

Disease Ecology: Past and Present for a Better Future

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DURING recent years, the emergence of infectious diseases has caused global concern due to its link with species extinctions and population declines (Jones et al., 2008; Frick et al., 2010; Fisher et al., 2012; Lorch et al., 2016). Although biodiversity losses have been documented globally across multiple taxonomic groups (Gibbons et al., 2000; Mooney, 2010), amphibians are recognized as a group of serious conservation concern (Houlahan et al., 2000; Alford et al., 2001; Stuart et al., 2004; Wake and Vredenburg, 2008; Kilpatrick et al., 2010; Grant et al., 2016), with extinction rates estimated to exceed 105 times the baseline for all species (Pechmann et al., 1991; McCallum, 2007; Alroy, 2015; Solow, 2016). Amphibian population declines have been reported on most continents (Berger et al., 1998; Hero and Morrison, 2004; Lips et al., 2005; Pasmans et al., 2006) and have been associated with multiple factors such as habitat loss, the introduction of non-native species, and emerging infectious diseases (Kats and Ferrer, 2003; Cushman, 2006; Blaustein et al., 2011; Hof et al., 2011).

Vast information on amphibian diseases has been collected from experimental and field research from scientists working in the United States (Briggs et al., 2010; Vredenburg et al., 2010; Searle et al., 2011; Blaustein et al., 2012, 2018; Gervasi et al., 2013; Rosenblum et al., 2013; Savage and Zamudio, 2016), Europe (Garner et al., 2005; Bosch and Martinez-Solano, 2006), and Australia (Woodhams et al., 2008; Voyles, 2011; Voyles et al., 2011; James et al., 2015). In Latin America, the topic of amphibian disease ecology is one of increasing concern, as multiple population declines and extinctions have been reported for this continent (Young et al., 2001; Crawford et al., 2010; Soto-Azat et al., 2013a, 2013b; Catenazzi et al., 2017; Valenzuela-Sánchez et al., 2017) that harbors half of all amphibian species on the planet (Stuart et al., 2008). Therefore, there is an urgent need to better understand the patterns and processes associated with these declines and extinctions. Currently, ecologists, conservationists, and herpetologists are making considerable efforts to advance this field of research in Latin America with the aim of preserving its unique amphibian biodiversity.

At the symposium “Disease Ecology: Past and Present for a Better Future” held as part of the XI Latin American Congress of Herpetology, experts from nine countries (Argentina, Brazil, Chile, Colombia, Ecuador, Mexico, Panama, Spain, and the United States of America) presented results of their ongoing research and most recent discoveries. Furthermore, they identified major gaps in the field and the necessary actions to fill these research gaps. Our goal here is to

summarize the main findings presented at the symposium and introduce a few research opportunities to advance the field of disease ecology in the region. We are not providing an exhaustive review of the field of disease ecology in Latin America, but we expect this communication will provide useful information for people interested in this area of research.

RECENT ADVANCES IN AMPHIBIAN DISEASE ECOLOGY

This symposium was planned to discuss a wide spectrum of diseases affecting the herpetofauna in Latin America, yet most of the presented studies were focused on amphibians and their infection by the chytrid fungus, *Batrachochytrium dendrobatidis* (Bd). This is despite the fact that there are different pathogens affecting amphibians in complex ways that can cause mortality or sublethal damage (Daszak et al., 1999; Blaustein and Kiesecker, 2002; Green et al., 2002; Romansic et al., 2009). Bacterial and viral diseases such as red-leg syndrome and ranaviruses affect both wild and captive amphibian populations (Cunningham et al., 2003; Densmore and Green, 2007; Schadich and Cole, 2010). Mycotic and mycotic-like organisms such as zygomycoses, chromomycoses, saprolegniasis, and ichthyophoniasis are also implicated as amphibian diseases (Speare et al., 1994; Longcore et al., 1999; Taylor et al., 1999; Kiesecker et al., 2001; Juopperi et al., 2002; Densmore and Green, 2007). Protozoan and metazoan parasites cause malformations, such as webbings, supernumerary digits and limbs, or missing limbs (Blaustein and Johnson, 2003a, 2003b; Johnson et al., 2003, 2010; Reeves et al., 2013). However, only a fraction of these pathogens are implicated in the decline of multiple populations of amphibians worldwide (Daszak et al., 1999; Wake and Vredenburg, 2008).

Presentations at the symposium addressed a wide range of questions and spanned multiple levels of biological organization (cellular, individual, population, community), taxa, and methodological approaches (experimental, theoretical, comparative; see Table 1 for details). Overall the presentations can be categorized in three broad topics: (i) host-microbiome interactions, (ii) macroecological patterns, and (iii) host-pathogen interactions, which we present below.

Host-microbiome interactions.—Several studies reported the key role that bacteria play as a defense mechanism against pathogens and specifically against Bd. The diversity of cutaneous bacteria of captive individuals of species of *Atelopus* from Colombia and Ecuador was similar to that of

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Table 1. List of participants and titles of presentations during the symposium, "Disease Ecology: Past and Present for a Better Future."

