



## **Amphibian Disease Ecology: Are We Just Scratching the Surface?**

Authors: Bienentreu, Joe-Felix, and Lesbarrères, David

Source: Herpetologica, 76(2) : 153-166

Published By: The Herpetologists' League

URL: <https://doi.org/10.1655/0018-0831-76.2.153>

---

BioOne Complete ([complete.BioOne.org](https://complete.BioOne.org)) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](https://www.bioone.org/terms-of-use).

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## Amphibian Disease Ecology: Are We Just Scratching the Surface?

JOE-FELIX BIENENTREU AND DAVID LESBARRÈRES<sup>1</sup>

Department of Biology, Laurentian University, Sudbury, ON P3E 2C6, Canada

**ABSTRACT:** Pathogen-induced population declines and extinction events have been recognized as main threats to amphibian species around the globe. However, the ecological drivers underlying epidemiological patterns are still poorly understood. In an attempt to assess the current knowledge on the ecological drivers of amphibian diseases, we identified 832 peer-reviewed publications on the ecology of amphibian pathogens and diseases published between 2009 and 2019. The vast majority of publications investigated either chytrid or ranavirus infections (79% of the articles), whereas other pathogens such as bacteria and helminths received considerably less attention. Just over half of the studies we reviewed included field research and 40% were experimental in nature, yet only 8% combined field and experimental approaches. More than half of the literature (56%) investigated postmetamorphic stages, whereas premetamorphic stages were considered in 23% of the reviewed studies, and only 13% included both life stages. Susceptibility and mortality have been assessed in almost every study (91%) whereas 37% of them tested for cellular, physiological, or immunological responses. However, other host characteristics such as growth/development, behavior, and specific mucosome/microbiome were considered in only one of four studies. Most research included at least one biotic factor (e.g., host and pathogen identity, species diversity, genetic adaptations), but only one-third considered environmental factors (e.g., temperature, landscape features, inorganic chemicals). Furthermore, there is no general consensus about the factors driving epidemiological patterns of pathogens in amphibian communities, and it is clear that the complexity and specificity of interactions between ecological factors and host–pathogen dynamics make conservation implications difficult and management decisions challenging. To this end, our review identifies some research gaps and proposes future directions to better understand one of the major threats to this class of vertebrates.

**Key words:** Chytrid; Helminths; Parasite; Pathogen; *Ranavirus*; Review

WORLDWIDE reports on emerging infectious diseases of ectothermic vertebrates have significantly increased over the last 30 yr (Dobson and Foufopoulos 2001; Gray and Chinchir 2015). By causing morbidity and mortality among populations, sometimes leading to the extinction of a whole species, some of these diseases are a serious threat to global biodiversity (Cunningham et al. 2017). The scientific community has been alarmed by disease-associated declines in amphibian populations all over the world (Daszak et al. 2003; Muths and Hero 2010; Grant et al. 2016; Cohen et al. 2019; Scheele et al. 2019), but the true scale of declines is unknown and knowledge on the spatiotemporal pattern remains limited (Brunner et al. 2015; Duffus et al. 2015; Scheele et al. 2019; McMillan et al. 2020). A key finding emerging from the literature is that environmental heterogeneity can strongly shape interactions between pathogens and their potential hosts by physiologically limiting vital processes of both host and parasite including growth, dispersal, and survival (Ostfeld et al. 2005; Altizer et al. 2013; McMillan et al. 2020), thus potentially driving disease outcomes in various ecological and evolutionary trajectories (Echaubard et al. 2014; Savage et al. 2015). However, the literature reveals multifaceted and even conflicting patterns (Smalling et al. 2019), providing a complex framework often difficult to translate into actions for conservation management. In this manuscript, we present results from a literature review designed to assess the current knowledge of amphibian disease ecology including the studied pathogens, common study designs, and the ecological factors associated with these host–pathogen relationships (Fig. 1).

### MATERIALS AND METHODS

To assess the current knowledge on the ecological drivers of amphibian diseases, we conducted a systematic literature search for relevant articles published between 2009 and 2019 on PubMed Central and Google Scholar on 2 September 2019. This time frame was chosen because in the years 2008 and 2009 several comprehensive modeling and reviews in the field of amphibian disease ecology, in particular on *Batrachochytrium dendrobatidis* (*Bd*) and ranaviruses, were published (e.g., Gahl and Calhoun 2008; Fisher et al. 2009; Gray et al. 2009; Lötters et al. 2009).

We used the following search terms: (“amphibia” AND “ecology”) AND (“disease” OR “pathogen” OR “parasite”). In addition we searched for common amphibian pathogens and pathogen groups: (“amphibia”) AND (“chytrid” OR “*Bd*” OR “*Bsal*” OR “*Ranavirus*” OR “ATV” OR “BIV” OR “CMTV” OR “FV3” OR “helminth” OR “trematode” OR “nematode” OR “*Ribeiroia*” OR “fungus” OR “*Achlya*” OR “*Saprolegnia*” OR “protist”).

We initially gathered approximately 12,000 search hits. We then excluded duplicates and scanned remaining titles for relevance to the topic. Subsequently, we excluded reviews, opinions, and synthesis articles, as well as studies based exclusively on modeling. We then applied the following selection criteria to the roughly 1400 remaining studies: (1) include amphibian host(s) and pathogen(s), (2) contain a field or experimental (e.g., lab or mesocosm) component, and (3) investigate ecological factors in the context of host–pathogen dynamics (listed below). After further inspection we were left with a pool of 832 peer-reviewed articles (hereafter, the literature; see Supplemental Materials available online for full list) for our review. From each of the included studies, we recorded journal, pathogen group (e.g., chytrid fungi, ranaviruses), and study design (field or experimental). We also scored the studies for the following ecological factors: (a)

<sup>1</sup> CORRESPONDENCE: e-mail, dlesbarreres@laurentian.ca

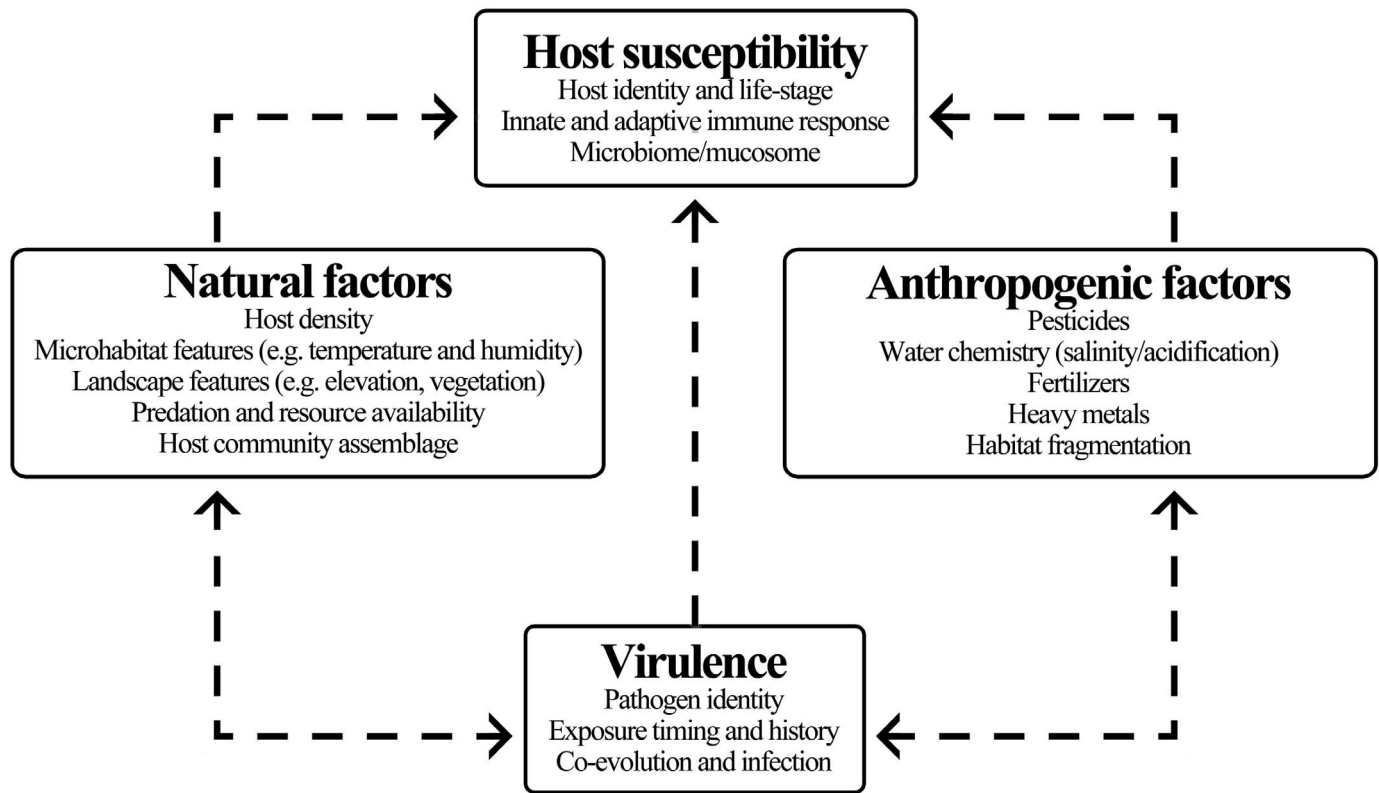


FIG. 1.—Flow diagram of basic relationships between amphibian host–pathogen systems and environmental factors. Adapted from Gray et al. 2009.

abiotic factors, including temperature, humidity, and precipitation; water parameters (e.g., salinity, pH, conductivity; dissolved oxygen); and light (e.g., ultraviolet [UV]B radiation, light:dark cycle); (b) biotic factors, including host community assemblage, population genetics, resources and predation, and density and abundance; (c) factors associated with landscape features, including slope, elevation, vegetation, and connectivity; and (d) factors of anthropogenic nature, including organic and inorganic chemicals, habitat fragmentation, infrastructural and industrial development, and trade and farming. We also included variables associated with (e) the host, such as species identity; life-history stage; susceptibility and mortality; growth and development; physiological, cellular, and immunological responses; behavior and host ecology; host microbiome or mucosome; and (f) the pathogen,

such as species identity, transmission mode, replication, and environmental persistence/viability.

WHAT PATHOGENS HAVE BEEN STUDIED?

Between 2009 and 2019, the most commonly investigated pathogens were chytrid fungi and ranaviruses, covering 78% of the publications examined. However, chytrid fungi (56% of all publications) received significantly more attention than ranaviruses (18% of all publications). Four percent of these publications investigated both pathogens, and only 3% were associated with more than two pathogen classes. Helminths, and in particular *Ribeiroia ondatrae*, were investigated in 15% of the publications and other pathogens such as protists/protozoans, bacteria, and other fungi were investigated in only 4% of the publications (Fig. 2A). Remarkably, more

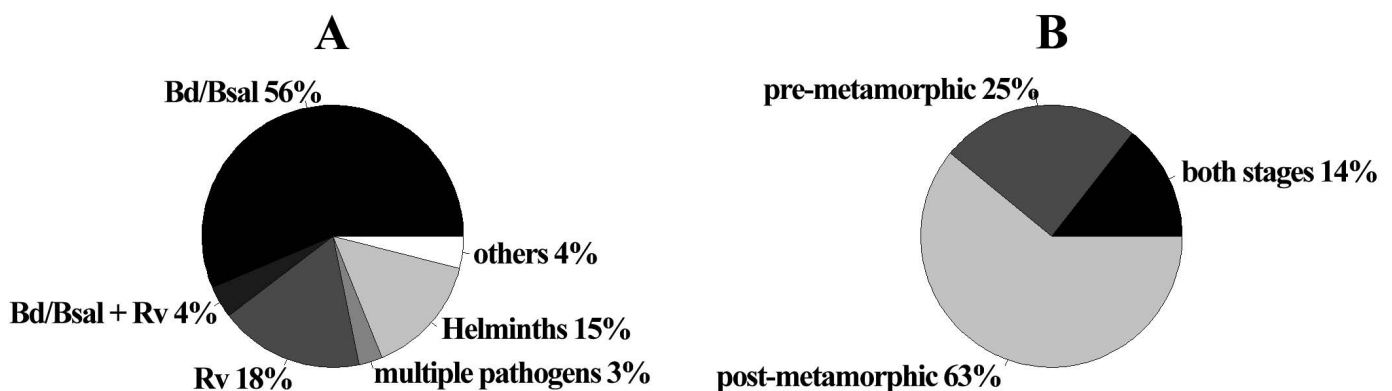


FIG. 2.—Percentage distribution of investigated pathogens (A) and host life stage (B) in the amphibian disease literature between 2009 and 2019.

