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## From the organismal to biosphere levels: environmental impacts on the amphibian microbiota

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**Title:** From the organismal to biosphere levels: environmental impacts on the amphibian microbiota

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**One sentence summary:**

This review synthesizes over a decade of knowledge, gaps, and future directions on the influence of environmental factors on amphibian microbiotas at multiple biological levels of organization.

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## **Abstract**

This review summarizes the role of environmental factors on amphibian microbiotas at the organismal, population, community, ecosystem, and biosphere levels. At the organismal-level, tissue source, disease status, and experimental manipulations were the strongest predictors of variation in amphibian microbiotas. At the population-level, habitat quality, disease status, and ancestry were commonly documented as drivers of microbiota turnover. At the community-level, studies focused on how species' niche influence microbiota structure and function. At the ecosystem-level, abiotic and biotic reservoirs were important contributors to microbiota structure. At the biosphere-level, databases, sample banks, and semi-natural experiments were commonly used to describe microbiota assembly mechanisms among temperate and tropical amphibians. Collectively, our review demonstrates that environmental factors can influence microbiotas through diverse mechanisms at all biological scales. Importantly, while environmental mechanisms occurring at each of the different scales can interact to shape microbiotas, the past ten years of research have mostly been characterized by targeted approaches at individual scales. Looking forward, efforts considering how environmental factors at multiple organizational levels interact to shape microbiota diversity and function are paramount. Generating opportunities for meaningful cross-disciplinary interactions and supporting infrastructure for research that spans biological scales are imperative to addressing this gap.

**Keywords:** frogs, salamanders, toads, microbial ecology, global change, reintegrating biology

## Introduction

Host-associated microbiomes play an essential role in the health of organisms, including immune system activation, metabolism and energy uptake (Baquero & Nombela, 2012). Changes in microbiome diversity or composition can influence the contributions these communities bestow to host physiological processes (Petersen & Round, 2014). It has been well established that wildlife microbial communities may differ depending on multiple host physiological and behavioral factors (i.e., life stage, natural history, habitat use, disease status; Wang *et al.*, 2011, Kohl *et al.*, 2013, Kueneman *et al.*, 2014, Walke *et al.*, 2014, Avena *et al.*, 2016, Jiménez & Sommer, 2017, Jani & Briggs, 2018). As our understanding of microbiomes continues to grow, the role the environment plays in structuring host-associated microbial communities continues to be documented (i.e. temperature, available diet, pollutants; Sanzo & Hecnar, 2006, Antwis *et al.*, 2014a, Heiman & Greenway, 2016, Kohl & Yahn, 2016, Zhang *et al.*, 2016, Fontaine *et al.*, 2018, Hernández-Gómez *et al.*, 2020b, Li *et al.*, 2020, Yang *et al.*, 2020a, Huang & Liao 2021, Huang *et al.*, 2021, Walke *et al.*, 2014, Avena *et al.*, 2016, Jani & Briggs, 2018). While the effects of environmental variation on host-associated microbiomes have been studied extensively in humans, ruminants and model organisms, this line of study has not been as deeply investigated in wildlife.

In the coming decades, wildlife populations are expected to face a multitude of threats associated with environmental change that can alter natural associations between hosts and microbiotas. For example, by altering natural sources of microbial symbionts in the environment, habitat degradation (i.e., fragmentation or deforestation) has been documented to alter microbiotas in amphibians, reptiles, birds, and mammals (Amato *et al.*, 2013, Jiménez *et al.*, 2020, Murray *et al.*, 2020, Beale *et al.*, 2022). Furthermore, in many cases, growing evidence suggests that shifts in microbial communities induced by environmental changes can result in cascading negative effects to host health (Redford *et al.*, 2012, Bahrndorff *et al.*, 2016, Jiménez & Sommer, 2017). Given the association between overall health and host-associated microbiomes, the ability to make *a priori* predictions about how environmental changes will alter host-associated microbiomes in wildlife, and importantly when changes to microbiomes are expected to modify health, is both of fundamental biological interest and has critical conservation implications.

To understand when and how environmental changes influence microbiota structure and function, reintegrating our understanding across the silos of biological disciplines and scales is a fundamental contemporary challenge. This review will (1) summarize current understanding of how environmental factors influence amphibian microbiota at the organismal, population, community, ecosystem, and biosphere levels, (2) highlight gaps in our understanding of how environmental factors influence amphibian microbiota and, (3) identify avenues for addressing these gaps.

## Amphibians as a Model for Microbiota Community Ecology

Amphibians are a useful model for understanding the role of environmental factors in shaping microbial communities. First, amphibian species vary in life history traits from fully aquatic species to species that undergo metamorphosis where larval stages are fully aquatic and adult stages are terrestrial. As such amphibians utilize a diversity of environments that influence both diversity and composition of host-associated microbial communities (Kueneman *et al.*, 2019).