Title of presentation	Authors	Affiliation
Efecto del cautiverio sobre las bacterias benéficas de la piel de tres especies del género <i>Atelopus</i> (Anura: Bufonidae)	Sandra V. Flechas ¹ Ailin Blasco-Zúñiga ² Andrés Merino-Viteri ³ Valeria Ramírez-Castañeda ¹ Miryan Rivera I ² Adolfo Amézquita ¹	¹ Departamento de Ciencias Biológicas, Universidad de los Andes ² Laboratorio de Investigaciones en Citogenética y Biomoléculas de Anfibios (LICBA), Centro de Investigación para la Salud en América Latina (CISEAL), Pontificia Universidad Católica del Ecuador ³ Museo de Zoología (QCAZ), Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador
El Grito Eltoniano de la quitridiomycosis	Aldo López-Velázquez ¹ Raquel Hernández-Austria ² Patricia Hernández-López ³ Gabriela Parra-Olea ¹	¹ Instituto de Biología, Universidad Nacional Autónoma de México ² Centro de Investigaciones Biológicas, UAEH ³ Red de Biología y Conservación de Vertebrados, INECOL
Estudios de patología comparada en anfibios ecuatorianos: Actualidad y perspectiva	Alexander Genoy-Puerto	Escuela de Medicina Veterinaria y Zootecnia, Universidad de Las América, Ecuador
<i>Ranavirus</i> : A surveillance study in wild native and invasive amphibians from Chile	Alexandra Peñafiel-Ricaurte ¹ Stephen J. Price ² Mario Alvarado-Rybak ¹ Andrew A. Cunningham ³ Claudio Soto-Azat ¹	¹ Universidad Andres Bello ² UCL Genetic Institute ³ Institute of Zoology, Zoological Society of London
Amphibian mucosal defenses against chytridiomycosis: Testing for selection in recovering populations in upland Panamá	Andreas Hertz Douglas C. Woodhams	University of Massachusetts, Boston
Spatial distribution of <i>Batrachochytrium dendrobatidis</i> in South American caecilians	Carolina Lambertini ¹ C. Guilherme Becker ¹ Cecilia Bardier ² Domingos da Silva Leite ¹ Luís Felipe Toledo ¹	¹ Universidade Estadual de Campinas ² Universidad de la Republica
Efecto inhibitorio de biocompuestos de hongos endófitos sobre el hongo patógeno <i>Batrachochytrium dendrobatidis</i>	Carolina Castro Carolina Portero Alexandra Narváez-Trujillo	Pontificia Universidad Católica del Ecuador
Diversidad de nematodos parásitos en anfibios del Gran Chaco Sudamericano: Avances y perspectivas	Cynthia Elizabeth González	Centro de Ecología Aplicada del Litoral (CECOAL) Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET-UNNE), Argentina
Exploring the amphibian microbiome within the context of infection by the pathogenic fungus <i>Batrachochytrium dendrobatidis</i>	Daniel Medina ¹ Josh Franklin ² Myra Hughey ¹ Jenifer Walke ¹ Matthew Becker ¹ Shan Sun ² Brian Badgley ² Lisa K. Belden ¹	¹ Virginia Tech, Department of Biological Sciences ² Virginia Tech, Crop & Soil Environmental Sciences Department
History of chytridiomycosis in Bolivia	Ignacio De la Riva ¹ Patricia A. Burrowes ²	¹ Museo Nacional de Ciencias Naturales-CSIC, Spain ² Department of Biology, University of Puerto Rico University of South Dakota
Gene expression in <i>Serratia marcescens</i> cutaneous bacteria from Costa Rican frogs in response to Bd	Jake Kerby Joseph Madison Jenny Urbina ¹ Evan Bredeweg ² Tiffany Garcia ² Andrew R. Blaustein ³	¹ Environmental Sciences, Oregon State University (OSU) ² Department of Fisheries and Wildlife, OSU ³ Department of Integrative Biology, OSU

Table 1. Continued.

Title of presentation	Authors	Affiliation
Effects of amphibian phylogeny, climate and human impact on the occurrence of the amphibian-killing chytrid fungus	Leonardo Bacigalupe ¹ Claudio Soto-Azat ² Cristobal Garcia-Vera ³ Ismael Barria-Oyarzo ¹ Enrico L. Rezende ⁴	¹ Instituto de Ciencias Ambientales y Evolutivas, Facultad de Ciencias, Universidad Austral de Chile, Valdivia, Chile ² Centro de Investigación para la Sustentabilidad, Facultad de Ecología y Recursos Naturales, Universidad Andrés Bello, Santiago, Chile ³ Dirección General de Aguas, Ministerio de Obras Públicas, Coyhaique, Chile ⁴ Department of Life Sciences, University of Roehampton, London, UK
12 years of chytrid and amphibian conservation research in Brazil and projections for the Anthropocene	Luis Felipe Toledo	Universidade Estadual de Campinas
Estudio morfológico de las células de Langerhans (CL) ATPasa+/MHC-II+ en las especies <i>Xenopus laevis</i> y <i>Lithobates montezumae</i>	Omar Betancourt-León Marcela Ariadne Delgado Gasca Armando Pérez Torres	Universidad Nacional Autónoma de México
Using metabolic theory to model climate impacts on multi-host diseases	Thomas R. Raffel Karie A. Altman Jason P. Scrabulis	Oakland University

individuals in the wild as reported by Blasco et al. This study also revealed that animals kept in captivity still harbored beneficial bacteria capable of inhibiting Bd growth, suggesting that reintroduction programs could be effective at least for this genus (Flechas et al., 2017). In subsequent presentations, authors focused on the potential influence of pathogens on the fungal diversity and community structure of the frog skin microbiome. During their presentations, Medina et al. and Hertz and Woodhams emphasized the relevance of identifying the types of interactions that occur between the host, pathogens, and other (beneficial/commensal) host skin microbiota, including bacteria and fungi. Kerby and Madison discussed the importance of sequencing genes of anti-Bd strains of bacteria to understand up-and-down gene regulation in response to Bd exposure (Madison et al., 2017).

Macroecological patterns.—Studies assessing the occurrence of Bd at regional scales provided new information on the current distribution of this pathogen and some historical factors that might have shaped it. Species-specific patterns of Bd prevalence, evidenced by a strong phylogenetic signal and a non-random geographic distribution of Bd throughout Chile was presented by Bacigalupe et al. Prevalence of Bd was shown to decrease with latitude and to increase in regions with high gross domestic product and high variability in rainfall regimes (Bacigalupe et al., 2017). De la Riva and Burrowes showed the earliest report of Bd in the world, which was found in a specimen of *Telmatobius* collected in 1863 in the Bolivian Andes, where amphibian declines have been linked to a new invasive strain of Bd. This finding highlighted the early presence of Bd in Latin America and the presence of both ancient endemic and recently introduced strains. Overall, the results suggested that some Bd strains have co-evolved with endemic amphibian fauna (Burrowes and De la Riva, 2017). During their presentation, Lambertini et al. found Bd prevalence of ~12% for caecilians from Brazilian Amazonia, the Atlantic Forest, and the Uruguayan Savannah, with Bd occurring even in areas considered to have low climatic suitability (Lambertini et al., 2017). The talk of López-Velázquez et al. called for caution regarding the interpretation of species distribution models that rely only

on climatic data for predicting the environmental suitability of Bd, suggesting that the role of the host must be included to disentangle new outbreaks. Finally, a historical analysis of Bd occurrence in Brazil including more than a decade of data was presented by Toledo, showing that Bd is widely distributed in the country and that both native and invasive amphibian species may act as hosts. Analyses of museum specimens revealed massive die-offs in the Atlantic Forest, and hypervirulent strains of Bd were shown to have resulted from the hybridization of an endemic strain (Bd-Brazil) with other strains in the world. Overall, it was suggested that human actions influence Bd epidemiology, and, therefore, urgent amphibian conservation actions must be planned and applied (Carvalho et al., 2017).