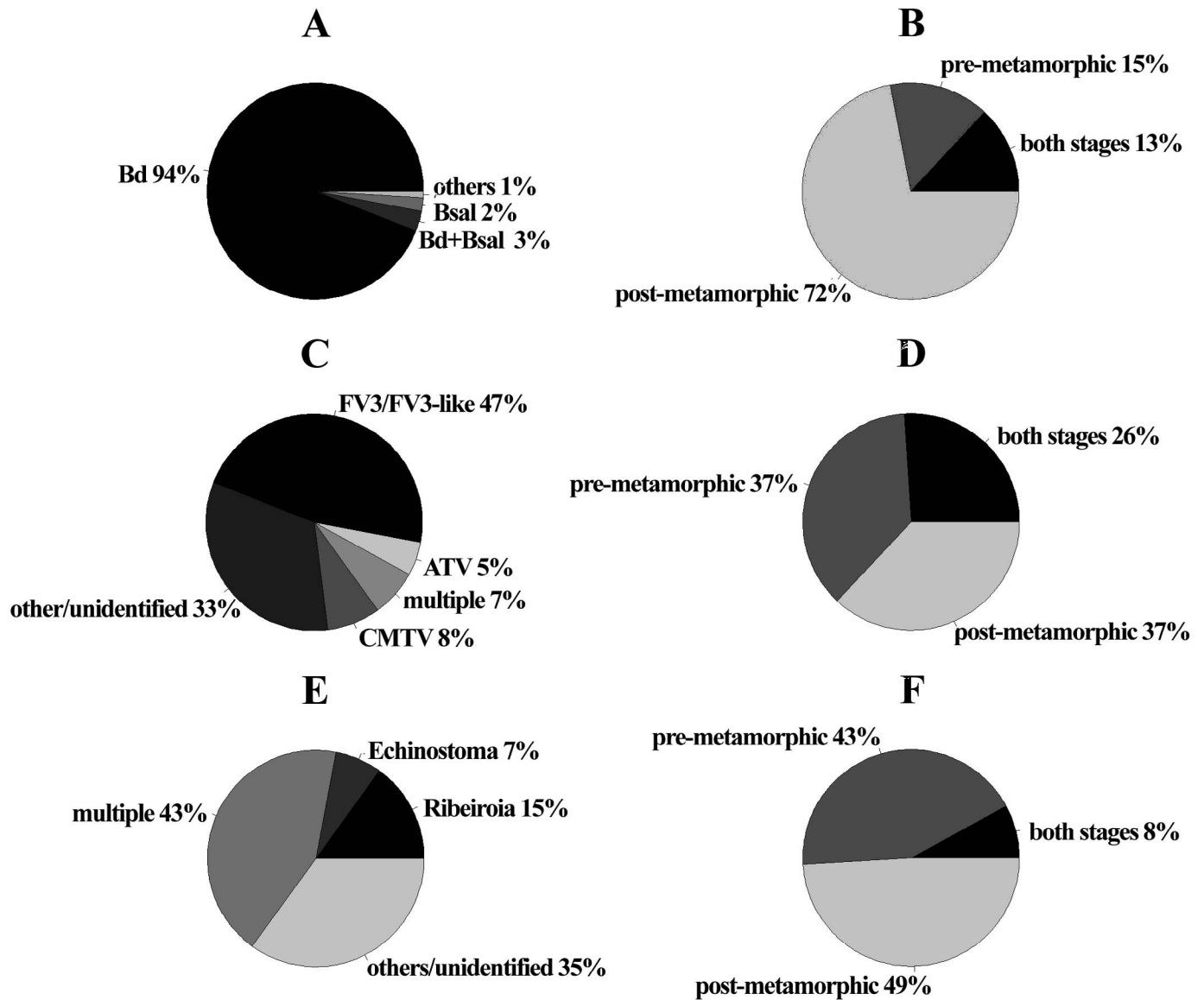


FIG. 3.—Percentage distribution of investigated pathogens and associated host life stage in chytridomycota (A, B), ranaviruses (C, D), and helminths (E, F) in the amphibian disease literature between 2009 and 2019.

than a third (35%) of all literature was published in only four journals (13%, 12%, 6%, and 4% for *Diseases of Aquatic Organisms*, *PLoS One*, *EcoHealth*, and *Journal of Wildlife Diseases*, respectively), although 173 journals have published research on amphibian diseases over this 10-yr period. This large diversity of journals shows the multidisciplinary research associated with these threats and accentuates the complex interplay between host, pathogens, and their environment in shaping disease dynamics (Echaubard et al. 2014; Kärvmö et al. 2018).

The chytrid fungi *Bd* and *B. salamandrivorans* (*Bsal*) belong to the phylum Chytridiomycota (Longcore et al. 1999; Martel et al. 2013), a group of heterotrophic and ubiquitous fungi, predominantly found in aquatic and semiaquatic habitats, as well as in moist soils (Sparrow 1960; Karling 1977). Many chytrids are obligate parasites of plants, fungi, and invertebrates, degrading substrates such as chitin, cellulose, and keratin (Berger et al. 1998). In

particular, *Bd* and *Bsal* affect keratinized tissue such as the superficial epidermis in juvenile and adult amphibians, as well as the mouth parts in tadpoles (Berger et al. 1998; Longcore et al. 1999; Fellers et al. 2001). Chytrid infections can be associated with multifocal erosion, irregular thickening of the epidermis, and severe ulcerations, which can disrupt osmotic regulation and cause cardiac arrest (Voyles et al. 2009; Martel et al. 2013). At least 500 amphibian species are affected by chytrid-related declines and extinctions, even in pristine environments (Olson et al. 2013; Becker et al. 2016; Scheele et al. 2019). The majority of the literature involving chytridomycota investigated *Bd* (94%), whereas only 2% considered *Bsal*, and 3% addressed both species together (Fig. 3A). Less than half (43%) of the literature identified chytrid lineages, which is somewhat surprising, considering more than 600 different isolates on GenBank and four main lineages are known (Bataille et al. 2013; Olson et al. 2013; O'Hanlon et al. 2018). This becomes

critical in the context of risk assessments when considering the variability in pathogenicity among different strains (Berger et al. 2005; Retallick and Miera 2007). Furthermore, strain identification would help to identify the source and origin of infection, subsequently aiding the implementation of measures to prevent further transmission and mitigate the outcomes of epizootics.

*Ranavirus* is a genus of viruses within the nucleocytoplasmic large deoxyribonucleic acid virus family Iridoviridae. Three species of *Ranavirus* are known to infect amphibians: *Ambystoma tigrinum virus* (ATV), *Common midwife toad virus* (CMTV), and *Frog virus 3* (FV3; for further taxonomy see Chinchar et al. 2017, 2018). They have been found in at least 105 species in 18 families of amphibians worldwide (Duffus et al. 2015) and are responsible for the majority of pathogen-associated amphibian die-off events in temperate climate regions such as North America and Europe (Kik et al. 2011; Lesbarrères et al. 2012). By inducing a potentially lethal systemic disease that involves organ necrosis and hemorrhages, ranaviruses have the potential to cause severe population declines, possibly leading to extirpation (Earl and Gray 2014; Price et al. 2014; Miller et al. 2015). Almost half of the research on ranaviruses (44%) focused on the FV3 lineage, whereas the other two species CMTV and ATV received considerably less attention (8% and 5% respectively; Fig. 3C). Yet, in 33% of the literature, ranaviruses remained unassigned to a lineage or unidentified despite being considered FV3-like isolates, and only 7% of the literature investigated multiple isolates.

Helminths are often detected in amphibians of all life stages, but the infection can be considered incidental since amphibians are normally not the target host (Miller et al. 2004). However, infestations may have severe consequences for infected hosts. In particular, the trematode *R. ondatrae* is known to induce severe limb malformations and mortality in developing amphibians (Johnson and McKenzie 2009; Roberts and Dickinson 2012). The majority of the helminth literature investigated either multiple species (43%) or did not specify the species (35%). One in five studies (22%) reported either *Echinostoma* sp. or *R. ondatrae* (Fig. 3E).

Among other pathogens, bacteria such as *Aeromonas hydrophila*, *Pseudomonas aeruginosa*, and *Klebsiella pneumoniae* can induce lethal dermatosepticemia, potentially leading to mass mortalities (Schadich 2009), and have been studied in 2% of the literature. However, these bacteria are often part of the natural internal and external microbiome of amphibians, only causing disease when the overall health and related immune functions of the host decrease (Schadich and Cole 2010). Finally, a limited number of papers investigated the role of water molds (1%), such as *Saprolegnia* sp. and *Achlya* sp., which can induce saprolegniasis in amphibians (Kiesecker et al. 2001; Ault et al. 2012). Water molds are ubiquitous saprotrophic oomycetes that can parasitize live and dead amphibians of all life stages (Romansic et al. 2011), potentially leading to death in embryonic and larval stages (Romansic et al. 2009; Fernández-Benítez et al. 2011; Ault et al. 2012). Fungal infections can also have a negative impact on host conditions, thus increasing vulnerability to secondary infections by other pathogens (Romansic et al. 2011).

TABLE 1.—Study design by major pathogen groups in the amphibian disease literature between 2009 and 2019, sorted by experimental studies, field studies, and a combination of approaches. Rows sum to 100%.

	Experiment	Field	Field + experiment
All pathogens	40%	52%	8%
Chytrid	41%	51%	9%
Ranaviruses	49%	46%	5%
Chytrid + ranaviruses	2%	96%	2%
Helminths	40%	49%	11%
Others	21%	68%	11%

#### WHAT STUDY DESIGNS HAVE BEEN USED?

More than half of the published studies included field sampling components, and slightly fewer were experimental in nature, but only a small number of these included both components, and even fewer conducted statistical modeling (Table 1). The same ratios were observed when considering chytrid fungi and helminths only, whereas for ranaviruses, slightly more experimental than fieldwork has been conducted (Table 1). It is interesting to note that for chytrid fungi, which received more and earlier attention than the ranaviruses, the majority of research is still fieldwork based, rather than conducted through specific experimental studies, as seen in ranavirus literature, highlighting both the geographical and knowledge gaps that remain.

#### WHAT ECOLOGICAL FACTORS HAVE BEEN STUDIED?

Overall, a large variety of ecological factors has been studied in amphibian disease research over the last decade. Besides specific host and pathogen characteristics, studies often included several environmental or anthropogenic factors. In general, studies often considered only a small suite of ecological factors, rather than taking a more holistic approach (Table 2), and the effects of host life stage and phylogeny, as well as community and density effects, received little attention.

#### Pathogen Characteristics

In general, the outcomes of epizootics in amphibian communities strongly depend on the respective pathogen strain (Brunner et al. 2015; Berger et al. 2016). Different pathogens are highly variable in their virulence (commonly measured as the time to the host's death; Berger et al. 2005; Brunner and Collins 2009; Farrer et al. 2011; Echaubard et al. 2014; Morrison et al. 2014), and recent studies have identified the circulation of highly recombinant pathogen lineages in wild populations (Farrer et al. 2011; Claytor et al. 2017; O'Hanlon et al. 2018; Vilaça et al. 2019). The origins of the different *Bd* lineages, as well as *Bsal*, are in northeast

TABLE 2.—Relative number of studies investigating zero, one, two, or more than two ecological factors in the amphibian disease literature between 2009 and 2019. Factors are separated into abiotic and biotic factors, and host and pathogen characteristics. Columns sum to 100%.

No. of factors	Abiotic factors	Biotic factors	Host characteristics	Pathogen characteristics
Zero	65%	10%	6%	38%
One	21%	51%	15%	51%
Two	8%	33%	46%	10%
More than two	6%	6%	33%	1%

Asia, where they infect native amphibians without causing severe epizootics, and most individuals sustain sublethal infections (Martel et al. 2014; O'Hanlon et al. 2018). This is likely explained by a coevolutionary history of the hosts and the pathogen, further supported by the detection of the fungi in museum specimens at least 100 yr old (Martel et al. 2014; Lips 2016). The geographical origin of ranaviruses is not clear, but phylogenetic analyses suggest that ranaviruses have been a natural part of amphibian host–pathogen systems in Asia for an extended period of time, and have been introduced into North America within the last 100 yr (Vilaça et al. 2019).

However, only half of the literature determined pathogen identity (e.g., *Bd* lineage or *Ranavirus* strain). Given the advancements in sequencing techniques and significant decrease in associated time and costs, we suggest routinely conducting isolate identification and providing sequences on GenBank. This would drastically increase the comparability among studies and provide a greater insight into the identity and diversity of pathogen strains circulating in wild and captive amphibian populations. Furthermore, this knowledge would greatly advance management and conservation strategies.

Other key factors for the outcomes of an epizootic in an amphibian population are the pathogen-specific replication and transmission modes (Kriger and Hero 2007; Gray et al. 2009). *Bd* infection occurs predominately through motile free-swimming zoospores in aquatic habitats, shed by infected individuals, but also through direct transmission (Rowley and Alford 2007; Chestnut et al. 2014). Similar routes of transmission are expected for the salamander fungus *Bsal* (Gray et al. 2015; Schmidt et al. 2017). Ranaviruses can be transmitted directly through contact with infectious individuals, but also through virions in water and on environmental substrates (Brunner et al. 2007; Cunningham et al. 2007; Robert et al. 2011; Brenes et al. 2014). Another plausible route of transmission, in particular for larval amphibians, is cannibalism (Brunner et al. 2015). This transmission route has been demonstrated in anurans (Pearman et al. 2004; Harp and Petranka 2006) and salamanders (Brunner et al. 2007). Vector-borne transmission can explain the spread of amphibian pathogens across the landscape, in particular over longer distances. *Bd* zoospores have been found on the feet and feathers of waterfowl (Garmyn et al. 2012; Burrowes and De la Riva 2017). A similar mode of landscape-level transmission would be plausible to expect for ranaviruses; however, there is no peer-reviewed literature testing this hypothesis. Interestingly, *Bd* as well as ranaviruses were found in mosquitos at sites with infected turtles (*Ranavirus*, Kimble et al. 2015; *Bd*, Gould et al. 2019). In addition, *Bd* has been found on lizard feet (Kilburn et al. 2011). For ranaviruses as a multiclass vertebrate pathogen there is a wide range of potential vector species including fish, reptiles, and amphibians (Duffus et al. 2015).