Second, amphibians are globally distributed and live in diverse habitats from vernal pools in the arctic to permanent temperate ponds to tropical ephemeral bromeliad microecosystems (Ficetola *et al.*, 2015). Additionally, populations of the same species can live in habitats that vary in environmental conditions. For example, North American wood frogs (*Rana sylvaticus*) live as far south as Alabama and as far north as Alaska; thus, wood frogs across their range can encounter drastically different abiotic and biotic environmental conditions (Larson *et al.*, 2014). Similarly, populations of wood frogs can be found in ponds that vary in quality from populations highly impacted by human activities such as agriculture to relatively pristine ponds found in protected state lands (Hua *et al.*, 2013). Therefore, the wide range of habitats utilized by amphibians make these taxa a useful model for understanding the effects of the environment on microbiotas.

Third, amphibians have long been established as useful model systems with research across biological scales and disciplines. For instance, the ability for some amphibian species to produce large numbers of offspring

and the relative ease of caring for amphibians in the lab makes these taxa ideal for experimental work. Indeed, amphibians such as African clawed frogs (*Xenopus laevis*), leopard frogs (*Rana* sp.), and common frogs (*Rana temporaria*), are well established across disciplines as laboratories and models for asking genetic, physiological, toxicological, developmental, infectious disease and numerous other research questions. In addition, amphibians are also useful models in the field of ecology and evolution since amphibian communities are well-described and the genome has been sequenced for both model and non-model species. Collectively, this past research across disciplines provides a strong foundation for evaluating how environmental effects on microbiotas across biological scale.

Lastly, amphibian microbiotas from captive and wild populations have received considerable attention in the literature over the past decade. The microbes that reside on (i.e., skin microbiota) or within (i.e., gut microbiota) amphibians are not only highly sensitive to environmental changes (Hughey *et al.*, 2016, Hughey *et al.*, 2017b, Hernández-Gómez *et al.*, 2020a; Wuerthner *et al.*, 2022), but studies indicate that changes to amphibian microbiota have important implications for amphibian susceptibility to disease (e.g., *Batrachochytrium dendrobatidis*; Bd; Bates *et al.*, 2018, Greenspan *et al.*, 2020). Indeed, a number of bacterial isolates from the skin of amphibians can produce metabolites that inhibit amphibian fungal pathogens associated with global amphibian declines (Woodhams *et al.*, 2015, Woodhams *et al.*, 2018). The link between changes to the skin microbiota and amphibian health, as well as the potential role of bacterial symbionts in disease dynamics, contribute to the useful nature of amphibians as a model.

### **Amphibian Microbiome Literature Collection**

We identified amphibian microbiota manuscripts published between 2011 and 2022 by searching the phrases “amphibian”, “tadpole”, “salamander”, “caecilian”, “toad”, “frog”, “microbes”, “microbial communities”, “16S rRNA”, “18S rRNA”, “bacteria”, “DNA sequencing”, “microbiome”, “microbiota”, and “amplicon sequencing” on webofscience.com. The last search was performed on December 19, 2022 and returned 4,337 hits. We performed an initial review of manuscript titles and abstracts to reduce the number of studies to those that implemented shotgun metagenomics or 16S rRNA amplicon sequencing to characterize the microbial communities. For the remaining 234 manuscripts, we evaluated each study’s methodology and assigned them to different biological categories based on their sampling strategies (Box 1). Studies may have been assigned to more than one category if the authors’ sampling strategy overlapped across multiple biological levels of organization (Table 1). Following characterization, we evaluated each study independently to determine the effect of environmental/individual factors on microbiota community diversity (i.e., alpha diversity), composition (i.e., beta diversity), and compositional heterogeneity (i.e., beta diversity dispersion).