The occurrence of other pathogens and parasites associated with infectious and non-infectious diseases was also presented at the symposium. In particular, in the study presented by Peñafiel-Ricarte et al. about the distribution of *Ranavirus* in Chile, a low prevalence of infection in native and invasive frogs was reported. However, an apparent association between *Xenopus laevis* and *Ranavirus* supported the role of this invasive amphibian species in the introduction, spread, and persistence of the virus (Soto-Azat et al., 2016). Preliminary results from a comparative pathology study of captive amphibians from Ecuador were presented by Genoy-Puerto, revealing the presence of at least six parasites, fungi, and bacterial clusters associated with non-infectious and infectious diseases. Finally, González found multiple nematode parasites in amphibians of the Gran Chaco in Argentina and stressed the need to improve our knowledge about parasites and their deleterious effects on the amphibian fauna.

Host–pathogen interactions.—The symposium also pointed out the utility of experimental and theoretical approaches to understanding Bd dynamics. The presentation of Urbina et al. showed that Bd strain, host identity, and timing of exposure to the pathogen have important impacts on the survival of embryos and larvae of both native and invasive species in captivity. The study presented by Betancourt-León et al. quantified and described the distribution of Langerhans

cells and their role in the immune response to chytrid fungus on *X. laevis* and *Lithobates montezumae*. During their presentation, Raffel et al. emphasized the advantages of using the metabolic theory of ecology as a framework to develop models that predict how temperature influences infectious diseases. These models consider the thermal biology of ectotherm hosts and their associated parasites and successfully describe multiple aspects of their temperature dependence (Rohr et al., 2013; Molnár et al., 2017).

RESEARCH OPPORTUNITIES FOR DISEASE ECOLOGY

Participants in the symposium “Disease Ecology: Past and Present for a Better Future” identified some research gaps and questions during a discussion session held at the end of the conference. The points presented here are neither an exhaustive nor specific list of future objectives, and although many of them are currently being addressed, there is still a huge amount of work needed to be done. However, they represent some topics discussed by participants of the symposium to improve research goals in this field over the next few years for Latin America. These topics were identified based on current world trends on the research of disease ecology or specific needs identified for this particular geographic area, and were recognized as they may lead to a better understanding of the ecology and evolution of emerging diseases and management actions for conservation in Latin America. We outline these topics below.

1) How do global change drivers, including climate change, biological invasions, and land-use change, affect emerging infectious diseases?—Several studies in Latin America have addressed the relationship between some of those global-change drivers and pathogens. For example, the prevalence of pathogens such as Bd and *Ranavirus* has been studied in Costa Rica in relation to temperature (Whitfield et al., 2012, 2013). Interactions of thermal physiology of amphibian hosts and their fungal pathogen and how environment can change infection risk has been assessed in Costa Rica (Nowakowski et al., 2016). Synthetic works have been published from Central America (Whitfield et al., 2016) and more than a decade ago for Latin America (Lips et al., 2005). Both studies indicated the need to evaluate different areas and the influence of different pathogens and other threats involved in amphibian declines.

2) How do features of the host immune system contribute to or defend against emerging infectious diseases?—In Panama, several studies have found inhibitory action of symbiotic bacteria from amphibian skin on the growth of Bd (Rebollar et al., 2016). The role of skin microbiota as a protection against microbial pathogens has been also explored in sympatric species of the Atlantic forest (Brazil) in fragmented and continuous forest (Assis et al., 2017). A recent study in Colombia demonstrated that symbiotic bacteria and antimicrobial peptides allow coexistence of Andean species with the global pandemic lineage of Bd (Flechas et al., 2019). Similarly, the use of alkaloid defenses against microbial pathogens has been recently evaluated, providing evidence of pathogen inhibition by these substances (Hovey et al., 2018). Future studies can focus on evaluating the actions of these bacteria or alkaloid substances against other emerging infectious diseases such as ranavirosis while understanding the impact of disease on the host immune system. It is urgent to evaluate

the role played by these symbiotic bacteria for potential use as probiotic treatment in amphibians.

3) What is the role of cutaneous bacterial genes in the resistance to infection by Bd?—Gene expression in anti-Bd bacterial strains reported from amphibian species recovering from outbreaks (Madison et al., 2017) and description of genetic metabolic pathways in skin microbiomes have been analyzed, presenting potential functions of metabolites that have anti-Bd properties (Rebollar et al., 2018). This field demands more exploration to generate an inclusive understanding of the inhibition function of these bacteria.

4) To what extent do endangered species in captivity contribute to a better understanding of the symptoms and treatment of diseases and the viability of potential reintroductions?—Captive amphibians have been used as models to understand aspects such as microbiomes and efficiency of probiotics (Becker et al., 2011). Bacterial communities have been reported to change in captive amphibians, but a limited number of species have been evaluated in Latin America (Becker et al., 2014; Flechas et al., 2017). However, considering chytridiomycosis, the viability of potential reintroduction efforts using captive individuals is unknown, especially as there is a lack of methods to control this disease in the wild (Becker et al., 2011). To our knowledge, the efficiency of antifungal treatments that have been done in other regions (Woodhams et al., 2011) remains poorly explored for species in Latin America (Becker et al., 2011). For other diseases, such as ranavirosis, there is no information reported in captive animals in Latin America. However, studies in other regions have shown concurrent infections of pathogens can affect captive amphibians (Miller et al., 2008; Shaw et al., 2011; Latney and Klaphake, 2013) and reptiles (Hepojoki et al., 2015; Sim et al., 2016). In Latin America, other infectious diseases need to be evaluated in captive animals, especially as those diseases can be potential threats for future reintroduction programs.

5) What is the current distribution of non-Bd emerging diseases such as ranavirosis? What role do these diseases play in population declines?—Information about *Ranavirus* has been reported for different countries in Latin America, suggesting a wide distribution. In the south, *Ranavirus* has been reported in Argentina (Fox et al., 2006) and Chile (Soto-Azat et al., 2016). Other countries in South America with reports of this pathogen are Brazil and Uruguay (Galli et al., 2006), Peru (Warne et al., 2016) and Venezuela (Zupanovic et al., 1998). In Central America, there are reports of *Ranavirus* from Costa Rica (Whitfield et al., 2013) and Nicaragua (Stark et al., 2014). Unfortunately, countries with a high diversity of amphibians including Ecuador and Colombia still need to be evaluated to get a better understanding of the distribution and impact of ranaviruses.