#### Host Characteristics

In general, amphibians exhibit high interspecific variation in susceptibility to pathogen infections (Schock et al. 2008; Hoverman et al. 2011; Searle et al. 2011; Ohmer et al. 2013). Therefore, host-identity can be a driving factor in the epidemiology of emerging pathogens in amphibian commu-

nities (e.g., chytrid in various North American amphibian species, Gahl et al. 2011; *Ranavirus* in Californian amphibian communities, Tornabene et al. 2018; Ranaviruses in amphibian communities in the boreal forest of northwestern Canada, Bienentreu 2019). Because of varying susceptibilities, some species experience devastating mortality events, whereas others sustain sublethal infections and potentially act as a reservoir for pathogens (Reeder et al. 2012; Scheele et al. 2016; Bacigalupe et al. 2017; Bienentreu 2019). In Australian amphibian communities, a high abundance of Common Eastern Froglets (*Crinia signifera*), a reservoir for *Bd*, amplified prevalence in sympatric Northern Corroboree Frogs (*Pseudophryne pengilleyi*, Scheele et al. 2017). A similar pattern has been found by Bienentreu (2019), where the presence of Canadian Toads (*Anaxyrus hemiophrys*) in a community of up to three hosts drastically increased ranavirus loads in Wood Frogs (*Lithobates sylvaticus*, or *Rana sylvatica*) and Boreal Chorus Frogs (*Pseudacris maculata*). With reservoir hosts potentially sustaining sublethal infections and acting as superspreaders for a pathogen, it becomes critical to consider host identity in epidemiological studies.

Additionally, the behavior and ecology of host species can have direct and indirect effects on pathogen dynamics in communities, and vice versa (Lips et al. 2003; Han et al. 2008; Daly and Johnson 2011; Haislip et al. 2012). Contact frequency with other individuals, as well as habitat preferences, can affect transmission (e.g., ATV in Tiger Salamanders [*Ambystoma tigrinum*], Brunner et al. 2004; *Bd* in Boreal Toads [*Anaxyrus boreas*], Hossack et al. 2013). For example, breeding aggregations can facilitate ranavirus transmission (Miller et al. 2011), and chytrid infection probability can be directly linked to thermal preferences of the host species (Rowley and Alford 2013).

Infected individuals (in particular, sublethally infected) may exhibit behavioral changes due to changes in morphology or physiology, subsequently altering transmission dynamics in a host community (Han et al. 2008). Such mechanisms were observed in relation to antipredator behavior, where Wood Frog tadpoles exposed to predator cues exhibited reduced *Bd* loads, likely due to a stress-induced upregulation of the immune system (Groner and Relyea 2015). When exposed to visual and chemical predator cues, Northern Leopard Frog (*Lithobates pipiens*, or *Rana pipiens*) tadpoles infected with *Bd* exhibited behavioral changes that decreased their risk of being preyed upon, as compared with uninfected individuals (Parris et al. 2006). In contrast, predator cues seemingly do not interact with disease dynamics in the amphibian–ranavirus system. Four larval North American anuran species did not experience elevated mortality or viral loads when exposed to predator cues (Haislip et al. 2012). Another study could not find any relationship between predator cues, resource availability, and ranavirus susceptibility of Wood Frog tadpoles (Reeve et al. 2013). It is also noteworthy that Tiger Salamander larvae infected with ATV, a *Ranavirus* species commonly found in salamanders, showed drastically increased mortality when exposed to predator cues (Kerby et al. 2011). For echinostomes, however, research showed that increased resource availability can be indirectly linked to the severity of infection in larval anurans by influencing host body size (Marino 2016). Therefore, infection-induced changes in

antipredator behavior become relevant when investigating predator–prey systems, where both parts are susceptible to the pathogen (e.g., *Bd* in frog–salamander system, Han et al. 2011). The vast majority of the literature (91%) included host-specific infection rates, susceptibility, or mortality. However, although 40% of the literature reported pathogen-induced changes in physiology, morphology, or at the cellular level, only 11% investigated effects on growth or development, another 6% investigated behavioral traits and specific host ecology, and only 4% focused on the effects of resource type and availability, as well as predation.

Intraspecific variation in susceptibility plays an important role in pathogen transmission and infection outcome (Echaubard et al. 2010, 2016; Tobler and Schmidt 2010). Such variation typically reflects phylogeny and life history of the host species and their related innate and adaptive immune responses (Grayfer et al. 2015a; Grogan et al. 2018), but also the number and timing of exposures to the pathogen (Hanlon and Parris 2014; Echaubard et al. 2016; Kirschman et al. 2018). The different amphibian life stages present distinct morphologies and physiologies, and their susceptibility to infection changes throughout development (Haislip et al. 2011; Warne et al. 2011). Premetamorphic and metamorphic stages (tadpoles and metamorphs) often exhibit reduced and delayed immune responses to infection in relation to postmetamorphic (juveniles and adults) individuals (Rollins-Smith 1998; Andino et al. 2012; Grogan et al. 2018). Therefore, late-stage tadpoles and metamorphs often show a high susceptibility and commonly succumb to ranavirus infection (Hoverman et al. 2011; Reeve et al. 2013; Grayfer et al. 2014), whereas postmetamorphic individuals can harbor considerably higher pathogen loads than premetamorphic individuals, sustaining sublethal infections without experiencing a terminal outcome (Landsberg et al. 2013; Grayfer et al. 2015b; An and Waldman 2016). The respective amphibian life stage at the time of exposure to a pathogen plays a significant role in infection outcome (Johnson et al. 2011; Echaubard et al. 2016; Kirschman et al. 2018) and despite the differences based on life history stage, only 25% of the literature assessed both pre- and postmetamorphic phases together. Overall, the postmetamorphic stages are more studied, with 63% of the literature compared with only 25% for premetamorphic stages, and only 14% investigating both stages (Fig. 2B). In studies of chytrid fungi, many studies focus on postmetamorphic host stages (72%), with only 15% of the literature investigating premetamorphic stages and 13% combining both stages (Fig. 3B).

In contrast, in the ranavirus literature, pre- and postmetamorphic stages are balanced (37% each), with 26% of the studies having both life stages combined (Fig. 3D). For helminths, approximately half of the literature (49%) investigated effects on premetamorphic individuals, in comparison with 43% for postmetamorphic individuals, and 8% for both stages (Fig. 3F). For other pathogens such as bacteria and water molds, the majority of the literature (94%) investigated infections in postmetamorphic individuals, and no study included both life stages.

Another important factor in the outcome of pathogen emergence is the phylogeny of the affected host population (Hoverman et al. 2011; Echaubard et al. 2014; Bradley et al. 2015; Bacigalupe et al. 2017). A repeated emergence of a

pathogen in a host population will lead to selection toward more resistant genotypes, overall increasing the resilience of the population against new or reintroduced pathogen lineages (Pearman and Garner 2005; Bacigalupe et al. 2017; Puschendorf et al. 2019). The rediscovery of relict amphibian populations of species that were believed to be extirpated or extinct due to epizootics and devastating die-offs (e.g., Armored Mist Frogs [*Litoria lorica*] and Waterfall Frogs [*Litoria nannotis*] in Australia, Puschendorf et al. 2011; amphibian communities in the Costa Rican highlands, García-Rodríguez et al. 2012; Harlequin Toads [*Atelopus varius*] in Costa Rica, González-Maya et al. 2013) may further indicate the coevolutionary history of the host–pathogen system. In fact, pathogens are often present in the host community, but positive individuals show no signs of disease, presumably sustaining sublethal infections (Whitfield et al. 2013; Warne et al. 2016; Puschendorf et al. 2019). However, the phylogenetic backgrounds of the hosts have only been investigated in 11% of the literature.

#### Host Community and Density

The diversity and dynamics of a community of host species can have a significant influence on pathogen dynamics and vice versa (Becker et al. 2014; Han et al. 2015; Bientreux 2019; Johnson et al. 2019). Pathogen transmission and infection prevalence are influenced by diversity, density, and abundance of suitable host species (and life stages) in the affected system (Miller et al. 2011; Venesky et al. 2014; Brunner et al. 2015; Muths et al. 2020). In the field of disease ecology, so-called dilution and amplification effects received a great deal of attention in recent years, whereby high host diversity dilutes disease risk and low diversity has amplifying effects (Ostfeld and Keesing 2012; Halliday et al. 2017). However, such relationships have been infrequently investigated in amphibian host–pathogen systems, and the sparse literature shows highly context-dependent interactions. For example, dilution effects were linked to specific tadpole feeding behavior, where the *Bd* zoospore abundance significantly decreased with an increase in filter-feeding Green Treefrog (*Hyla cinerea*) and Eastern Narrowmouth Toad (*Gastrophryne carolinensis*) tadpole diversity (Venesky et al. 2014). A more general relationship was shown in wild Californian amphibian communities of up to six hosts, where an increase in community richness decreased the number of competent host species for the trematode *R. ondatrae*, reducing the overall infection risk (Johnson et al. 2013). Interestingly, the opposite pattern has been observed for *Ranavirus* in the same system, where an increase in community richness was positively correlated with ranavirus prevalence (Tornabene et al. 2018).

The effects of community composition become relevant when considering human-mediated species translocations, as well as climate change-induced migration of amphibian species to previously unsuitable habitats. Predictive modeling showed that climate-driven amphibian migrations are expected to be more rapid and advancing farther north than most other vertebrates (Araújo et al. 2006; Lawler et al. 2009). Changes in community diversity can thus lead to the introduction of new pathogens, but also change the dynamics of the pathogens present, by an increase or decrease in competent host species. (Schock et al. 2010; Johnson et al. 2013). In addition, the majority (>80%) of amphibian

pathogens is capable of infecting multiple host species within a community, and hosts in natural communities are likely to be infected with multiple pathogens (Blaustein et al. 2011; Olori et al. 2018). In addition, pathogen diversity and abundance in amphibian communities can be increased or decreased by human-mediated habitat fragmentation (King et al. 2007, 2008; McKenzie 2007). Yet, less than half of the literature assessed more than one host species (44%) and only 9% reported more than one pathogen. Furthermore, most of these studies did not directly address potential combined effects of multiple pathogens, and simply stated their co-occurrence. Therefore, epidemiological studies, risk assessments, and management strategies should routinely consider potential effects of host community assemblage and pathogen diversity.

Host density can potentially affect disease dynamics, but only 3% of the literature has considered such effects. In the Sierra Nevada system, higher densities of Mountain Yellow-legged Frogs (*Rana muscosa*) were positively correlated with a higher number of environmental *Bd* zoospores and increased infection and mortality (Rachowitz and Briggs 2007; Briggs et al. 2010). Experimental trials with Northern Leopard Frog tadpoles showed that higher density had negative effects on the overall fitness (growth and development), and as a result, animals died faster and at a higher rate when exposed to *Ranavirus* (Echaubard et al. 2010). By contrast, ranavirus epizootics in Wood Frog populations in Connecticut were strongly influenced by tadpole developmental stage and water temperature, rather than by density (Hall et al. 2018). Similarly, in amphibian communities in Missouri, there was no correlation between *Bd* presence and community density or species density (Strauss and Smith 2013). Overall, these contradicting patterns show our limited knowledge of density effects on amphibian host–pathogen systems and underline the necessity for further research.

#### Environmental Factors

Environmental factors influence amphibian host–pathogen systems (Kiesecker 2002; Blaustein et al. 2003), further contributing to population declines (Daszak et al. 2003; Kiesecker et al. 2004; Lips et al. 2006). Over the last decade, environmental factors were considered in 41% of the research on amphibian pathogens. In particular, a third of these studies (32%) investigated landscape features such as slope and elevation, habitat characteristics such as vegetation type and canopy cover, and also natural disturbances such as wildfires and severe weather events, which can potentially affect pathogen dynamics in amphibian communities (Becker et al. 2012; Hossack et al. 2013; Muths et al. 2020). These alterations are mediated by changes in temperature, environmental humidity, and light intensity. At amphibian breeding sites in Maine, low canopy cover was positively associated with ranavirus presence and mortality (Gahl and Calhoun 2010), likely due to a higher mean water temperature. The opposite effects have been observed in endangered rain-forest frogs (*Litoria rheocola*) in Australia, where the reduction of canopy cover drastically decreased the *Bd* infection risk for the frogs, mediated by an increase in microhabitat mean temperature and related decrease in environmental humidity (Roznik et al. 2015).

In general, climate is considered a major factor driving amphibian disease dynamics (Rohr et al. 2013). In particular,

temperature received increased attention and is a factor in 37% of the literature. Temperature is believed to directly influence the dynamics of emerging pathogens such as *Bd* in wild amphibian populations (Kiesecker et al. 2001; Woodhams et al. 2003; Berger et al. 2004). Chytrid fungi and ranaviruses are extremely temperature dependent, as reflected in their spatiotemporal distribution patterns (Olson et al. 2013; Feldmeier et al. 2016; Hall et al. 2018; Youker-Smith et al. 2018). Chytrid fungi occur mostly in regions with low mean temperatures and *Bd*-related declines occur predominantly at higher altitudes (Ron 2005; Woodhams and Alford 2005), whereas *Bsal*-related declines are currently restricted to forested areas in central Europe (Feldmeier et al. 2016; Watts et al. 2019). Chytrid fungi show optimal growth at temperatures between 10°C and 20°C and decreased growth between 25°C and 28°C, with temperatures over 30°C killing the fungus (Piotrowski et al. 2004; Martel et al. 2013; Stevenson et al. 2013). Ranavirus epizootics often occur in mid- to late summer in temperate regions of the Northern Hemisphere when water temperatures surpass 25°C (Brunner et al. 2015). In fact, ranaviruses show optimal growth at temperatures of 28°C but do not replicate over 31°C (Ariel et al. 2009; Nazir et al. 2012). At temperatures below 12°C, infection loads are low and mortality is drastically reduced (Brand et al. 2016).