### **Organismal Level**

The vast majority of work evaluating the effects of environmental factors on amphibian microbiotas falls into the organismal level. We categorize organismal-level studies as those that focus on measuring how environmental factors influence the microbiotas of individuals of a particular species. The environmental factors considered in the literature are diverse including studies that evaluate the effects of diet (Antwis *et al.*, 2014a, Antwis *et al.*, 2014c; Kohl *et al.*, 2014, Chang *et al.*, 2016, Edwards *et al.*, 2017, Knutie *et al.*, 2017b, Wang *et al.*, 2020, Zhang *et al.*, 2020, Huang & Liao, 2021, Wang *et al.*, 2021), temperature (Kohl & Yahn, 2016, Longo & Zamudio 2017a, Longo & Zamudio 2017b, Fontaine *et al.*, 2018, Muletz-Wolz *et al.*, 2019, Li *et al.*, 2020, Fontaine *et al.*, 2020, Carter *et al.*, 2021, Zhu *et al.*, 2021), housing conditions (Loudon *et al.*, 2014, Kueneman *et al.*, 2016a, Loudon *et al.*, 2016, Kearns *et al.*, 2017, Tong *et al.*, 2019a, Wuerthner *et al.*, 2019, Michaels & Preziosi 2020, Jones *et al.*, 2021, Piccinni *et al.*, 2021, Walke *et al.*, 2021, Zhu *et al.*, 2022c), habitat choice/life-stage (i.e. aquatic – terrestrial habitat use correlates with developmental stages; Kueneman *et al.*, 2014, Kueneman *et al.*, 2016b, Vences *et al.*, 2016, Bletz *et al.*, 2017d, Davis *et al.*, 2017, Sabino-Pinto *et al.*, 2017, Sanchez *et al.*, 2017, Bataille *et al.*, 2018, Chai *et al.*, 2018, Prest *et al.*, 2018, Zhang *et al.*, 2019, Flechas *et al.*, 2019, Long *et al.*, 2020, Tong *et al.*, 2020c, Xu *et al.*, 2020b, Yang *et al.*, 2020b, Alexiev *et al.*, 2021, Fontaine *et al.*, 2021, Chai *et al.*, 2022b, Hou *et al.*

*al.*, 2022, Martinez-Ugalde *et al.*, 2022, Michaels & Preziosi 2022, Wuerthner *et al.*, 2022, Yang *et al.*, 2022), social interactions (Hughey *et al.*, 2017a, McGrath-Blaser *et al.*, 2021, Kruger & Roth 2022), pathogen exposure/infection status (Jani & Briggs 2014, Becker *et al.*, 2015, Federici *et al.*, 2015, Walker *et al.*, 2015, Longo & Zamudio 2017a; Longo & Zamudio 2017b, Lopez *et al.*, 2017, Jani & Briggs 2018, Becker *et al.*, 2019, Harrison *et al.*, 2019, Shu *et al.*, 2019a, Hernández-Gómez *et al.*, 2020b, Kruger 2020, Weeks *et al.*, 2020, Jani *et al.*, 2021, Jones *et al.*, 2021, Medina *et al.*, 2021, Hu *et al.*, 2022, Jiang *et al.*, 2022, Schmeller *et al.*, 2022), pollutants (Kohl *et al.*, 2015, Hughey *et al.*, 2016, Knutie *et al.*, 2018, Mu *et al.*, 2018, Wiebler *et al.*, 2018, Wang *et al.*, 2019, Ya *et al.*, 2019, Yao *et al.*, 2019, Bie *et al.*, 2020, Hernández-Gómez *et al.*, 2020b, Xie *et al.*, 2020, Ya *et al.*, 2020, Yang *et al.*, 2020a, Zheng *et al.*, 2020, Evariste *et al.*, 2021, Gust *et al.*, 2021, Gutierrez-Villagomez *et al.*, 2021, Huang *et al.*, 2021, Jiménez *et al.*, 2021, Zhao *et al.*, 2021, Chai *et al.*, 2022a, Chai *et al.*, 2022b, Chapman *et al.*, 2022, Huang *et al.*, 2022a, Huang *et al.*, 2022b, Li *et al.*, 2022, Lin *et al.*, 2022, Liu *et al.*, 2022a, Liu *et al.*, 2022b, Liu *et al.*, 2022c, Lv *et al.*, 2022, Shen *et al.*, 2022, Wan *et al.*, 2022, Zhu *et al.*, 2022a, Zhu *et al.*, 2022b), seasonal variation (Longo *et al.*, 2015, Tong *et al.*, 2019b, Tong *et al.*, 2020a, Tong *et al.*, 2020b, Walke *et al.*, 2021; Longo 2022, Xu *et al.*, 2022), and supplementation or removal of microorganisms (Rebollar *et al.*, 2016b, Pereira *et al.*, 2017, Weng *et al.*, 2017 Madison *et al.*, 2019, Kenison *et al.*, 2020, Woodhams *et al.*, 2020, Becker *et al.*, 2021, Christian *et al.*, 2021, Tong *et al.*, 2021).

Aside from the wide range in environmental conditions evaluated in the literature, many of these studies utilize a similar approach: characterizing and comparing the diversity (alpha and beta) of the skin or gut microbes in amphibians experiencing different environmental conditions. For example, Huang *et al.*, (2021) exposed *Pelophylax nigromaculatus* tadpoles to atrazine and found that 500ug/L of atrazine altered the composition and diversity of intestinal microbiota after 20 days. Using a similar study design, Walke *et al.*, (2021) found that altering habitat structure by adding substrate into a pond shifted the composition of the microbiota community on the tadpole skin. Collectively, across these studies, there is an overwhelmingly consistent conclusion that environmental factors influence microbiota diversity and structure among individuals.