6) What kind of actions can we as scientists take to integrate the knowledge generated by researchers on amphibian disease ecology with conservation actions in Latin America?—Publications of reviews with information about the conservation status of species can help further the understanding of the role played by diseases as well as providing guidelines for conservation actions. Reviews about the status of species in Argentina (Vaira et al., 2017), Bolivia (De la Riva and Reichle, 2014), Chile (Diaz-Paez and Ortiz, 2003), Ecuador (Ron et al., 2011), Peru (Catenazzi and von May, 2014), and Uruguay

(Canavero et al., 2010) emphasized the need to continuously collect population data to properly quantify potential amphibian declines as well as to establish a baseline of information. However, in the field of disease ecology, we have only found one synthetic work that examines chytridiomycosis in Mexico (Mendoza-Almeralla et al., 2015).

There is a need to compile information containing the main topics that each research group is working on in Latin America, to integrate and share knowledge among countries, and to establish collaborations. For example, studies of *Ranavirus* in Chile have generated key information that can provide guidelines for other countries where there is a lack of information related to this topic. Collaborative work will strengthen the knowledge base and avoid unnecessarily using resources. A successful example of this type of collaboration is the annual meeting held in Arizona (Integrated Research Challenges in Environmental Biology, Amphibian Declines), where different researchers working in topics related to amphibian diseases meet, share, and discuss their most recent advances as well as prioritize actions to be done in the near future. Hosted by the Partners in Amphibian and Reptile Conservation (PARC), this meeting integrates members from federal and state levels, zoos, the pet industry, conservationists, and researchers.

Another mechanism of communication to reach a broader audience more efficiently is the generation of networks. An example of a network in Latin America was the Research and Analysis Network for Neotropical Amphibians (RANA), also known in Spanish as the Red de Análisis sobre Anfibios Neotropicales Amenazados (Young and Lips, 2002). Launched in 2002 with economic support from the National Science Foundation (NSF), NatureServe, and the Universidad de Costa Rica, this network was funded until 2007. Research and Analysis Network for Neotropical Amphibians coordinated research on different causes of amphibian population declines, synthesized, and disseminated information collected from understudied geographical areas. The result was more than 50 publications (peer-reviewed papers and book chapters) and multiple presentations at international and national conferences (National Science Foundation Award 0130273, RCN: Coordinated Research on Amphibian Population Declines in the Neotropics; https://nsf.gov/awardsearch/showAward?AWD_ID=0130273). Strong collaborations with other networks such as the Declining Amphibian Population Task Force (DAPTF) part of the Species Survival Commission (SSC) of the International Union for Conservation of Nature (IUCN) were equally impactful.

The participants in this symposium concluded that progress in the field of disease ecology in Latin America definitely requires that more areas such as immunology, pathology, bioinformatics, co-infection, and new pathogen surveillance be included in research agendas going forward. Approaches from different fields will enrich our perspectives and improve existing actions to face the invisible threat of emerging infectious diseases. Additionally, promoting networking, exchanges, and knowledge transfer at national and international meetings can be possible if a Disease Ecology Section for the Latin American Congress of Herpetology is created to connect efforts for collaborative projects and management actions. A successful example of these efforts is the chapter of disease ecology formed in the Ecological Society of America (ESA) that has offered several workshops each year at their annual meeting, facilitating collaborative links for group members while promoting the integration of

disease ecology into the general study of ecology. Almost a decade ago, after the annual meeting of the Wildlife Disease Association (WDA) held in Argentina in 2010, the Latin America section was created. Professionals working in the disease ecology field decided to combine efforts for expanding research activities under the One Health concept.

ACTIONS PROPOSED TO ADVANCE THE FIELD OF DISEASE ECOLOGY IN LATIN AMERICA

Integrating knowledge of disease ecology with conservation actions is urgent. Very little research effort, particularly in Latin America, has resulted in conservation policies or concrete management plans. This was the main message that all the participants of the symposium agreed upon. In this context, three important actions were proposed as fundamental to the inclusion of basic knowledge of disease ecology in conservation and management efforts.

First, in order to have inclusive representation in management and decision-making, multidisciplinary groups must be created to include research specialists, scientific communicators, and government members. For example, efforts and actions made by the *Batrachochytrium salamandrivorans* group have shown how inclusion of different sectors can result in effective management decisions to prevent disease spread and population declines (Gray et al., 2015).

Second, scientists involved in primary research need to be actively involved in conservation decision-making and political topics that affect conservation (Ellison, 2016). It was agreed upon that increased basic research would not protect any threatened species. Although the conservation status of a number of amphibian species in Latin America has been documented as part of the Red Lists compiled by the IUCN, there is a need to document and follow up on the status of species in relation to diseases to better understand disease trends and risk factors as well as to implement actions and develop guidelines in disease management.

Scientists also need to make a better effort to communicate with politicians and managers to generate interest and reduce existing gaps between science and society. In Panama, for example, the joint action of representatives of the Ministry of the Environment (MiAmbiente), Panama Amphibian Rescue and Conservation project (PARC), and the Smithsonian Tropical Research Institute (STRI) have made advances in amphibian conservation plans after policy makers and scientists cooperated to provide a science-based framework for these conservation actions. Science and policy are still disconnected in most countries in Latin America (Ciocca and Delgado, 2017), and extensive work is needed to engage scientists and government.

Third, the scientific community needs to improve their communication skills and take further steps to clearly present their research to the general public. Workshops in social media and leadership can be useful to communicate research effectively. In other regions, non-profit, non-advocacy organizations such as COMPASS (<https://www.compasscomm.org>) and AAAS (<https://www.aaas.org>) have been offering training and coaching, leading to better networking and improving the relationship between scientists and the general public (Smith et al., 2013). Some of the programs have even resulted in extensive participation of citizens in science projects with great results. For example, data collection for disease surveillance has been accomplished at larger scales than if done by a group of scientists alone (Freifeld et al., 2010; Laaksonen et al., 2017) and has

simultaneously increased citizen engagement in the process of generating scientific knowledge (Pocock et al., 2017).

In conclusion, the symposium "Disease Ecology: Past and Present for a Better Future" at the XI Latin American Congress of Herpetology emphasized the current research in the field of disease ecology in different countries, revealing multiple research advances and opportunities and suggesting actions to advance the field. Integrating generated knowledge, increasing collaborative efforts among researchers, and improving the communication of research findings to the general public and decision makers seem to be the best starting points to provide guidelines for management plans of pathogen surveillance and conservation priorities in the region. Creating awareness about disease ecology will link conservation managers and decision makers to make science-based decisions; however, creating this link will require participation on both sides. These are some of the steps needed to help ensure the health and preservation of the impressive amphibian diversity of Latin America.