Environmental substrates and humidity strongly influence the environmental persistence of pathogens (Nazir et al. 2012; Kolby et al. 2015a) and have been investigated in 20% of the literature. In particular, the type of substrate (e.g., inorganic and organic) as well as humidity (e.g., precipitation, water connectivity, substrate moisture) affect the short-term viability of the pathogens (Johnson and Brunner 2014; Kolby et al. 2015b; Munro et al. 2016; Stoler et al. 2016). Therefore, it is unlikely that pathogens show long-term persistence in environmental substrates. Ranaviruses and chytrid fungi may rely therefore on reservoirs, such as sublethally infected individuals, for long-term persistence in amphibian communities (Gray et al. 2009; Blaustein et al. 2011; Bosch et al. 2015; Schmidt et al. 2017; Brannelly et al. 2018). In fact, the amphibian-reservoir hypothesis is strongly supported by reoccurring pathogen emergence in amphibian communities inhabiting semipermanent and ephemeral wetlands (Hunter et al. 2010; Hall et al. 2018; McMillan et al. 2020), as well as after environmental chemical disinfection (Bosch et al. 2015). Furthermore, *Bd* and ranaviruses can persist in overwintering individuals (Brunner et al. 2004; Narayan et al. 2014).

UVB radiation can also cause an increased vulnerability to infection by impairing growth and development and possibly inducing malformations (Blaustein et al. 2003; Searle et al. 2010). Ambient UVB radiation significantly decreased *Bd* prevalence in infected larval Common Toads (*Bufo bufo*) and European Midwife Toads (*Alytes obstetricans*, Ortiz-Santaliestra et al. 2011), but no such connection was found for ranaviruses (Gahl and Calhoun 2010). However, only 1% of the literature assessing environmental factors associated with amphibian pathogens considered UVB radiation as a potential explanatory variable for epidemiological patterns. Similarly, as little as 4% of the literature has assessed water parameters such as salinity, conductivity, pH, or dissolved oxygen. Elevated salinity significantly reduced pathogen transmission and infection loads and increased survival rates among *Bd*-



infected amphibians in Australia (Stockwell et al. 2015a,b; Clulow et al. 2018). The opposite pattern was observed in a Wood Frog–ranavirus system, whereby an increase in chloride concentrations slightly increased the chances for a mortality event (Hall et al. 2018). Other factors such as pH and conductivity had no significant effects on amphibian host–pathogen systems (e.g., *Ranavirus* in Wood Frogs in Connecticut, Hall et al. 2018; *Bd* in ranids in Missouri, Strauss and Smith 2013). However, in a study across the continental United States, *Bd* loads of swabbed frogs were lower at sites with elevated pH levels (Battaglin et al. 2016).

Overall, there is very little support for general effects of natural water characteristics such as pH, conductivity, and salinity on pathogen dynamics. The literature clearly shows that interactions are highly context dependent. Yet, water characteristics can indirectly influence pathogen dynamics through alteration of the microbiome involved in *Bd* tolerance (Varela et al. 2018) or by directly affecting hosts' overall body condition and related resilience and immunity, making additional research on these relationships necessary.

#### Anthropogenic Factors

There is substantial evidence for a direct correlation between anthropogenic factors and epidemiological patterns in amphibian populations (e.g., Schotthoefler et al. 2011; Koprivnikar and Redfern 2012; Tornabene et al. 2018). Sixteen percent of the literature investigated such relationships and found that industrial and infrastructural development has strong effects on host–pathogen dynamics by altering habitats and host community structures (St-Amour et al. 2008; Belasen et al. 2018; Davis et al. 2019).

Highly virulent pathogen lineages from commercial trade and breeding facilities (Farrer et al. 2011; Claytor et al. 2017; Vilaça et al. 2019) and human-mediated species translocation (e.g., use as bait) accompanied by the introduction of new pathogens represents a severe threat to naïve populations, and can lead to fast and devastating mass mortality events (Picco and Collins 2008; Price et al. 2014; Earl et al. 2016). Research showed that commercial frog farms facilitated strain recombination events (*Bd*, Schloegel et al. 2012; Greenspan et al. 2018; Ranaviruses, Claytor et al. 2017; Vilaça et al. 2019) and can release ecologically relevant amounts of infectious agents in the adjoining ecosystem by discharge of untreated wastewater (e.g., *Bd* zoospores, Ribeiro et al. 2019). Similar mechanisms of pathogen spread were suggested for the amphibian–ranavirus system (Saucedo et al. 2019). In addition, ranavirus isolates collected from epizootics in commercial frog-breeding facilities (Majji et al. 2006; Miller et al. 2007) showed significantly increased virulence in a variety of different amphibian species in comparison with wild-type isolates (Hoverman et al. 2010, 2011; Peace et al. 2019).

In addition to breeding facilities, the associated trade of the animals contributes significantly to the global spread of amphibian pathogens such as *Bd* and ranaviruses (Picco and Collins 2008; Kolby et al. 2014). A study investigating the presence of common pathogens in commercially traded amphibians at the Hong Kong International Airport revealed that about 1 in 10 individuals was infected with *Bd*, and more than half tested positive for ranaviruses (Kolby et al. 2014). High densities during import and export can amplify virulence and transmission among individuals (Pavlin et al. 2009). For example, Tiger Salamanders in the North

American fishing bait trade were infected with highly virulent strains of the *Ranavirus* species ATV (Jancovich et al. 2005; Picco and Collins 2008; Epstein and Storfer 2016). Furthermore, invasive Bullfrogs (*Lithobates catesbeianus*, or *Rana catesbeiana*) can act as reservoir hosts and can contribute to the emergence and spread of common amphibian pathogens *Bd* (Garner et al. 2006; O'Hanlon et al. 2018) and ranaviruses (Schloegel et al. 2009).

Pollution from fertilizer, herbicides, and pesticides may indirectly affect pathogen dynamics in aquatic communities by eutrophication and subsequent increase in host density and prevalence (Johnson et al. 2007). Furthermore, many of the commonly used herbicides and pesticides negatively affected the body condition of amphibians (Egea-Serrano et al. 2012), and therefore can influence disease dynamics in host communities. For example, Northern Leopard Frogs exposed to environmentally relevant doses of the insecticide carbaryl harbored significantly higher trematode loads than unexposed individuals (Pochini and Hoverman 2017a). Interestingly, the authors did not observe any direct effects on infection rates. Another study used larval Wood Frogs to investigate the effects of the insecticides carbaryl and thiamethoxam on ranavirus transmission and susceptibility (Pochini and Hoverman 2017b). The animals experienced increased mortality; however, the effects on pathogen transmission and prevalence were negligible. In contrast, five North American anuran species exposed to mixtures of commonly used insecticides or herbicides did not experience increased mortality rates, but showed alterations of *Bd* loads (Buck et al. 2015). Another study conducted across the United States showed a positive correlation of *Bd* prevalence in amphibian hosts and total fungicide concentrations in the environment (Battaglin et al. 2016). Furthermore, *Bd* zoospore loads in ranid and hylid frogs increased with dissolved organic carbon, nitrogen, and phosphorus (Battaglin et al. 2016). Although their impacts on the overall health of amphibians are known, certain pesticides have been used in disease control and outbreak management. *Bd* was eliminated at several wetlands in Spain through a combination of artificial draining, environmental chemical disinfection, and ex situ treatment of individuals with fungicides (Bosch et al. 2015).

A major threat to amphibian populations worldwide, anthropogenic habitat fragmentation can also control host–pathogen interactions by modifying host community structure and density (Beasley et al. 2005; King et al. 2007; Greer and Collins 2008; St-Amour et al. 2008; Becker et al. 2016). For example, deforestation can directly influence amphibian community diversity, richness, and density by alteration of microhabitat climate and species interactions, in turn variously increasing or decreasing the infection risk for *Bd* (Becker et al. 2016). Increased microhabitat temperatures can suppress the growth of the fungus and negatively affect its environmental persistence (Raffel et al. 2010; Becker et al. 2012). Similarly, spatial and temporal variation of ranavirus transmission and prevalence was indirectly influenced by land use pattern in Tiger Salamanders (Greer and Collins 2008). An increase in ranavirus infection was correlated with the increase in contact rates between hosts, induced by anthropogenic modifications of the wetland structure (Greer and Collins 2008). Amphibian populations inhabiting fragmented habitats in urban settings in the UK also showed an increased ranavirus prevalence influenced by

various anthropogenic factors (e.g., level of urbanization, use of chemicals, invasive species; North et al. 2015), and a direct relationship between industrial and infrastructural activity and ranavirus prevalence was observed in Green Frogs (*Lithobates clamitans*, or *Rana clamitans*) in Canada, yet not with *Bd* (St-Amour et al. 2008). A large study among amphibian populations across the United States revealed a similar relationship (Battaglin et al. 2016).

Overall, anthropogenic factors play a significant role in amphibian disease ecology by directly and indirectly altering host–pathogen dynamics. This underlines the importance of comprehensive ecological assessments and subsequent implementation of management and mitigation strategies when conducting infrastructural and industrial development. Furthermore, biosafety measures, such as disinfection protocols at recreational and commercial facilities (e.g., marinas and harbors), should be implemented to limit pathogen spread through contaminated equipment. Finally, stricter regulations need to be imposed on commercially bred and traded amphibians to prevent the further spread of pathogens and their establishment into wild populations.

#### PERSPECTIVES AND CONCLUSIONS

Emerging infectious diseases are a serious threat to global amphibian diversity as well as to the economy (e.g., aquaculture: Gilbert et al. 2012; Waltzek et al. 2014; Saucedo et al. 2019). Despite an extensive suite of intrinsic (host and pathogen) and environmental (biotic and abiotic) factors investigated in the amphibian disease literature over the last 10 yr, the specific factors driving epidemiological patterns and processes remain unknown for the majority of amphibian pathogens. This can be attributed to the complexity of host–pathogen systems, but also to the lack of standardization in approaches. Nonetheless, factors such as temperature and humidity are directly associated with epidemiological patterns of amphibian diseases (Bustamante et al. 2010; Brunner et al. 2015; Roznik et al. 2015), and landscape features such as slope, elevation (Kriger and Hero 2007; Gahl and Cahoun 2008), and vegetation (canopy cover; Becker et al. 2012) drive differences in microclimate and microhabitat conditions, in turn influencing pathogen dynamics in host communities. These relationships become of particular importance in a climate-change context, when considering the potentially rapid and extensive northward migration of amphibian species (and their pathogens) into naïve amphibian communities (Araújo et al. 2006; Lawler et al. 2009; Schock et al. 2010). There is also accumulated evidence that the variation in virulence among pathogen species and strains and the inter- and intraspecific variations in infection susceptibility are key factors for emergence and transmission of most amphibian diseases (Hoverman et al. 2011; Ohmer et al. 2013; Echaubard et al. 2016; Grogan et al. 2018). Despite this, many studies fail to identify their pathogen(s) of study at the molecular level, and do not consider the full host community but rather focus on selected host species.

Anthropogenic pressures such as industrial/infrastructural development have been shown to influence pathogen dynamics, in particular through habitat fragmentation (Becker and Zamudio 2011; Becker et al. 2016), and may thus lead to epizootics. Interestingly, inorganic chemicals (e.g., pesticides and herbicides) seem to only have negligible effects on chytrid

dynamics (Buck et al. 2015), but show significant effects on other common amphibian pathogens such as ranaviruses (Pochini and Hoverman 2017a) and helminths (Pochini and Hoverman 2017b). Therefore, inorganic chemicals should more often be taken into consideration when conducting studies on amphibian populations in anthropogenically disturbed environments (e.g., industrial activity; St-Amour et al. 2008). Furthermore, most of the aforementioned factors influence epidemiological patterns on a local scale, but fail to fully explain how pathogens spread across the landscape and globally. At a local scale, the spread of infectious agents is likely mediated by human activities (e.g., *Ranavirus* on contaminated equipment, Casais et al. 2019; and fishing bait, Picco et al. 2010; Wimsatt et al. 2014), but waterfowl can facilitate pathogen translocation in more complex landscapes (e.g., *Bd*; Garmyn et al. 2012; Burrowes and De la Riva 2017; Hanlon et al. 2017). At a continental scale, amphibian pathogens are regularly spread through commercial activities (pet and food trade; Kolby et al. 2014; Wombwell et al. 2016; O’Hanlon et al. 2018; Yuan et al. 2018), and this needs to be rigorously prevented.

Overall, the complex and context-dependent interactions of amphibian host–pathogen systems with ecological drivers are often difficult to disentangle, and knowledge gaps remain. Decision analysis and quantitative modeling can help to develop, evaluate, and compare disease management strategies for amphibian communities threatened by disease (Grant et al. 2017; Smalling et al. 2019). We recommend that future studies of amphibian disease ecology routinely include (1) characterization of the host community assemblage, (2) life stage and species-specific effects therein, (3) the identification of the pathogen(s) at a molecular level, and (4) an assessment of environmental factors potentially contributing to pathogen emergence. In addition, experimental trials to determine the specific role of different hosts (e.g., reservoir host) as well as to test the persistence of pathogens in the ecosystem should be considered. Such standardized and comprehensive approaches are ultimately required to allow the identification of key factors driving epidemiological patterns and advance the successful development and implementation of proactive disease management as well as conservation strategies, rather than solely reactive outbreak management.

