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Amphibian Disease Ecology: Are We Just Scratching the Surface?

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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 Chinchar 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).

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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)

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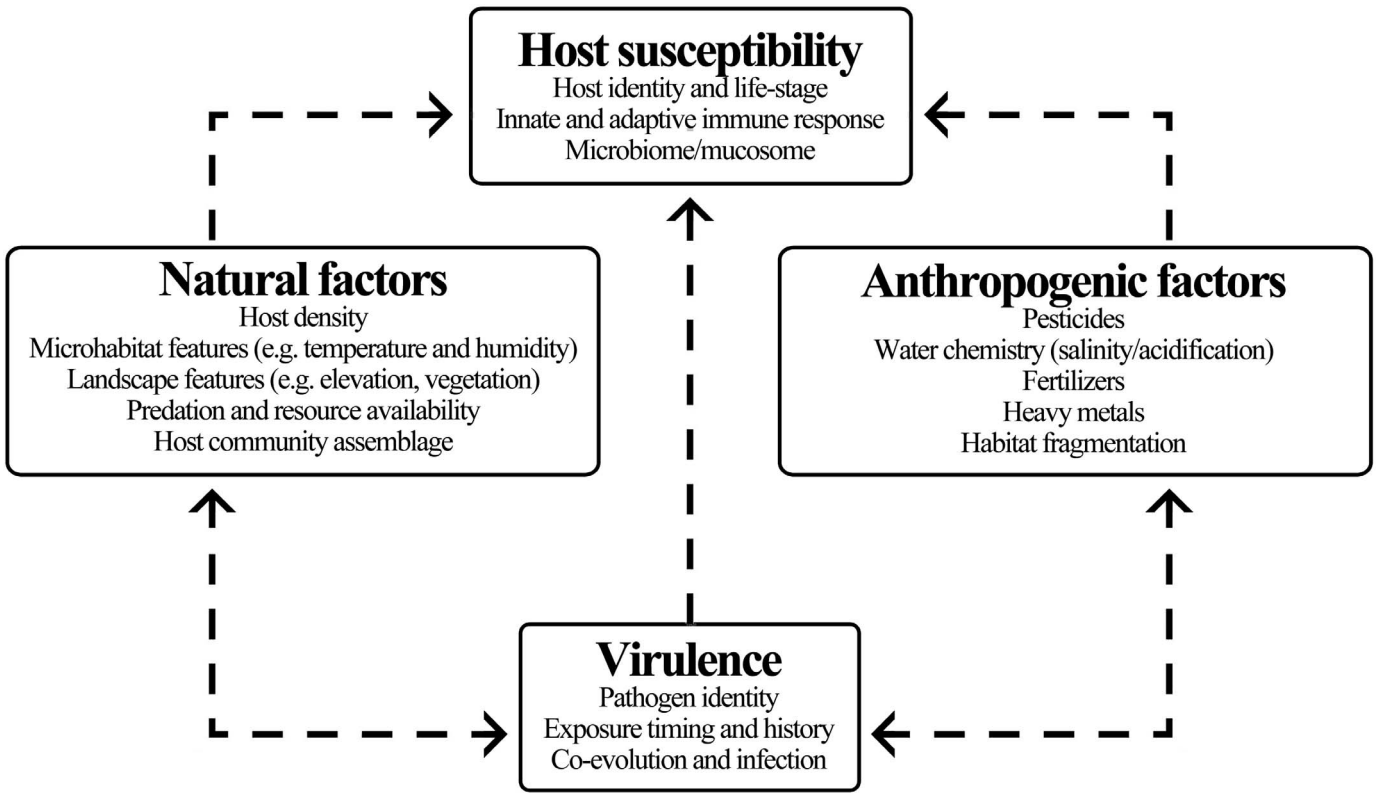


Fig. 1.—Flow diagram of basic relationships between amphibian host–pathogen systems and environmental factors. Adapted from Gray et al. 2009.

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

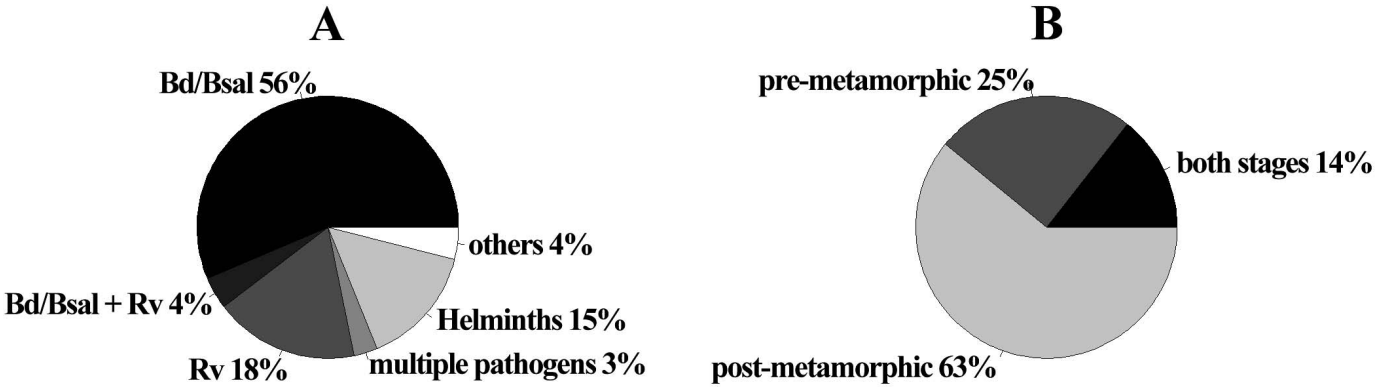


Fig. 2.—Percentage distribution of investigated pathogens (A) and host life stage (B) in the amphibian disease literature between 2009 and 2019.