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LITERATURE CITED

- Alford, R. A., P. M. Dixon, and J. H. K. Pechmann. 2001. Ecology: global amphibian population declines. *Nature* 412:499–500.
- Alroy, J. 2015. Current extinction rates of reptiles and amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 112:13003–13008.
- Assis, A. B. de, C. C. Barreto, and C. A. Navas. 2017. Skin microbiota in frogs from the Brazilian Atlantic forest: species, forest type, and potential against pathogens. *PLoS ONE* 12:e0179628.
- Bacigalupe, L. D., C. Soto-Azat, C. García-Vera, I. Barriá-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.
- Becker, M. H., R. N. Harris, K. P. C. Minbiole, C. R. Schwantes, L. A. Rollins-Smith, L. K. Reinert, R. M. Brucker, R. J. Domangue, and B. Gratwicke. 2011. Towards a better understanding of the use of probiotics for preventing chytridiomycosis in Panamanian golden frogs. *EcoHealth* 8:501–506.
- Becker, M. H., C. L. Richards-Zawacki, B. Gratwicke, and L. K. Belden. 2014. The effect of captivity on the cutaneous bacterial community of the critically endangered Panamanian golden frog (*Atelopus zeteki*). *Biological Conservation* 176:199–206.
- Berger, L., R. Speare, P. Daszak, D. E. Green, A. A. Cunningham, C. L. Goggin, R. Slocombe, M. A. Ragan, A. D. Hyatt, K. R. McDonald, H. B. Hines, K. R. Lips, G. Marantelli, and H. Parkes. 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.
- Blaustein, A. R., S. S. Gervasi, P. T. J. Johnson, J. T. Hoverman, L. K. Belden, P. W. Bradley, and G. Y. Xie. 2012. Ecophysiology meets conservation: understanding the role of disease in amphibian population declines. *Philosophical Transactions of the Royal Society B: Biological Sciences* 367:1688.
- Blaustein, A. R., B. A. Han, R. A. Relyea, P. T. J. 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.
- Blaustein, A. R., and P. Johnson. 2003a. Explaining frog deformities. *Scientific American* 288:60–65.
- Blaustein, A. R., and P. T. Johnson. 2003b. The complexity of deformed amphibians. *Frontiers in Ecology and the Environment* 1:87–94.
- Blaustein, A. R., and J. M. Kiesecker. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. *Ecology Letters* 5:597–608.
- Blaustein, A. R., J. Urbina, P. W. Snyder, E. Reynolds, T. Dang, J. T. Hoverman, B. Han, D. H. Olson, C. Searle, and N. M. Hambalek. 2018. Effects of emerging infectious diseases on amphibians: a review of experimental studies. *Diversity* 10:81.
- Bosch, J., and I. Martínez-Solano. 2006. Chytrid fungus infection related to unusual mortalities of *Salamandra salamandra* and *Bufo bufo* in the Penalara Natural Park, Spain. *Oryx* 40:84–89.
- 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.
- Burrowes, P. A., and I. De la Riva. 2017. Unraveling the historical prevalence of the invasive chytrid fungus in the Bolivian Andes: implications in recent amphibian declines. *Biological Invasions* 19:1781–1794.
- Canavero, A., S. Carreira, J. Langone, F. Achaval, C. Borteiro, A. Camargo, I. da Rosa, A. Estrades, A. Fallabrino, F. Kolenc, M. M. López-Mendilaharsu, R. Maneyro, M. Meneghel, D. Nuñez...L. Ziegler. 2010. Conservation status assessment of the amphibians and reptiles of Uruguay. *Iheringia. Série Zoologia* 100:5–12.
- Carvalho, T., C. G. Becker, and L. F. Toledo. 2017. Historical amphibian declines and extinctions in Brazil linked to chytridiomycosis. *Proceedings of the Royal Society B: Biological Sciences* 284:20162254.
- Catenazzi, A., and R. von May. 2014. Conservation status of amphibians in Peru. *Herpetological Monographs* 28:1–23.
- Catenazzi, A., A. Swei, J. Finkle, E. Foreyt, L. Wyman, and V. T. Vredenburg. 2017. Epizootic to enzootic transition of a fungal disease in tropical Andean frogs: Are surviving species still susceptible? *PLoS ONE* 12:e0186478.
- Ciocca, D. R., and G. Delgado. 2017. The reality of scientific research in Latin America; an insider's perspective. *Cell Stress and Chaperones* 22:847–852.
- Crawford, A. J., K. R. Lips, and E. Bermingham. 2010. Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of