**Acknowledgments.**—We thank David Green, the Redpath Museum and the Canadian Herpetological Society for organizing the symposium “Global Amphibian Population Declines—30 yr of Progress in Confronting a Complex Problem” from which this publication stems.

#### SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-19-00064.S1>.

#### LITERATURE CITED

- Altizer, S., R.S. Ostfeld, P.T. Johnson, S. Kutz, and C.D. Harvell. 2013. Climate change and infectious diseases: From evidence to a predictive framework. *Science* 341:514–519.
- An, D., and B. Waldman. 2016. Enhanced call effort in Japanese Tree Frogs infected by amphibian chytrid fungus. *Biology Letters* 12:20160018.
- Andino, F.D.J., G. Chen, Z. Li, L. Grayfer, and J. Robert. 2012. Susceptibility of *Xenopus laevis* tadpoles to infection by the *Ranavirus*

- Frog virus 3 correlates with a reduced and delayed innate immune response in comparison with adult frogs. *Virology* 432:435–443.
- Araújo, M.B., W. Thuiller, and R.G. Pearson. 2006. Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography* 33:1712–1728.
- Ariel, E., J. Kielgast, H.E. Svart, K. Larsen, H. Tapiovaara, B.B. Jensen, and R. Holopainen. 2009. Ranavirus in wild edible frogs *Pelophylax* kl. *esculentus* in Denmark. *Diseases of Aquatic Organisms* 85:7–14.
- Ault, K.K., J.E. Johnson, H.C. Pinkart, and R.S. Wagner. 2012. Genetic comparison of water molds from embryos of amphibians *Rana cascadae*, *Bufo boreas* and *Pseudacris regilla*. *Diseases of Aquatic Organisms* 99:127–137.
- Bacigalupe, L.D., C. Soto-Azat, C. García-Vera, I. Barría-Oyarzo, and E.L. Rezende. 2017. Effects of amphibian phylogeny, climate and human impact on the occurrence of the amphibian-killing chytrid fungus. *Global Change Biology* 23:3543–3553.
- Bataille, A., J.J. Fong, M. Cha, G.O. Wogan, H.J. Baek, H. Lee, M.S. Min, and B. Waldman. 2013. Genetic evidence for a high diversity and wide distribution of endemic strains of the pathogenic chytrid fungus *Batrachochytrium dendrobatidis* in wild Asian amphibians. *Molecular Ecology* 22:4196–4209.
- Battaglin, W.A., K.L. Smalling, C. Anderson, D. Calhoun, T. Chestnut, and E. Muths. 2016. Potential interactions among disease, pesticides, water quality and adjacent land cover in amphibian habitats in the United States. *Science of the Total Environment* 566:320–332.
- Beasley, V.R., S.A. Faeh, B. Wikoff, C. Staehle, J. Eisold, D. Nichols, R. Cole, A.M. Schotthoefer, M. Greenwell, and L.E. Brown. 2005. Risk factors and declines in Northern Cricket Frogs (*Acris crepitans*). Pp. 75–86 in *Amphibian Declines: The Conservation Status of United States Species* (M.J. Lannoo, ed.). University of California Press, USA.
- Becker, C.G., and K.R. Zamudio. 2011. Tropical amphibian populations experience higher disease risk in natural habitats. *Proceedings of the National Academy of Sciences of the United States of America* 108:9893–9898.
- Becker, C.G., D. Rodriguez, A.V. Longo, A.L. Talaba, and K.R. Zamudio. 2012. Disease risk in temperate amphibian populations is higher at closed-canopy sites. *PloS One* 7:e48205.
- Becker, C.G., D. Rodriguez, L.F. Toledo, A.V. Longo, C. Lambertini, D.T. Corrêa, D.S. Leite, C.F. Haddad, and K.R. Zamudio. 2014. Partitioning the net effect of host diversity on an emerging amphibian pathogen. *Proceedings of the Royal Society B: Biological Sciences* 281:20141796.
- Becker, C.G., D. Rodriguez, A.V. Longo, L.F. Toledo, C. Lambertini, D.S. Leite, C.F. Haddad, and K.R. Zamudio. 2016. Deforestation, host community structure, and amphibian disease risk. *Basic and Applied Ecology* 17:72–80.
- Belasen, A.M., M.C. Bletz, D.D.S. Leite, L.F. Toledo, and T.Y. James. 2018. Long-term habitat fragmentation is associated with reduced MHC IIB diversity and increased infections in amphibian hosts. *Frontiers in Ecology and Evolution* 6:236.
- Berger, L., R. Speare, P. Daszak, H.B. Hines. 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *Proceedings of the National Academy of Sciences of the United States of America* 95:9031–9036.
- Berger, L., R. Speare, H.B. Hines, M. Mahony. 2004. Effect of season and temperature on mortality in amphibians due to chytridiomycosis. *Australian Veterinary Journal* 82:434–439.
- Berger, L., G. Marantelli, L.F. Skerratt, and R. Speare. 2005. Virulence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* varies with the strain. *Diseases of Aquatic Organisms* 68:47–50.
- Berger, L., A.A. Roberts, J. Voyles, J.E. Longcore, K.A. Murray, and L.F. Skerratt. 2016. History and recent progress on chytridiomycosis in amphibians. *Fungal Ecology* 19:89–99.
- Bienentrou, J.F. 2019. Epidemiology of Ranaviruses in Amphibian Populations in the Boreal Forest of Northwestern Canada. Ph.D. dissertation, Laurentian University, Canada.
- Blaustein, A.R., J.M. Romansic, J.M. Kiesecker, and A.C. Hatch. 2003. Ultraviolet radiation, toxic chemicals and amphibian population declines. *Diversity and Distributions* 9:123–140.
- Blaustein, A.R., B.A. Han, R.A. Relyea, P.T. Johnson, J.C. Buck, S.S. Gervasi, and L.B. Kats. 2011. The complexity of amphibian population declines: Understanding the role of cofactors in driving amphibian losses. *Annals of the New York Academy of Sciences* 1223:108–119.
- Bosch, J., E. Sanchez-Tomé, A. Fernández-Loras, J.A. Oliver, M.C. Fisher, and T.W. Garner. 2015. Successful elimination of a lethal wildlife infectious disease in nature. *Biology Letters* 11:20150874.
- Bradley, P.W., S.S. Gervasi, J. Hua, R.D. Cothran, R.A. Relyea, D.H. Olson, and A.R. Blaustein. 2015. Differences in sensitivity to the fungal pathogen *Batrachochytrium dendrobatidis* among amphibian populations. *Conservation Biology* 29:1347–1356.
- Brand, M.D., R.D. Hill, R. Brenes, J.C. Chaney, R.P. Wilkes, L. Grayfer, D.L. Miller, and M.J. Gray. 2016. Water temperature affects susceptibility to *Ranavirus*. *EcoHealth* 13:350–359.
- Brannelly, L.A., R.J. Webb, D.A. Hunter, N. Clemann, K. Howard, L.F. Skerratt, L. Berger, and B.C. Scheele. 2018. Non-declining amphibians can be important reservoir hosts for amphibian chytrid fungus. *Animal Conservation* 21:91–101.
- Brenes, R., M.J. Gray, T.B. Waltzek, R.P. Wilkes, and D.L. Miller. 2014. Transmission of *Ranavirus* between ectothermic vertebrate hosts. *PloS One* 9:e92476.
- Briggs, C.J., R.A. Knapp, and V.T. Vredenburg. 2010. Enzootic and epizootic dynamics of the chytrid fungal pathogen of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 107:9695–9700.
- Brunner, J.L., and J.P. Collins. 2009. Testing assumptions of the trade-off theory of the evolution of parasite virulence. *Evolutionary Ecology Research* 11:1169–1188.
- Brunner, J.L., D.M. Schock, E.W. Davidson, and J.P. Collins. 2004. Intraspecific reservoirs: Complex life history and the persistence of a lethal *Ranavirus*. *Ecology* 85:560–566.
- Brunner, J.L., D.M. Schock, and J.P. Collins. 2007. Transmission dynamics of the amphibian *Ranavirus Ambystoma tigrinum virus*. *Diseases of Aquatic Organisms* 77:87–95.
- Brunner, J.L., A. Storfer, M.J. Gray, and J.T. Hoverman. 2015. *Ranavirus* ecology and evolution: From epidemiology to extinction. Pp. 71–104 in *Ranaviruses: Lethal Pathogens of Ectothermic Vertebrates* (M.J. Gray and V.G. Chinchar, eds.). Springer, USA.
- Buck, J.C., J. Hua, W.R. Brogan, III, T.D. Dang, J. Urbina, R.J. Bendis, A.B. Stoler, A.R. Blaustein, and R.A. Relyea. 2015. Effects of pesticide mixtures on host–pathogen dynamics of the amphibian chytrid fungus. *PloS One* 10:e0132832.
- Burrowes, P.A., and I. De la Riva. 2017. Detection of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in museum specimens of Andean aquatic birds: Implications for pathogen dispersal. *Journal of Wildlife Diseases* 53:349–355.
- Bustamante, H.M., L.J. Livo, and C. Carey. 2010. Effects of temperature and hydric environment on survival of the Panamanian Golden Frog infected with a pathogenic chytrid fungus. *Integrative Zoology* 5:143–153.
- Casais, R., A.R. Larrinaga, K.P. Dalton, P.D. Lapido, I. Márquez, E. Bécáres, E.D. Carter, M.J. Gray, D.L. Miller, and A. Balseiro. 2019. Water sports could contribute to the translocation of ranaviruses. *Scientific Reports* 9:2340.
- Chestnut, T., C. Anderson, R. Popa, A.R. Blaustein, M. Voytek, D.H. Olson, and J. Kirshstein. 2014. Heterogeneous occupancy and density estimates of the pathogenic fungus *Batrachochytrium dendrobatidis* in waters of North America. *PloS One* 9:e106790.
- Chinchar, V.G., P. Hick, I.A. Ince, Q.Y. Zhang. 2017. ICTV virus taxonomy profile: Iridoviridae. *Journal of General Virology* 98:890–891.
- Chinchar, V.G., P. Hick, J. Jancovich, K. Subramaniam, T. Waltzek, R. Whittington, and T. Williams. 2018. Create eight new species, remove three existing species in the family Iridoviridae. Available at ICTV [https://talk.ictvonline.org/ictv/proposals/2018.007D.A.v1.Iridoviridae\\_8sp3sprem.zip](https://talk.ictvonline.org/ictv/proposals/2018.007D.A.v1.Iridoviridae_8sp3sprem.zip). Accessed on 5 March 2020.
- Claytor, S.C., K. Subramaniam, N. Landrau-Giovannetti, V.G. Chinchar, M.J. Gray, D.L. Miller, C. Mavian, M. Salemi, S. Wisely, and T.B. Waltzek. 2017. Ranavirus phylogenomics: Signatures of recombination and inversions among bullfrog ranaculture isolates. *Virology* 511:330–343. DOI: <http://dx.doi.org/10.1016/j.virol.2017.07.028>
- Clulow, S., J. Gould, H. James, M. Stockwell, J. Clulow, and M. Mahony. 2018. Elevated salinity blocks pathogen transmission and improves host survival from the global amphibian chytrid pandemic: Implications for translocations. *Journal of Applied Ecology* 55:830–840.
- Cohen, J.M., D.J. Civitello, M.D. Venesky, T.A. McMahon, and J.R. Rohr. 2019. An interaction between climate change and infectious disease drove widespread amphibian declines. *Global Change Biology* 25:927–937.
- Cunningham, A.A., A.D. Hyatt, P. Russell, and P.M. Bennett. 2007. Emerging epidemic diseases of frogs in Britain are dependent on the source of ranavirus agent and the route of exposure. *Epidemiology & Infection* 135:1200–1212.
- Cunningham, A.A., P. Daszak, and J.L. Wood. 2017. One Health, emerging

