richter, J. Jiang, B.E. Youree, J.H. Bowie, M.J. Tyler, J.M. Conlon, D. Wade, C. Aiken, et al. 2005. Antimicrobial peptides from amphibian skin potently inhibit human immunodeficiency virus infection and transfer of virus from dendritic cells to T cells. Journal of Virology 79:11598–11606.

Wake, D.B., and V.T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. Proceedings of the National Academy of Sciences 105:11466–11473.

Walton, B.M. 2005. Salamanders in forest-floor food webs: environmental heterogeneity affects the strength of top-down effects. Pedobiologia 49:381–393.

Walton, B.M., and S. Steckler. 2005. Contrasting effects of salamanders on forest-floor macro- and mesofauna in laboratory microcosms. Pedobiologia 49:51–60.

Walton, B.M., D. Tsatiris, and M. Rivera-Sostre. 2006. Salamanders in forest-floor food webs: invertebrate species composition influences top-down effects. Pedobiologia 50:313–321.

Ward, E.J., B.X. Semmens, D.L. Phillips, J.W. Moore, and N. Bouwes. 2011. A quantitative approach to combine sources in stable isotope mixing models. Ecosphere 2:art19.

Wardle, D.A., W.M. Williamson, G.W. Yeates, and K.I. Bonner. 2005. Trickle-down effects of aboveground trophic cascades on the soil food web. Oikos 111:348–358.

Warkentin, I.G., D. Bickford, N.S. Sodhi, and C.J.A. Bradshaw. 2009. Eating frogs to extinction. Conservation Biology 23:1056–1059.

Weng, S.P., J.G. He, X.H. Wang, L. Lü, M. Deng, and S.M. Chan. 2002. Outbreaks of an iridovirus disease in cultured Tiger Frog, *Rana tigrina rugulosa*, in southern China. Journal of Fish Diseases 25:423–427.

Werner, E.E. 1986. Amphibian metamorphosis: growth rate, predation risk, and the optimal size at transformation. The American Naturalist 128:319–341.

Whiles, M.R., M.I. Gladyshev, N.N. Sushchik, O.N. Makhutova, G.S. Kalachova, S.D. Peterson, and K.J. Regester. 2010. Fatty acid analyses reveal high degrees of omnivory and dietary plasticity in pond-dwelling tadpoles. Freshwater Biology 55:1533–1547.

Whiles, M.R., R.O. Hall, W.K. Dodds, P. Verburg, A.D. Huryn, C.M. Pringle, K.R. Lips, S.S. Kilham, J.C. Colón-Gaud, A.T. Rugenski, et al. 2013. Disease-driven amphibian declines alter ecosystem processes in a tropical stream. Ecosystems 16:146–157.

Whiles, M.R., K.R. Lips, C.M. Pringle, S.S. Kilham, R.J. Bixby, R. Brenes, S. Connelly, J.C. Colon-Gaud, M. Hunte-Brown, A.D. Huryn, et al. 2006. The effects of amphibian population declines on the structure and function of neotropical stream ecosystems. Frontiers in Ecology and the Environment 4:27–34.

Wilbur, H.M. 1980. Complex life cycles. Annual Review of Ecology and Systematics 11:67–93.

Wilson, E.O. 1992. The Diversity of Life. Harvard University Press, Cambridge, Massachusetts, USA.

Wilson, E.O. 2002. The Future of Life. Vintage Books, New York, New York, USA.

Wood, S., and J. Richardson. 2010. Evidence for ecosystem engineering in a lentic habitat by tadpoles of the Western Toad. Aquatic Sciences - Research Across Boundaries 72:499–508.

Wyman, R.L. 1998. Experimental assessment of salamanders as predators of detrital food webs: effects on invertebrates, decomposition and the carbon cycle. Biodiversity and Conservation 7:641–650.

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