- central Panama. *Proceedings of the National Academy of Sciences of the United States of America* 107:13777–13782.
- Cunningham, A., P. Danzak, and J. Rodriguez. 2003. Pathogen pollution: defining a parasitological threat to biodiversity conservation. *Journal of Parasitology* 89(suppl.):S78–83.
- Cushman, S. A. 2006. Effects of habitat loss and fragmentation on amphibians: a review and prospectus. *Biological Conservation* 128:231–240.
- Daszak, P., L. Berger, A. A. Cunningham, A. D. Hyatt, D. E. Green, and R. Speare. 1999. Emerging infectious diseases and amphibian population declines. *Emerging Infectious Diseases* 5:735–748.
- De la Riva, I., and S. Reichle. 2014. Diversity and conservation of the amphibians of Bolivia. *Herpetological Monographs* 28:46–65.
- Densmore, C. L., and D. E. Green. 2007. Diseases of amphibians. *ILAR Journal* 48:235–254.
- Diaz-Paez, H., and J. C. Ortiz. 2003. Assessment of the conservation status of amphibians in Chile. *Revista Chilena De Historia Natural* 76:509–525.
- Ellison, A. M. 2016. It's time to get real about conservation. *Nature* 538:141.
- Fisher, M. C., D. A. Henk, C. J. Briggs, J. S. Brownstein, L. C. Madoff, S. L. McCraw, and S. J. Gurr. 2012. Emerging fungal threats to animal, plant and ecosystem health. *Nature* 484:186–194.
- Flechas, S. V., A. Acosta-González, L. A. Escobar, J. G. Kueneman, Z. A. Sánchez-Quitian, C. M. Parra-Giraldo, L. A. Rollins-Smith, L. K. Reinert, V. T. Vredenburg, A. Amézquita, and D. C. Woodhams. 2019. Microbiota and skin defense peptides may facilitate coexistence of two sympatric Andean frog species with a lethal pathogen. *The ISME Journal* 13:361–373.
- Flechas, S. V., A. Blasco-Zúñiga, A. Merino-Viteri, V. Ramírez-Castañeda, M. Rivera, and A. Amézquita. 2017. The effect of captivity on the skin microbial symbionts in three *Atelopus* species from the lowlands of Colombia and Ecuador. *PeerJ* 5:e3594.
- Fox, S., A. Greer, R. Torres-Cervantes, and J. P. Collins. 2006. First case of ranavirus-associated morbidity and mortality in natural populations of the South American frog *Atelognathus patagonicus*. *Diseases of Aquatic Organisms* 72:87–92.
- Freifeld, C. C., R. Chunara, S. R. Mekaru, E. H. Chan, T. Kass-Hout, A. Ayala Iacucci, and J. S. Brownstein. 2010. Participatory epidemiology: use of mobile phones for community-based health reporting. *PLoS Medicine* 7: e1000376.
- Frick, W. F., J. F. Pollock, A. C. Hicks, K. E. Langwig, D. S. Reynolds, G. G. Turner, C. M. Butchkoski, and T. H. Kunz. 2010. An emerging disease causes regional population collapse of a common North American bat species. *Science* 329:679.
- Galli, L., A. Pereira, A. Márquez, and R. Mazzoni. 2006. Ranavirus detection by PCR in cultured tadpoles (*Rana catesbeiana* Shaw, 1802) from South America. *Aquaculture* 257:78–82.
- Garner, T. W. J., S. Walker, J. Bosch, A. D. Hyatt, A. A. Cunningham, and M. C. Fisher. 2005. Chytrid fungus in Europe. *Emerging Infectious Disease Journal* 11:1639–1641.
- Gervasi, S., C. Gondhalekar, D. H. Olson, and A. R. Blaustein. 2013. Host identity matters in the amphibian-*Batrachochytrium dendrobatidis* system: fine-scale patterns of variation in responses to a multi-host pathogen. *PLoS ONE* 8:e54490.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *Bioscience* 50:653–666.
- Grant, E. H. C., D. A. W. Miller, B. R. Schmidt, M. J. Adams, S. M. Amburgey, T. Chambert, S. S. Cruickshank, R. N. Fisher, D. M. Green, B. R. Hossack, P. T. J. Johnson, M. B. Joseph, T. A. G. Rittenhouse, M. E. Ryan...E. Muths. 2016. Quantitative evidence for the effects of multiple drivers on continental-scale amphibian declines. *Scientific Reports* 6:25625.
- Gray, M. J., J. P. Lewis, P. Nanjappa, B. Klocke, F. Pasmans, A. Martel, C. Stephen, G. Parra Olea, S. A. Smith, A. Sacerdote-Velat, M. R. Christman, J. M. Williams, and D. H. Olson. 2015. *Batrachochytrium salamandrivorans*: the North American response and a call for action. *PLoS Pathogens* 11:e1005251.
- Green, D. E., K. A. Converse, and A. K. Schrader. 2002. Epizootiology of sixty-four amphibian morbidity and mortality events in the USA, 1996–2001. *Annals of the New York Academy of Sciences* 969:323–339.
- Hepojoki, J., P. Salmenperä, T. Sironen, U. Hetzel, Y. Korzyukov, A. Kipar, and O. Vapalahti. 2015. Arenavirus coinfections are common in snakes with boid inclusion body disease. *Journal of Virology* 89:8657.
- Hero, J. M., and C. Morrison. 2004. Frog declines in Australia: global implications. *Herpetological Journal* 14: 175–186.
- Hof, C., M. B. Araújo, W. Jetz, and C. Rahbek. 2011. Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature* 480:516.
- Houlahan, J. E., C. S. Findlay, B. R. Schmidt, A. H. Meyer, and S. L. Kuzmin. 2000. Quantitative evidence for global amphibian population declines. *Nature* 404:752–755.
- Hovey, K. J., E. M. Seiter, E. E. Johnson, and R. A. Saporito. 2018. Sequestered alkaloid defenses in the dendrobatid poison frog *Oophaga pumilio* provide variable protection from microbial pathogens. *Journal of Chemical Ecology* 44:312–325.
- James, T. Y., L. F. Toledo, D. Rödder, D. da Silva Leite, A. M. Belasen, C. M. Betancourt-Román, T. S. Jenkinson, C. Soto-Azat, C. Lambertini, A. V. Longo, J. Ruggeri, J. P. Collins, P. A. Burrowes, K. R. Lips...J. E. Longcore. 2015. Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. *Ecology and Evolution* 5:4079–4097.
- Johnson, P., M. K. Reeves, S. K. Krest, and A. E. Pinkney. 2010. A decade of deformities: advances in our understanding of amphibian malformations and their implications, p. 511–536. *In: Ecotoxicology of Amphibians and Reptiles*. Second edition. D. W. Sparling, G. Linder, C. A. Bishop, and S. K. Krest (eds.). CRC Press, Taylor & Francis Group, Boca Raton, Florida.
- Johnson, P. T. J., K. B. Lunde, D. A. Zelmer, and J. K. Werner. 2003. Limb deformities as an emerging parasitic disease in amphibians: evidence from museum specimens and resurvey data. *Conservation Biology* 17:1724–1737.
- Jones, K. E., N. G. Patel, M. A. Levy, A. Storeygard, D. Balk, J. L. Gittleman, and P. Daszak. 2008. Global trends in emerging infectious diseases. *Nature* 451:990–993.