- infectious diseases and wildlife: Two decades of progress? *Philosophical Transactions of the Royal Society B: Biological Sciences* 372:20160167.
- Daly, E.W., and P.T. Johnson. 2011. Beyond immunity: Quantifying the effects of host anti-parasite behavior on parasite transmission. *Oecologia* 165:1043–1050.
- Daszak, P., A.A. Cunningham, and A.D. Hyatt. 2003. Infectious disease and amphibian population declines. *Diversity and Distributions* 9:141–150.
- Davis, D.R., J.K. Farkas, T.R. Kruesselbrink, J.L. Watters, E.D. Ellsworth, J.L. Kerby, and C.D. Siler. 2019. Prevalence and distribution of *Ranavirus* in amphibians from southeastern Oklahoma, USA. *Herpetological Conservation and Biology* 14:360–369.
- Dobson, A., and J. Foufopoulos. 2001. Emerging infectious pathogens of wildlife. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 356:1001–1012.
- Duffus, A.L., T.B. Waltzek, A.C. Stöhr, M.C. Allender, M. Gotesman, R.J. Whittington, P. Hick, M.K. Hines, and R.E. Marschang. 2015. Distribution and host range of ranaviruses. Pp. 9–57 in *Ranaviruses: Lethal Pathogens of Ectothermic Vertebrates* (M.J. Gray and V.G. Chinchar, eds.). Springer, USA.
- Earl, J.E., and M.J. Gray. 2014. Introduction of *Ranavirus* to isolated Wood Frog populations could cause local extinction. *EcoHealth* 11:581–592.
- Earl, J.E., J.C. Chaney, W.B. Sutton, M.J. Gray. 2016. *Ranavirus* could facilitate local extinction of rare amphibian species. *Oecologia* 182:611–623.
- Echaubard, P., K. Little, B. Pauli, and D. Lesbarrères. 2010. Context-dependent effects of ranaviral infection on Northern Leopard Frog life history traits. *PLoS One* 5:e13723.
- Echaubard, P., J. Leduc, B. Pauli, V.G. Chinchar, J. Robert, and D. Lesbarrères. 2014. Environmental dependency of amphibian–ranavirus genotypic interactions: Evolutionary perspectives on infectious diseases. *Evolutionary Applications* 7:723–733.
- Echaubard, P., B.D. Pauli, V.L. Trudeau, and D. Lesbarrères. 2016. *Ranavirus* infection in Northern Leopard Frogs: The timing and number of exposures matter. *Journal of Zoology* 298:30–36.
- Egea-Serrano, A., R.A. Relyea, M. Tejedo, and M. Torralva. 2012. Understanding of the impact of chemicals on amphibians: A meta-analytic review. *Ecology and Evolution* 2:1382–1397.
- Epstein, B., and A. Storfer. 2016. Comparative genomics of an emerging amphibian virus. *G3: Genes, Genomes, Genetics* 6:15–27.
- Farrer, R.A., L.A. Weinert, J. Biellby, L. Anderson. 2011. Multiple emergences of genetically diverse amphibian-infecting chytrids include a globalized hypervirulent recombinant lineage. *Proceedings of the National Academy of Sciences of the United States of America* 108:18732–18736.
- Feldmeier, S., L. Schefczyk, N. Wagner, G. Heinemann, M. Veith, and S. Loetters. 2016. Exploring the distribution of the spreading lethal salamander chytrid fungus in its invasive range in Europe—A macro-ecological approach. *PLoS One* 11:e0165682.
- Fellers, G.M., D.E. Green, and J.E. Longcore. 2001. Oral chytridiomycosis in the Mountain Yellow-legged Frog (*Rana muscosa*). *Copeia* 2001:945–953.
- Fernández-Benítez, M.J., M.E. Ortiz-Santaliestra, M. Lizana, and J. Diéguez-Urbeondo. 2011. Differences in susceptibility to *Saprolegnia* infections among embryonic stages of two anuran species. *Oecologia* 165:819–826.
- Fisher, M.C., T.W. Garner, and S.F. Walker. 2009. Global emergence of *Batrachochytrium dendrobatidis* and amphibian chytridiomycosis in space, time, and host. *Annual Review of Microbiology* 63:291–310.
- Gahl, M.K., and A.J. Calhoun. 2008. Landscape setting and risk of *Ranavirus* mortality events. *Biological Conservation* 141:2679–2689.
- Gahl, M.K., and A.J.K. Calhoun. 2010. The role of multiple stressors in *Ranavirus*-caused amphibian mortalities in Acadia National Park wetlands. *Canadian Journal of Zoology* 88:108–121.
- Gahl, M.K., B.D. Pauli, and J.E. Houlahan. 2011. Effects of chytrid fungus and a glyphosate-based herbicide on survival and growth of Wood Frogs (*Lithobates sylvaticus*). *Ecological Applications* 21:2521–2529.
- García-Rodríguez, A., G. Chaves, C. Benavides-Varela, and R. Puschendorf. 2012. Where are the survivors? Tracking relictual populations of endangered frogs in Costa Rica. *Diversity and Distributions* 18:204–212.
- Garmyn, A., P. Van Rooij, F. Pasmans, T. Hellebuyck, W. Van Den Broeck, F. Haesebrouck, and A. Martel. 2012. Waterfowl: Potential environmental reservoirs of the chytrid fungus *Batrachochytrium dendrobatidis*. *PLoS One* 7:e0035038.
- Garner, T.W., M.W. Perkins, P. Govindarajulu, D. Seglie, S. Walker, A.A. Cunningham, and M.C. Fisher. 2006. The emerging amphibian pathogen *Batrachochytrium dendrobatidis* globally infects introduced populations of the North American Bullfrog, *Rana catesbeiana*. *Biology Letters* 2:455–459.
- Gilbert, M., D. Bickford, L. Clark, S. Robertson. 2012. Amphibian pathogens in Southeast Asian frog trade. *EcoHealth* 9:386–398.
- González-Maya, J.F., J.L. Belant, S.A. Wyatt, A. Fischer. 2013. Renewing hope: The rediscovery of *Atelopus varius* in Costa Rica. *Amphibia-Reptilia* 34:573–578.
- Gould, J., J. Valdez, M. Stockwell, S. Clulow, and M. Mahony. 2019. Mosquitoes as a potential vector for the transmission of the amphibian chytrid fungus. *Zoology and Ecology* 29:38–44.
- Grant, E.H.C., D.A. Miller, B.R. Schmidt, P.T. Johnson. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports* 6:1–9.
- Grant, E.H.C., E. Muths, R.A. Katz, M.C. Harris. 2017. Using decision analysis to support proactive management of emerging infectious wildlife diseases. *Frontiers in Ecology and the Environment* 15:214–221.
- Gray, M.J., and V.G. Chinchar. 2015. Introduction: History and future of ranaviruses. Pp. 1–7 in *Ranaviruses: Lethal Pathogens of Ectothermic Vertebrates* (M.J. Gray and V.G. Chinchar, eds.). Springer, USA.
- Gray, M.J., D.L. Miller, and J.T. Hoverman. 2009. Ecology and pathology of amphibian ranaviruses. *Diseases of Aquatic Organisms* 87:243–266.
- Gray, M.J., J.P. Lewis, P. Nanjappa, M.R. Christman. 2015. *Batrachochytrium salamandrivorans*: The North American response and a call for action. *PLoS Pathogens* 11:e1005251.
- Graifer, L., F.D.J. Andino, and J. Robert. 2014. The amphibian (*Xenopus laevis*) Type I interferon response to frog virus 3: New insight into ranavirus pathogenicity. *Journal of Virology* 88:5766–5777.
- Graifer, L., E.S. Edholm, F.D.J. Andino, V.G. Chinchar, and J. Robert. 2015a. *Ranavirus* host immunity and immune evasion. Pp. 141–170 in *Ranaviruses: Lethal Pathogens of Ectothermic Vertebrates* (M.J. Gray and V.G. Chinchar, eds.). Springer, USA.
- Graifer, L., F.D.J. Andino, and J. Robert. 2015b. Prominent amphibian (*Xenopus laevis*) tadpole Type III interferon response to the frog virus 3 *Ranavirus*. *Journal of Virology* 89:5072–5082.
- Greenspan, S.E., C. Lambertini, T. Carvalho, T.Y. James, L.F. Toledo, C.F.B. Haddad, and C.G. Becker. 2018. Hybrids of amphibian chytrid show high virulence in native hosts. *Scientific Reports* 8:9600.
- Greer, A.L., and J.P. Collins. 2008. Habitat fragmentation as a result of biotic and abiotic factors controls pathogen transmission throughout a host population. *Journal of Animal Ecology* 77:364–369.
- Grogan, L.F., J. Robert, L. Berger, L.F. Skerratt, B.C. Scheele, J.G. Castley, D.A. Newell, and H.I. McCallum. 2018. Review of the amphibian immune response to chytridiomycosis, and future directions. *Frontiers in Immunology* 9:2536.
- Groner, M.L., and R.A. Relyea. 2015. Predators reduce *Batrachochytrium dendrobatidis* infection loads in their prey. *Freshwater Biology* 60:1699–1704.
- Haislip, N.A., M.J. Gray, J.T. Hoverman, and D.L. Miller. 2011. Development and disease: How susceptibility to an emerging pathogen changes through anuran development. *PLoS One* 6:e22307.
- Haislip, N.A., J.T. Hoverman, D.L. Miller, and M.J. Gray. 2012. Natural stressors and disease risk: Does the threat of predation increase amphibian susceptibility to *Ranavirus*? *Canadian Journal of Zoology* 90:893–902.
- Hall, E.M., C.S. Goldberg, J.L. Brunner, and E.J. Crespi. 2018. Seasonal dynamics and potential drivers of ranavirus epidemics in Wood Frog populations. *Oecologia* 188:1253–1262.
- Halliday, F.W., R.W. Heckman, P.A. Wilfahrt, and C.E. Mitchell. 2017. A multivariate test of disease risk reveals conditions leading to disease amplification. *Proceedings of the Royal Society B: Biological Sciences* 284:20171340.
- Han, B.A., P.W. Bradley, and A.R. Blaustein. 2008. Ancient behaviors of larval amphibians in response to an emerging fungal pathogen, *Batrachochytrium dendrobatidis*. *Behavioral Ecology and Sociobiology* 63:241–250.
- Han, B.A., C.L. Searle, and A.R. Blaustein. 2011. Effects of an infectious fungus, *Batrachochytrium dendrobatidis*, on amphibian predator–prey interactions. *PLoS One* 6:e0016675.
- Han, B.A., J.L. Kerby, C.L. Searle, A. Storfer, and A.R. Blaustein. 2015. Host species composition influences infection severity among amphibians in the absence of spillover transmission. *Ecology and Evolution* 5:1432–1439.
- Hanlon, S.M., and M.J. Parris. 2014. The interactive effects of chytrid