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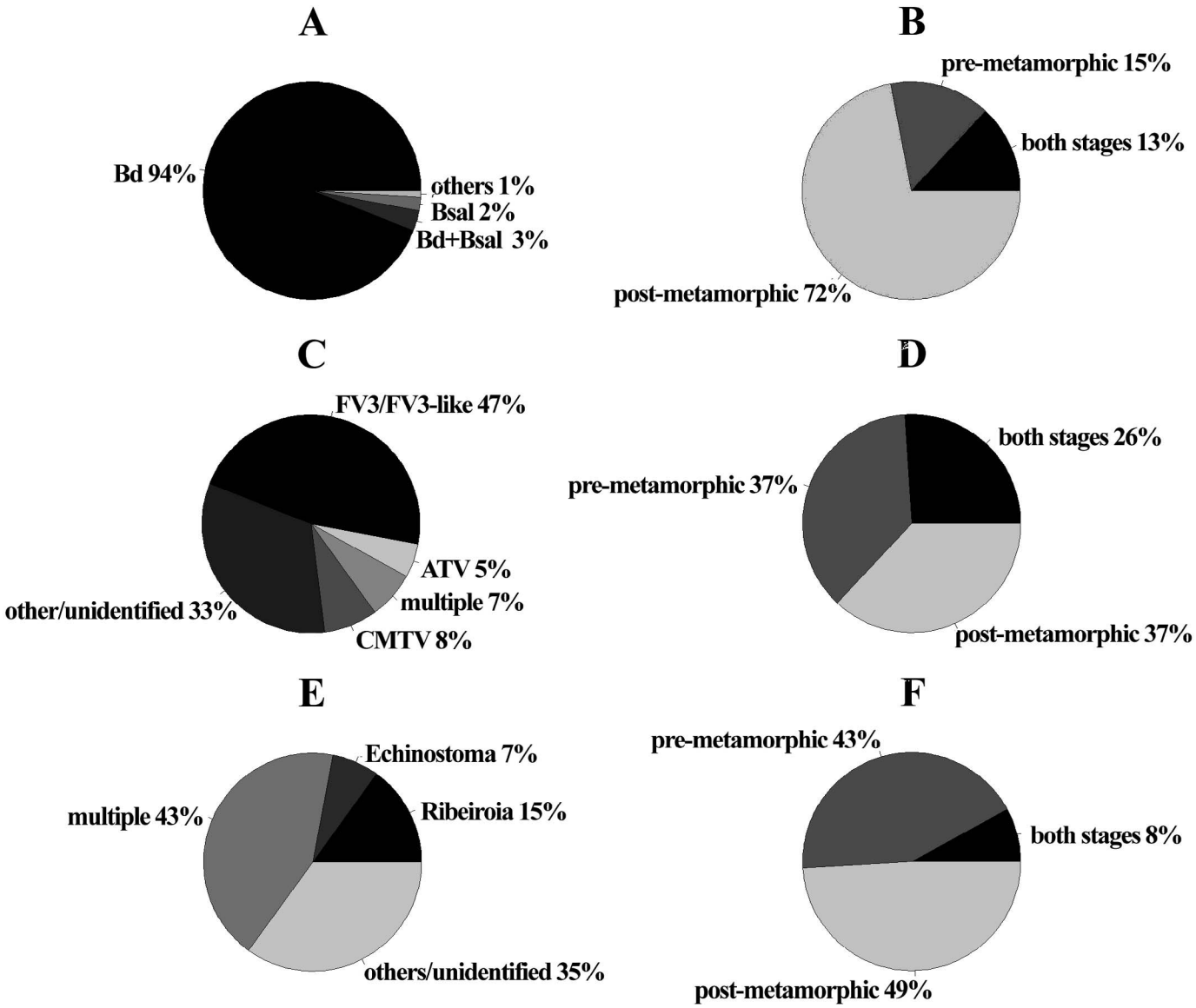


Fig. 3.—Percentage distribution of investigated pathogens and associated host life stage in chytridomycota (A, B), ranaviruses (C, D), and helminths (E, F) in the amphibian disease literature between 2009 and 2019.

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; Kärvemo 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

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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-Benéitez 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%

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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 communities (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

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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% invetigating 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; Bienentreu 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

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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*-

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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., Schotthoefer 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

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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 Cahloun 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.

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Supplemental Material

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