- Juopperi, T., K. Karli, R. De Voe, and C. B. Grindem. 2002. Granulomatous dermatitis in a spadefoot toad (*Scaphiopus holbrooki*). *Veterinary Clinical Pathology* 31:137–139.
- Kats, L. B., and R. P. Ferrer. 2003. Alien predators and amphibian declines: review of two decades of science and the transition to conservation. *Diversity and Distributions* 9:99–110.
- Kiesecker, J. M., A. R. Blaustein, and C. L. Miller. 2001. Transfer of a pathogen from fish to amphibians. *Conservation Biology* 15:1064–1070.
- Kilpatrick, A. M., C. J. Briggs, and P. Daszak. 2010. The ecology and impact of chytridiomycosis: an emerging disease of amphibians. *Trends in Ecology & Evolution* 25: 109–118.
- Laaksonen, M., E. Sajanti, J. J. Sormunen, R. Penttinen, J. Hänninen, K. Ruohomäki, I. Sääksjärvi, E. J. Vesterinen, I. Vuorinen, J. Hytönen, and T. Klemola. 2017. Crowd-sourcing-based nationwide tick collection reveals the distribution of *Ixodes ricinus* and *I. persulcatus* and associated pathogens in Finland. *Emerging Microbes Infections* 6:e31.
- Lambertini, C., C. G. Becker, C. Bardier, D. da Silva Leite, and L. F. Toledo. 2017. Spatial distribution of *Batrachochytrium dendrobatidis* in South American caecilians. *Diseases of Aquatic Organisms* 124:109–116.
- Latney, L. V., and E. Klaphake. 2013. Selected emerging diseases of amphibia. *New and Emerging Diseases* 16:283–301.
- Lips, K. R., P. A. Burrowes, J. R. Mendelson, and G. Parra-Olea. 2005. Amphibian population declines in Latin America: a synthesis. *Biotropica* 37:222–226.
- 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.
- Lorch, J. M., S. Knowles, J. S. Lankton, K. Michell, J. L. Edwards, J. M. Kapfer, R. A. Staffen, E. R. Wild, K. Z. Schmidt, A. E. Ballmann, D. Blodgett, T. M. Farrell, B. M. Glorioso, L. A. Last...D. S. Blehert. 2016. Snake fungal disease: an emerging threat to wild snakes. *Philosophical Transactions of the Royal Society B: Biological Sciences* 371:20150457.
- Madison, J. D., E. A. Berg, J. G. Abarca, S. M. Whitfield, O. Gorbatenko, A. Pinto, and J. L. Kerby. 2017. Characterization of *Batrachochytrium dendrobatidis* inhibiting bacteria from amphibian populations in Costa Rica. *Frontiers in Microbiology* 8:290.
- McCallum, M. L. 2007. Amphibian decline or extinction? Current declines dwarf background extinction rate. *Journal of Herpetology* 41:483–491.
- Mendoza-Almeralla, C., P. Burrowes, and G. Parra-Olea. 2015. La quitridiomycosis en los anfibios de México: una revisión. *Revista Mexicana de Biodiversidad* 86:238–248.
- Miller, D. L., S. Rajeev, M. Brookins, J. Cook, L. Whittington, and C. A. Baldwin. 2008. Concurrent infection with Ranavirus, *Batrachochytrium dendrobatidis*, and *Aeromonas* in a captive anuran colony. *Journal of Zoo and Wildlife Medicine* 39:445–449.
- Molnár, P. K., J. P. Sckrabulis, K. A. Altman, and T. R. Raffel. 2017. Thermal performance curves and the metabolic theory of ecology—a practical guide to models and experiments for parasitologists. *Journal of Parasitology* 103:423–439.
- Mooney, H. A. 2010. The ecosystem-service chain and the biological diversity crisis. *Philosophical Transactions of the Royal Society B: Biological Sciences* 365:31–39.
- Nowakowski, A. J., S. M. Whitfield, E. A. Eskew, M. E. Thompson, J. P. Rose, B. L. Caraballo, J. L. Kerby, M. A. Donnelly, and B. D. Todd. 2016. Infection risk decreases with increasing mismatch in host and pathogen environmental tolerances. *Ecology Letters* 19:1051–1061.
- Pasmans, F., F. Mutschmann, T. Halliday, and P. Zwart. 2006. Amphibian decline: the urgent need for amphibian research in Europe. *The Veterinary Journal* 171:18–19.
- Pechmann, J. H. K., D. E. Scott, R. D. Semlitsch, J. P. Caldwell, L. J. Vitt, and J. W. Gibbons. 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253:892–895.
- Pocock, M. J. O., J. C. Tweddle, J. Savage, L. D. Robinson, and H. E. Roy. 2017. The diversity and evolution of ecological and environmental citizen science. *PLoS ONE* 12:e0172579.
- Rebollar, E. A., A. Gutiérrez-Preciado, C. Noecker, A. Eng, M. C. Hughey, D. Medina, J. B. Walke, E. Borenstein, R. V. Jensen, L. K. Belden, and R. N. Harris. 2018. The skin microbiome of the neotropical frog *Craugastor fitzingeri*: inferring potential bacterial-host-pathogen interactions from metagenomic data. *Frontiers in Microbiology* 9:466.
- Rebollar, E. A., M. C. Hughey, D. Medina, R. N. Harris, R. Ibáñez, and L. K. Belden. 2016. Skin bacterial diversity of Panamanian frogs is associated with host susceptibility and presence of *Batrachochytrium dendrobatidis*. *The ISME Journal* 10:1682–1695.
- Reeves, M. K., K. A. Medley, A. E. Pinkney, M. Holyoak, P. T. J. Johnson, and M. J. Lannoo. 2013. Localized hotspots drive continental geography of abnormal amphibians on U.S. wildlife refuges. *PLoS ONE* 8:e77467.
- Rohr, J. R., T. R. Raffel, A. R. Blaustein, P. T. J. 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: cot022.
- 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.
- Ron, S. R., J. Guayasamin, and P. Menéndez-Guerrero. 2011. Biodiversity and conservation status of Ecuadorian amphibians, p. 129–170. *In: Amphibian Biology*. Vol. 9. Part 2. H. Heatwole, C. L. Barrio-Amoros, and H. W. Wilkinson (eds.). Surrey Beatty & Sons PTY Limited, Baulkham Hills, Australia.
- Rosenblum, E. B., T. Y. James, K. R. Zamudio, T. J. Poorten, D. Ilut, D. Rodriguez, J. M. Eastman, K. Richards-Hrdlicka, S. Joneson, T. S. Jenkinson, J. E. Longcore, G. Parra Olea, L. F. Toledo, M. L. Arellano...J. E. Stajich. 2013. Complex history of the amphibian-killing chytrid fungus revealed with genome resequencing data. *Proceedings of the National Academy of Sciences of the United States of America* 110:9385–9390.
- Savage, A. E., and K. R. Zamudio. 2016. Adaptive tolerance to a pathogenic fungus drives major histocompatibility complex evolution in natural amphibian populations. *Proceedings of the Royal Society B: Biological Sciences* 283:20153115.
- 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.
- Searle, C. L., S. S. Gervasi, J. Hua, J. I. Hammond, R. A. Relyea, D. H. Olson, and A. R. Blaustein. 2011.