- fungus, pesticides, and exposure timing on Gray Treefrog (*Hyla versicolor*) larvae. *Environmental Toxicology and Chemistry* 33:216–222.
- Hanlon, S.M., J.R. Henson, and J.L. Kerby. 2017. Detection of amphibian chytrid fungus on waterfowl integument in natural settings. *Diseases of Aquatic Organisms* 126:71–74.
- Harp, E.M., and J.W. Petranka. 2006. *Ranavirus* in wood frogs (*Rana sylvatica*): Potential sources of transmission within and between ponds. *Journal of Wildlife Diseases* 42:307–318.
- Hossack, B.R., W.H. Lowe, J.L. Ware, and P.S. Corn. 2013. Disease in a dynamic landscape: Host behavior and wildfire reduce amphibian chytrid infection. *Biological Conservation* 157:293–299.
- Hoverman, J.T., M.J. Gray, and D.L. Miller. 2010. Anuran susceptibilities to ranaviruses: Role of species identity, exposure route, and a novel virus isolate. *Diseases of Aquatic Organisms* 89:97–107.
- Hoverman, J.T., M.J. Gray, N.A. Haislip, and D.L. Miller. 2011. Phylogeny, life history, and ecology contribute to differences in amphibian susceptibility to ranaviruses. *EcoHealth* 8:301–319.
- Hunter, D.A., R. Speare, G. Marantelli, D. Mendez, R. Pietsch, and W. Osborne. 2010. Presence of the amphibian chytrid fungus *Batrachochytrium dendrobatidis* in threatened Corroboree Frog populations in the Australian Alps. *Diseases of Aquatic Organisms* 92:209–216.
- Jancovich, J.K., E.W. Davidson, N. Parameswaran, J. Mao, V.G. Chinchar, J.P. Collins, B.L. Jacobs, and A. Storfer. 2005. Evidence for emergence of an amphibian iridoviral disease because of human-enhanced spread. *Molecular Ecology* 14:213–224.
- Johnson, A.F., and J.L. Brunner. 2014. Persistence of an amphibian ranavirus in aquatic communities. *Diseases of Aquatic Organisms* 111:129–138.
- Johnson, P.T., and V.J. McKenzie. 2009. Effects of environmental change on helminth infections in amphibians: Exploring the emergence of *Ribeiroia* and *Echinostoma* infections in North America. Pp. 249–280 in *The Biology of Echinostomes* (J.Y. Chai, ed.). Springer, USA.
- Johnson, P.T., J.M. Chase, K.L. Dosch, R.B. Hartson, J.A. Gross, D.J. Larson, D.R. Sutherland, and S.R. Carpenter. 2007. Aquatic eutrophication promotes pathogenic infection in amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 104:15781–15786.
- Johnson, P.T., V.J. McKenzie, A.C. Peterson, J.L. Kerby, J. Brown, A.R. Blaustein, and T. Jackson. 2011. Regional decline of an iconic amphibian associated with elevation, land-use change, and invasive species. *Conservation Biology* 25:556–566.
- Johnson, P.T., D.L. Preston, J.T. Hoverman, and K.L. Richgels. 2013. Biodiversity decreases disease through predictable changes in host community competence. *Nature* 494:230–233.
- Johnson, P.T., D.M. Calhoun, T. Riepe, T. McDevitt-Galles, and J. Koprivnikar. 2019. Community disassembly and disease: Realistic—but not randomized—biodiversity losses enhance parasite transmission. *Proceedings of the Royal Society B: Biological Sciences* 286:20190260.
- Karling, J.S. (ed.). 1977. *Chytridiomycetorum Iconographia: An Illustrated and Brief Descriptive Guide to the Chytridiomycetous Genera with a Supplement of the Hyphochytriomycetes*. Cramer, USA.
- Kärveemo, S., S. Meurling, D. Berger, J. Höglund, and A. Laurila. 2018. Effects of host species and environmental factors on the prevalence of *Batrachochytrium dendrobatidis* in northern Europe. *PLoS One* 13:e0199852.
- Kerby, J.L., A.J. Hart, and A. Storfer. 2011. Combined effects of virus, pesticide, and predator cue on the larval Tiger Salamander (*Ambystoma tigrinum*). *EcoHealth* 8:46–54.
- Kiesecker, J.M. 2002. Synergism between trematode infection and pesticide exposure: A link to amphibian limb deformities in nature? *Proceedings of the National Academy of Sciences of the United States of America* 99:9900–9904.
- Kiesecker, J.M., A.R. Blaustein, and L.K. Belden. 2001. Complex causes of amphibian population declines. *Nature* 410:681.
- Kiesecker, J.M., L.K. Belden, K. Shea, and M.J. Rubbo. 2004. Amphibian decline and emerging disease: What can sick frogs teach us about new and resurgent diseases in human populations and other species of wildlife? *American Scientist* 92:138–147.
- Kik, M., A. Martel, A. Spitzen-van der Sluijs, F. Pasmans, P. Wohlsein, A. Gröne, and J.M. Rijks. 2011. Ranavirus-associated mass mortality in wild amphibians, The Netherlands. 2010: A first report. *Veterinary Journal* 190:284–286.
- Kilburn, V.L., R. Ibáñez, and D.M. Green. 2011. Reptiles as potential vectors and hosts of the amphibian pathogen *Batrachochytrium dendrobatidis* in Panama. *Diseases of Aquatic Organisms* 97:127–134.
- Kimble, S.J., A.K. Karna, A.J. Johnson, J.T. Hoverman, and R.N. Williams. 2015. Mosquitoes as a potential vector of ranavirus transmission in terrestrial turtles. *EcoHealth* 12:334–338.
- King, K.C., J.D. McLaughlin, A.D. Gendron, B.D. Pauli, I. Giroux, B. Rondeau, M. Boily, P. Juneau, and D.J. Marcogliese. 2007. Impacts of agriculture on the parasite communities of Northern Leopard Frogs (*Rana pipiens*) in southern Quebec, Canada. *Parasitology* 134:2063–2080.
- King, K.C., A.D. Gendron, J.D. McLaughlin, I. Giroux, P. Brousseau, D. Cyr, S.M. Ruby, M. Fournier, and D.J. Marcogliese. 2008. Short-term seasonal changes in parasite community structure in Northern Leopard Froglets (*Rana pipiens*) inhabiting agricultural wetlands. *Journal of Parasitology* 94:13–22.
- Kirschman, L.J., E.J. Crespi, and R.W. Warne. 2018. Critical disease windows shaped by stress exposure alter allocation trade-offs between development and immunity. *Journal of Animal Ecology* 87:235–246.
- Kolby, J.E., K.M. Smith, L. Berger, W.B. Karesh, A. Preston, A.P. Pessier, and L.F. Skerratt. 2014. First evidence of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) and ranavirus in Hong Kong amphibian trade. *PLoS One* 9:e90750.
- Kolby, J.E., S.D. Ramirez, L. Berger, K.L. Richards-Hrdlicka, M. Jocque, and L.F. Skerratt. 2015a. Terrestrial dispersal and potential environmental transmission of the amphibian chytrid fungus (*Batrachochytrium dendrobatidis*). *PLoS One* 10:e0125386.
- Kolby, J.E., S.D. Ramirez, L. Berger, D.W. Griffin, M. Jocque, and L.F. Skerratt. 2015b. Presence of amphibian chytrid fungus (*Batrachochytrium dendrobatidis*) in rainwater suggests aerial dispersal is possible. *Aerobiologia* 31:411–419.
- Koprivnikar, J., and J.C. Redfern. 2012. Agricultural effects on amphibian parasitism: Importance of general habitat perturbations and parasite life cycles. *Journal of Wildlife Diseases* 48:925–936.
- Kruger, K.M., and J.M. Hero. 2007. The chytrid fungus *Batrachochytrium dendrobatidis* is non-randomly distributed across amphibian breeding habitats. *Diversity and Distributions* 13:781–788.
- Landsberg, J.H., Y. Kiryu, M. Tabuchi, T.B. Waltzek, K.M. Enge, S. Reintjes-Tolen, A. Preston, and A.P. Pessier. 2013. Co-infection by alveolate parasites and frog virus 3-like ranavirus during an amphibian larval mortality event in Florida, USA. *Diseases of Aquatic Organisms* 105:89–99.
- Lawler, J.J., S.L. Shafer, B.A. Bancroft, and A.R. Blaustein. 2009. Projected climate impacts for the amphibians of the Western Hemisphere. *Conservation Biology* 24:38–50.
- Lesbarrères, D., A. Balseiro, J. Brunner, M.J. Gray. 2012. Ranavirus: Past, present and future. *Biology Letters* 8:481–483.
- Lips, K.R. 2016. Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150465.
- Lips, K.R., J.D. Reeve, and L.R. Witters. 2003. Ecological traits predicting amphibian population declines in Central America. *Conservation Biology* 17:1078–1088.
- Lips, K.R., F. Brem, R. Brenes, J.D. Reeve, R.A. Alford, J. Voyles, C. Carey, L. Livo, A.P. Pessier, and J.P. Collins. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences of the United States of America* 103:3165–3170.
- Longcore, J.E., A.P. Pessier, and D.K. Nichols. 1999. *Batrachochytrium dendrobatidis* gen. et sp. nov., a chytrid pathogenic to amphibians. *Mycologia* 91:219–227.
- Lötters, S., J. Kielgast, J. Bielby, S. Schmidlein, J. Bosch, M. Veith, S.F. Walker, M.C. Fisher, and D. Rödder. 2009. The link between rapid enigmatic amphibian decline and the globally emerging chytrid fungus. *EcoHealth* 6:358–372.
- Majji, S., S. LaPatra, S.M. Long, R. Sample, L. Bryan, A. Sinning, and V.G. Chinchar. 2006. *Rana catesbeiana* virus Z (RCV-Z): A novel pathogenic ranavirus. *Diseases of Aquatic Organisms* 73:1–11.
- Marino, J.A. 2016. Host food resource supplementation increases echinostome infection in larval anurans. *Parasitology Research* 115:4477–4483.
- Martel, A., A. Spitzen-van der Sluijs, M. Blooi, F. Pasmans. 2013. *Batrachochytrium salamandricorans* sp. nov. causes lethal chytridiomycosis in amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 110:15325–15329.
- Martel, A., M. Blooi, C. Adriaensen, K.R. Lips. 2014. Recent introduction of a chytrid fungus endangers Western Palearctic salamanders. *Science* 346:630–631.
- McKenzie, V.J. 2007. Human land use and patterns of parasitism in tropical amphibian hosts. *Biological Conservation* 137:102–116.

- McMillan, K., D. Lesbarrères, X.A. Harrison, and T.W.J. Garner. 2020. Spatiotemporal heterogeneity decouples infection parameters of amphibian chytridiomycosis. *Journal of Animal Ecology* 00:1–13. <https://doi.org/10.1111/1365-2656.13170>
- Miller, D., M. Gray, and A. Storfer. 2011. Ecopathology of ranaviruses infecting amphibians. *Viruses* 3:2351–2373.
- Miller, D.L., C.R. Bursey, M.J. Gray, and L.M. Smith. 2004. Metacercariae of *Clinostomum attenuatum* in *Ambystoma tigrinum mavortium*, *Bufo cognatus* and *Spea multiplicata* from west Texas. *Journal of Helminthology* 78:373–376.
- Miller, D.L., S. Rajeev, M.J. Gray, and C.A. Baldwin. 2007. Frog virus 3 infection, cultured American bullfrogs. *Emerging Infectious Diseases* 13:342.
- Miller, D.L., A.P. Pessier, P. Hick, and R.J. Whittington. 2015. Comparative pathology of ranaviruses and diagnostic techniques. Pp. 171–208 in *Ranaviruses: Lethal Pathogens of Ectothermic Vertebrates* (M.J. Gray and V.G. Chinchar, eds.). Springer, USA.
- Morrison, E.A., S. Garner, P. Echaubard, D. Lesbarrères, C.J. Kyle, and C.R. Brunetti. 2014. Complete genome analysis of a frog virus 3 (FV3) isolate and sequence comparison with isolates of differing levels of virulence. *Virology Journal* 11:46.
- Munro, J., A.E. Bayley, N.J. McPherson, and S.W. Feist. 2016. Survival of frog virus 3 in freshwater and sediment from an English lake. *Journal of Wildlife Diseases* 52:138–142.
- Muths, E., and J.M. Hero. 2010. Amphibian declines: Promising directions in understanding the role of disease. *Animal Conservation* 13:33–35.
- Muths, E., B.R. Hossack, E.H. Campbell Grant, D.S. Pilliod, and B.A. Mosher. 2020. Effects of snowpack, temperature, and disease on demography in a wild population of amphibians. *Herpetologica* 76:132–143.
- Narayan, E.J., C. Graham, H. McCallum, and J.M. Hero. 2014. Overwintering tadpoles of *Mixophyes fasciolatus* act as reservoir host for *Batrachochytrium dendrobatidis*. *PLoS One* 9:e92499.
- Nazir, J., M. Spengler, and R.E. Marschang. 2012. Environmental persistence of amphibian and reptilian ranaviruses. *Diseases of Aquatic Organisms* 98:177–184.
- North, A.C., D.J. Hodgson, S.J. Price, and A.G. Griffiths. 2015. Anthropogenic and ecological drivers of amphibian disease (ranavirosis). *PLoS One* 10:e0127037.
- O'Hanlon, S.J., A. Rieux, R.A. Farrer, M.D. Martin. 2018. Recent Asian origin of chytrid fungi causing global amphibian declines. *Science* 360:621–627.
- Ohmer, M.E., S.M. Herbert, R. Speare, and P.J. Bishop. 2013. Experimental exposure indicates the amphibian chytrid pathogen poses low risk to New Zealand's threatened endemic frogs. *Animal Conservation* 16:422–429.
- Olori, J.C., R. Netzband, N. McKean, J. Lowery, K. Parsons, and S.T. Windstam. 2018. Multi-year dynamics of ranavirus, chytridiomycosis, and co-infections in a temperate host assemblage of amphibians. *Diseases of Aquatic Organisms* 130:187–197.
- Olson, D.H., D.M. Aanensen, K.L. Ronnenberg, C.I. Powell, S.F. Walker, J. Bielby, T.W. Garner, G. Weaver, and M.C. Fisher. 2013. Mapping the global emergence of *Batrachochytrium dendrobatidis*, the amphibian chytrid fungus. *PLoS One* 8:e56802.
- Ortiz-Santaliestra, M.E., M.C. Fisher, S. Fernández-Beakoetxea, M.J. Fernández-Benítez, and J. Bosch. 2011. Ambient ultraviolet B radiation and prevalence of infection by *Batrachochytrium dendrobatidis* in two amphibian species. *Conservation Biology* 25:975–982.
- Ostfeld, R.S., and F. Keesing. 2012. Effects of host diversity on infectious disease. *Annual Review of Ecology, Evolution, and Systematics* 43:157–182.
- Ostfeld, R.S., G.E. Glass, and F. Keesing. 2005. Spatial epidemiology: An emerging (or re-emerging) discipline. *Trends in Ecology & Evolution* 20:328–336.
- Parris, M.J., E. Reese, and A. Storfer. 2006. Antipredator behavior of chytridiomycosis-infected Northern Leopard Frog (*Rana pipiens*) tadpoles. *Canadian Journal of Zoology* 84:58–65.
- Pavlin, B.I., L.M. Schloegel, and P. Daszak. 2009. Risk of importing zoonotic diseases through wildlife trade, United States. *Emerging Infectious Diseases* 15:1721.
- Peace, A., S.M. O'Regan, J.A. Spatz, P.N. Reilly, R.D. Hill, E.D. Carter, R.P. Wilkes, T.B. Waltzek, D.L. Miller, and M.J. Gray. 2019. A highly invasive chimeric ranavirus can decimate tadpole populations rapidly through multiple transmission pathways. *Ecological Modelling* 410:108777.
- Pearman, P.B., and T.W. Garner. 2005. Susceptibility of Italian agile frog populations to an emerging strain of *Ranavirus* parallels population genetic diversity. *Ecology Letters* 8:401–408.
- Pearman, P.B., T.W. Garner, M. Straub, and U.F. Greber. 2004. Response of the Italian Agile Frog (*Rana latastei*) to a *Ranavirus*, Frog virus 3: A model for viral emergence in naïve populations. *Journal of Wildlife Diseases* 40:660–669.
- Picco, A.M., and J.P. Collins. 2008. Amphibian commerce as a likely source of pathogen pollution. *Conservation Biology* 22:1582–1589.
- Picco, A.M., A.P. Karam, and J.P. Collins. 2010. Pathogen host switching in commercial trade with management recommendations. *EcoHealth* 7:252–256.
- Piotrowski, J.S., S.L. Annis, and J.E. Longcore. 2004. Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. *Mycologia* 96:9–15.
- Pochini, K.M., and J.T. Hoverman. 2017a. Reciprocal effects of pesticides and pathogens on amphibian hosts: The importance of exposure order and timing. *Environmental Pollution* 221:359–366.
- Pochini, K.M., and J.T. Hoverman. 2017b. Immediate and lag effects of pesticide exposure on parasite resistance in larval amphibians. *Parasitology* 144:817–822.
- Price, S.J., T.W. Garner, R.A. Nichols, F. Balloux, C. Ayres, A.M.C. de Alba, and J. Bosch. 2014. Collapse of amphibian communities due to an introduced *Ranavirus*. *Current Biology* 24:2586–2591.
- Puschendorf, R., C.J. Hoskin, S.D. Cashins, K. McDonald, L.F. Skerratt, J. Vanderwal, and R.A. Alford. 2011. Environmental refuge from disease-driven amphibian extinction. *Conservation Biology* 25:956–964.
- Puschendorf, R., M. Wallace, M.M. Chavarria, A.J. Crawford, F. Wynne, M. Knight, D.H. Janzen, W. Hallwachs, C.V. Palmer, and S.J. Price. 2019. Cryptic diversity and ranavirus infection of a critically endangered Neotropical frog before and after population collapse. *Animal Conservation* 22:515–524.
- Rachowicz, L.J., and C.J. Briggs. 2007. Quantifying the disease transmission function: Effects of density on *Batrachochytrium dendrobatidis* transmission in the Mountain Yellow-legged Frog *Rana muscosa*. *Journal of Animal Ecology* 76:711–721.
- Raffel, T.R., P.J. Michel, E.W. Sites, and J.R. Rohr. 2010. What drives chytrid infections in newt populations? Associations with substrate, temperature, and shade. *EcoHealth* 7:526–536.
- Reeder, N.M.M., A.P. Pessier, and V.T. Vredenburg. 2012. A reservoir species for the emerging amphibian pathogen *Batrachochytrium dendrobatidis* thrives in a landscape decimated by disease. *PLoS One* 7:e33567.
- Reeve, B.C., E.J. Crespi, C.M. Whipps, and J.L. Brunner. 2013. Natural stressors and ranavirus susceptibility in larval Wood Frogs (*Rana sylvatica*). *EcoHealth* 10:190–200.
- Retallick, R.W., and V. Miera. 2007. Strain differences in the amphibian chytrid *Batrachochytrium dendrobatidis* and non-permanent, sub-lethal effects of infection. *Diseases of Aquatic Organisms* 75:201–207.
- Ribeiro, L.P., T. Carvalho, C.G. Becker, T.S. Jenkinson, D. da Silva Leite, T.Y. James, S.E. Greenspan, and L.F. Toledo. 2019. Bullfrog farms release virulent zoospores of the frog-killing fungus into the natural environment. *Scientific Reports* 9:1–10.
- Robert, J., E. George, F.D.J. Andino, and G. Chen. 2011. Waterborne infectivity of the *Ranavirus* Frog virus 3 in *Xenopus laevis*. *Virology* 417:410–417.
- Roberts, C.D., and T.E. Dickinson. 2012. *Ribeiroia ondatrae* causes limb abnormalities in a Canadian amphibian community. *Canadian Journal of Zoology* 90:808–814.
- Rohr, J.R., T.R. Raffel, A.R. Blaustein, P.T. Johnson, S.H. Paull, and S. Young. 2013. Using physiology to understand climate-driven changes in disease and their implications for conservation. *Conservation Physiology* 1:1–15.
- Rollins-Smith, L.A. 1998. Metamorphosis and the amphibian immune system. *Immunological Reviews* 166:221–230.
- Romansic, J.M., K.A. Diez, E.M. Higashi, J.E. Johnson, and A.R. Blaustein. 2009. Effects of the pathogenic water mold *Saprolegnia ferax* on survival of amphibian larvae. *Diseases of Aquatic Organisms* 83:187–193.
- Romansic, J.M., P.T. Johnson, C.L. Searle, J.E. Johnson, T.S. Tunstall, B.A. Han, J.R. Rohr, and A.R. Blaustein. 2011. Individual and combined effects of multiple pathogens on Pacific Treefrogs. *Oecologia* 166:1029–1041.
- Ron, S.R. 2005. Predicting the distribution of the amphibian pathogen *Batrachochytrium dendrobatidis* in the New World. *Biotropica: Journal of Biology and Conservation* 37:209–221.
- Rowley, J.J., and R.A. Alford. 2007. Behaviour of Australian rainforest

- stream frogs may affect the transmission of chytridiomycosis. *Diseases of Aquatic Organisms* 77:1–9.
- Rowley, J.J., and R.A. Alford. 2013. Hot bodies protect amphibians against chytrid infection in nature. *Scientific Reports* 3:1515.
- Roznik, E.A., S.J. Sapsford, D.A. Pike, L. Schwarzkopf, and R.A. Alford. 2015. Natural disturbance reduces disease risk in endangered rainforest frog populations. *Scientific Reports* 5:13472.
- Saucedo, B., J. Serrano, M. Jacinto-Maldonado, R. Leuven, A. Rocha García, A. Méndez Bernal, A. Gröne, S. van Beurden, and C. Escobedo-Bonilla. 2019. Pathogen risk analysis for wild amphibian populations following the first report of a ranavirus outbreak in farmed American Bullfrogs (*Lithobates catesbeianus*) from Northern Mexico. *Viruses* 11:26.
- Savage, A.E., C.G. Becker, and K.R. Zamudio. 2015. Linking genetic and environmental factors in amphibian disease risk. *Evolutionary Applications* 8:560–572.
- Schadich, E. 2009. Skin peptide activities against opportunistic bacterial pathogens of the African clawed frog (*Xenopus laevis*) and three *Litoria* frogs. *Journal of Herpetology* 43:173–184.
- Schadich, E., and A.L. Cole. 2010. Pathogenicity of *Aeromonas hydrophila*, *Klebsiella pneumoniae*, and *Proteus mirabilis* to Brown Tree Frogs (*Litoria ewingii*). *Comparative Medicine* 60:114–117.
- Scheele, B.C., D.A. Hunter, S.C. Banks, J.C. Pierson, L.F. Skerratt, R. Webb, and D.A. Driscoll. 2016. High adult mortality in disease-challenged frog populations increases vulnerability to drought. *Journal of Animal Ecology* 85:1453–1460.
- Scheele, B.C., D.A. Hunter, L.A. Brannelly, L.F. Skerratt, and D.A. Driscoll. 2017. Reservoir-host amplification of disease impact in an endangered amphibian. *Conservation Biology* 31:592–600.
- Scheele, B.C., F. Pasmans, L.F. Skerratt, .I. De la Riva. 2019. Amphibian fungal panzootic causes catastrophic and ongoing loss of biodiversity. *Science* 363:1459–1463.
- 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.
- Schloegel, L.M., L.F. Toledo, J.E. Longcore, .A.J. Davies. 2012. Novel, panzootic and hybrid genotypes of amphibian chytridiomycosis associated with the bullfrog trade. *Molecular Ecology* 21:5162–5177.
- Schmidt, B.R., C. Bozzuto, S. Lötters, and S. Steinfartz. 2017. Dynamics of host populations affected by the emerging fungal pathogen *Batrachochytrium salamandricorans*. *Royal Society Open Science* 4:160801.
- Schock, D.M., T.K. Bollinger, V.G. Chinchar, J.K. Jancovich, and J.P. Collins. 2008. Experimental evidence that amphibian ranaviruses are multi-host pathogens. *Copeia* 2008:133–143.
- Schock, D.M., G.R. Ruthig, J.P. Collins, .D.G. Allaire. 2010. Amphibian chytrid fungus and ranaviruses in the Northwest Territories, Canada. *Diseases of Aquatic Organisms* 92:231–240.
- Schotthoefler, A.M., J.R. Rohr, R.A. Cole, A.V. Koehler, C.M. Johnson, L.B. Johnson, and V.R. Beasley. 2011. Effects of wetland vs. landscape variables on parasite communities of *Rana pipiens*: Links to anthropogenic factors. *Ecological Applications* 21:1257–1271.
- Searle, C.L., L.K. Belden, B.A. Bancroft, B.A. Han, L.M. Biga, and A.R. Blaustein. 2010. Experimental examination of the effects of Ultraviolet-B radiation in combination with other stressors on frog larvae. *Oecologia* 162:237–245.
- Searle, C.L., L.M. Biga, J.W. Spatafora, and A.R. Blaustein. 2011. A dilution effect in the emerging amphibian pathogen *Batrachochytrium dendrobatidis*. *Proceedings of the National Academy of Sciences of the United States of America* 108:16322–16326.
- Smalling, K.L., C.W. Anderson, R.K. Honeycutt, I.M. Cozzarelli, T. Preston, and B.R. Hossack. 2019. Associations between environmental pollutants and larval amphibians in wetlands contaminated by energy-related brines are potentially mediated by feeding traits. *Environmental Pollution* 248:260–268.
- Sparrow, F.K., Jr. 1960. *Aquatic Phycomycetes*. Arbor, USA.
- St-Amour, V., W.M. Wong, T.W. Garner, and D. Lesbarrères. 2008. Anthropogenic influence on prevalence of 2 amphibian pathogens. *Emerging Infectious Diseases* 14:1175.
- Stevenson, L.A., R.A. Alford, S.C. Bell, E.A. Roznik, L. Berger, and D.A. Pike. 2013. Variation in thermal performance of a widespread pathogen, the amphibian chytrid fungus *Batrachochytrium dendrobatidis*. *PLoS One* 8:e73830.
- Stockwell, M.P., J. Clulow, and M.J. Mahony. 2015a. Evidence of a salt refuge: Chytrid infection loads are suppressed in hosts exposed to salt. *Oecologia* 177:901–910.
- Stockwell, M.P., L.J. Storrle, C.J. Pollard, J. Clulow, and M.J. Mahony. 2015b. Effects of pond salinization on survival rate of amphibian hosts infected with the chytrid fungus. *Conservation Biology* 29:391–399.
- Stoler, A.B., K.A. Berven, and T.R. Raffel. 2016. Leaf litter inhibits growth of an amphibian fungal pathogen. *EcoHealth* 13:392–404.
- Strauss, A.E., and K.G. Smith. 2013. Why does amphibian chytrid (*Batrachochytrium dendrobatidis*) not occur everywhere? An exploratory study in Missouri ponds. *PLoS One* 8:e76035.
- Tobler, U., and B.R. Schmidt. 2010. Within-and among-population variation in chytridiomycosis-induced mortality in the toad *Alytes obstetricans*. *PLoS One* 5:e10927.
- Tornabene, B.J., A.R. Blaustein, C.J. Briggs, D.M. Calhoun, P.T. Johnson, T. McDevitt-Galles, J.R. Rohr, and J.T. Hoverman. 2018. The influence of landscape and environmental factors on ranavirus epidemiology in a California amphibian assemblage. *Freshwater Biology* 63:639–651.
- Varela, B.J., D. Lesbarrères, R. Ibáñez, and D.M. Green. 2018. Environmental and host effects on skin bacterial community composition in Panamanian frogs. *Frontiers in Microbiology* 9:298.
- Venesky, M.D., X. Liu, E.L. Sauer, and J.R. Rohr. 2014. Linking manipulative experiments to field data to test the dilution effect. *Journal of Animal Ecology* 83:557–565.
- Vilaça, S.T., J.F. Bientreux, C.R. Brunetti, D. Lesbarrères, D.L. Murray, and C.J. Kyle. 2019. Frog virus 3 genomes reveal prevalent recombination between ranavirus lineages and their origins in Canada. *Journal of Virology* 93:e00765–19.
- Voyles, J., S. Young, L. Berger, .R. Speare. 2009. Pathogenesis of chytridiomycosis, a cause of catastrophic amphibian declines. *Science* 326:582–585.
- Waltzek, T.B., D.L. Miller, M.J. Gray, .K.V. Malm. 2014. New disease records for hatchery-reared sturgeon: Expansion of frog virus 3 host range into *Saccharinichthys albus*. *Diseases of Aquatic Organisms* 111:219–227.
- Warne, R.W., E.J. Crespi, and J.L. Brunner. 2011. Escape from the pond: Stress and developmental responses to ranavirus infection in wood frog tadpoles. *Functional Ecology* 25:139–146.
- Warne, R.W., B. LaBumbard, S. LaGrange, V.T. Vredenburg, and A. Catenazzi. 2016. Co-infection by chytrid fungus and ranaviruses in wild and harvested frogs in the tropical Andes 11:1.
- Watts, A., D. Olson, R. Harris, and M. Mandica. 2019. The deadly amphibian *Bsal* disease: How science-management partnerships are forestalling amphibian biodiversity losses. *Science Findings* 214:1–5.
- Whitfield, S.M., E. Geerdes, I. Chacon, E.B. Rodriguez, R.R. Jimenez, M.A. Donnelly, and J.L. Kerby. 2013. Infection and co-infection by the amphibian chytrid fungus and ranavirus in wild Costa Rican frogs. *Diseases of Aquatic Organisms* 104:173–178.
- Wimsatt, J., S.H. Feldman, M. Heffron, M. Hammond, M.P.R. Ruehling, K.L. Grayson, and J.C. Mitchell. 2014. Detection of pathogenic *Batrachochytrium dendrobatidis* using water filtration, animal and bait testing. *Zoo Biology* 33:577–585.
- Wombwell, E.L., T.W. Garner, A.A. Cunningham, R. Quest, S. Pritchard, J.M. Rowcliffe, and R.A. Griffiths. 2016. Detection of *Batrachochytrium dendrobatidis* in amphibians imported into the UK for the pet trade. *EcoHealth* 13:456–466.
- Woodhams, D.C., and R.A. Alford. 2005. Ecology of chytridiomycosis in rainforest stream frog assemblages of tropical Queensland. *Conservation Biology* 19:1449–1459.
- Woodhams, D.C., R.A. Alford, and G. Marantelli. 2003. Emerging disease of amphibians cured by elevated body temperature. *Diseases of Aquatic Organisms* 55:65–67.
- Youker-Smith, T.E., P.H. Boersch-Supan, C.M. Whipps, and S.J. Ryan. 2018. Environmental drivers of ranavirus in free-living amphibians in constructed ponds. *EcoHealth* 15:608–618.
- Yuan, Z., A. Martel, J. Wu, S. Van Praet, S. Canessa, and F. Pasmans. 2018. Widespread occurrence of an emerging fungal pathogen in heavily traded Chinese urodelan species. *Conservation Letters* 11:e12436.

Accepted on 9 March 2020  
Associate Editor: David M. Green