- Differential host susceptibility to *Batrachochytrium dendrobatidis*, an emerging amphibian pathogen. *Conservation Biology* 25:965–974.
- Shaw, S., R. Speare, D. H. Lynn, G. Yeates, Z. Zhao, L. Berger, and R. Jakob-Hoff. 2011. Nematode and ciliate nasal infection in captive Archey's Frogs (*Leiopelma archeyi*). *Journal of Zoo and Wildlife Medicine* 42:473–479.
- Sim, R. R., M. C. Allender, L. K. Crawford, A. N. Wack, K. J. Murphy, J. L. Mankowski, and E. Bronson. 2016. *Ranavirus* epizootic in captive eastern box turtles (*Terrapene carolina carolina*) with concurrent herpesvirus and mycoplasma infection: management and monitoring. *Journal of Zoo and Wildlife Medicine* 47:256–270.
- Smith, B., N. Baron, C. English, H. Galindo, E. Goldman, K. McLeod, M. Miner, and E. Neeley. 2013. COMPASS: navigating the rules of scientific engagement. *PLoS Biology* 11:e1001552.
- Solow, A. R. 2016. On Bayesian inference about extinction. *Proceedings of the National Academy of Sciences of the United States of America* 113:E1132.
- Soto-Azat, C., A. Peñafiel-Ricaurte, S. J. Price, N. Sallaberry-Pincheira, M. P. García, M. Alvarado-Rybak, and A. A. Cunningham. 2016. *Xenopus laevis* and emerging amphibian pathogens in Chile. *EcoHealth* 13:775–783.
- Soto-Azat, C., A. Valenzuela-Sánchez, B. T. Clarke, K. Busse, J. C. Ortiz, C. Barrientos, and A. A. Cunningham. 2013a. Is chytridiomycosis driving Darwin's frogs to extinction? *PLoS ONE* 8:e79862.
- Soto-Azat, C., A. Valenzuela-Sánchez, B. Collen, J. M. Rowcliffe, A. Veloso, and A. A. Cunningham. 2013b. The population decline and extinction of Darwin's frogs. *PLoS ONE* 8:e66957.
- Speare, R., A. D. Thomas, P. O'Shea, and W. A. Shipton. 1994. *Mucor amphibiorum* in the toad, *Bufo marinus*, in Australia. *Journal of Wildlife Diseases* 30:399–407.
- Stark, T., C. Laurijssens, M. Weterings, A. Spitzen-van der Sluijs, A. Martel, and F. Pasmans. 2014. Death in the clouds: *Ranavirus* associated mortality in assemblage of cloud forest amphibians in Nicaragua. *Acta Herpetologica* 9:125–127.
- Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman, and R. W. Waller. 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* 306:1783–1786.
- Stuart, S. N., J. Hoffman, J. S. Chanson, N. A. Cox, R. Berridge, R. Ramani, and B. E. Young. 2008. *Threatened Amphibians of the World*. Lynx Edicions, Barcelona, Spain; IUCN, Gland, Switzerland; and Conservation International, Arlington, Virginia.
- Taylor, S. K., E. S. Williams, A. C. Pier, K. W. Mills, and M. D. Bock. 1999. Mucormycotic dermatitis in captive adult Wyoming toads. *Journal of Wildlife Diseases* 35:70–74.
- Vaira, M., L. C. Pereyra, M. S. Akmentins, and J. Bielby. 2017. Conservation status of amphibians of Argentina: an update and evaluation of national assessments. *Amphibian & Reptile Conservation* 11:36–44.
- Valenzuela-Sánchez, A., B. R. Schmidt, D. E. Uribe-Rivera, F. Costas, A. A. Cunningham, and C. Soto-Azat. 2017. Cryptic disease-induced mortality may cause host extinction in an apparently stable host–parasite system. *Proceedings of the Royal Society B: Biological Sciences* 284: 20171176.
- Voyles, J. 2011. Phenotypic profiling of *Batrachochytrium dendrobatidis*, a lethal fungal pathogen of amphibians. *Fungal Ecology* 4:196–200.
- Voyles, J., E. B. Rosenblum, and L. Berger. 2011. Interactions between *Batrachochytrium dendrobatidis* and its amphibian hosts: a review of pathogenesis and immunity. *Microbes and Infection* 13:25–32.
- Vredenburg, V. T., R. A. Knapp, T. S. Tunstall, and C. J. Briggs. 2010. Dynamics of an emerging disease drive large-scale amphibian population extinctions. *Proceedings of the National Academy of Sciences of the United States of America* 107:9689–9694.
- Wake, D. B., and V. T. Vredenburg. 2008. Are we in the midst of the sixth mass extinction? A view from the world of amphibians. *Proceedings of the National Academy of Sciences of the United States of America* 105:11466–11473.
- 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. *PLoS ONE* 11:e0145864.
- Whitfield, S. M., E. Geerdes, I. Chacon, E. Ballesteros 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.
- Whitfield, S. M., J. Kerby, L. R. Gentry, and M. A. Donnelly. 2012. Temporal variation in infection prevalence by the amphibian chytrid fungus in three species of frogs at La Selva, Costa Rica. *Biotropica* 44:779–784.
- Whitfield, S. M., K. R. Lips, and M. A. Donnelly. 2016. Amphibian decline and conservation in Central America. *Copeia* 104:351–379.
- Woodhams, D. C., R. A. Alford, C. J. Briggs, M. Johnson, and L. A. Rollins-Smith. 2008. Life-history trade-offs influence disease in changing climates: strategies of an amphibian pathogen. *Ecology* 89:1627–1639.
- Woodhams, D. C., J. Bosch, C. J. Briggs, S. Cashins, L. R. Davis, A. Lauer, E. Muths, R. Puschendorf, B. R. Schmidt, B. Sheafor, and J. Voyles. 2011. Mitigating amphibian disease: strategies to maintain wild populations and control chytridiomycosis. *Frontiers in Zoology* 8:8.
- Young, B. E., and K. R. Lips. 2002. RANA: the research and analysis network for neotropical amphibians. *Froglog* 53: 1–3.
- Young, B. E., K. R. Lips, J. K. Reaser, R. Ibáñez, A. W. Salas, J. R. Cedeño, L. A. Coloma, S. Ron, E. La Marca, J. R. Meyer, A. Muñoz, F. Bolaños, G. Chaves, and D. Romo. 2001. Population declines and priorities for amphibian conservation in Latin America. *Conservation Biology* 15: 1213–1223.
- Zupanovic, Z., C. Musso, G. Lopez, C.-L. Louriero, A. D. Hyatt, S. Hengstberger, and A. J. Robinson. 1998. Isolation and characterization of iridoviruses from the giant toad *Bufo marinus* in Venezuela. *Diseases of Aquatic Organisms* 33:1–9.