Despite consensus that shifts in environmental factors can induce shifts in microbiota diversity, how, when, and the mechanisms for how environmental change influences microbiota diversity and structure is not well understood. This is complicated by the challenge that a shift in the same environmental factor can induce different directional changes in microbiota diversity. For example, Li *et al.*, (2020), Fontaine and Kohl (2020), and Kohl and Yahn (2016) found that shifts in temperature had no effect on microbiota alpha diversity. In contrast, Fontaine *et al.*, (2018), Fontaine *et al.*, (2022), Muletz-Wolz *et al.*, (2019), and Longo & Zamudio, (2017a) found that increasing temperatures caused a decrease in the microbiota alpha diversity. In addition, Carter *et al.*, (2021) found richer bacteriome communities at intermediate temperatures (e.g., 14°C) compared to low (6°C) and high temperatures (22°C) in experimental manipulations. The equivocal nature of these studies highlight a significant challenge in these types of investigations, while studies may manipulate the same environmental factor (temperature), variation in other environmental factors associated with experimental methods (field vs. lab), housing conditions (experimental unit size, water source), host source (i.e., host-associated factors-species used, population) make developing generalizations about how specific environmental factors influence microbiota challenging. Collectively, this work underscores the importance of integrated approaches that work to standardize experimental work across disciplines, regions, etc.

Lastly, while a number of studies evaluate how environmental factors modify microbiota diversity and composition changes, only a handful consider the functional consequences of these shifts in microbial communities. Of these studies, the most common response variable assessed is the effect of shifting microbial communities' on amphibian disease outcomes, specifically, amphibian susceptibility to the amphibian pathogenic fungal disease, Chytridiomycosis (Becker *et al.*, 2015, Federici *et al.*, 2015, Longo *et al.*, 2015, Walke *et al.*, 2015, Kueneman *et al.*, 2016b, Edwards *et al.*, 2017, Bletz *et al.*, 2018, Madison *et al.*, 2019, Tong *et al.*, 2020b, Woodhams *et al.*, 2020, Jani *et al.*, 2021, Jiménez *et al.*, 2021, Chen *et al.*, 2022a, Estrada *et al.*, 2022). Five other studies evaluated disease susceptibility to other amphibian pathogens: one using ranavirus (Harrison *et al.*, 2019), three using nematodes (Knutie *et al.*, 2017a, Knutie *et al.*, 2017b, Shu *et al.*, 2019a), and one using trematodes (Hernández-

Gómez *et al.*, 2020b). We need more studies that focus on how shifts in microbiota diversity influence other relevant functional metrics such as intestinal histology or morphology (as in Ya *et al.*, 2019, Ya *et al.*, 2020, Huang *et al.*, 2021, and Liu *et al.*, 2022c), reproductive success, growth/development (as in Hernández-Gómez *et al.*, 2020b), metabolism (Chapman *et al.*, 2022), and survival (as in Knutie *et al.*, 2018, Harrison *et al.*, 2019, and Chai *et al.*, 2022).

### Population Level

Studies that incorporate population components into their amphibian design sampled microbiotas of a particular variety across more than one population of the same species. Much of this work used natural observations to compare microbiotas across geographically distant populations within the range of a particular taxon. Across the range of multiple aquatic and terrestrial amphibian species, numerous studies document a distance decay relationship in the similarity of microbiotas among populations (Griffiths *et al.*, 2018, Loudon *et al.*, 2020, Walker *et al.*, 2020, Song *et al.*, 2021). The negative relationship between distance and microbiota similarity across broad host ranges suggests that there are limits to the dispersal of bacteria among populations, that likely result from dispersal barriers or environmental change. Microbial turnover among populations has been associated with differences in disease histories (Jani & Briggs, 2014, Rebollar *et al.*, 2016a, Hernández-Gómez *et al.*, 2017b, Jani *et al.*, 2017, Kueneman *et al.*, 2017, Bletz *et al.*, 2018, Jani & Briggs, 2018, Campbell *et al.*, 2019, Ellison *et al.*, 2019b, Wilber *et al.*, 2020, Jani *et al.*, 2021, Jervis *et al.*, 2021, Bates *et al.*, 2022, Basanta *et al.*, 2022a), habitat type (Medina *et al.*, 2017, Sanchez *et al.*, 2017, Hernández-Gómez *et al.*, 2020a, Belasen *et al.*, 2021, Basanta *et al.*, 2022a, Basanta *et al.*, 2022b), and habitat quality (Becker *et al.*, 2017; Hughey *et al.*, 2017b, Muletz-Wolz *et al.*, 2018, Assis *et al.*, 2020, Goff *et al.*, 2020, Jiménez *et al.*, 2020, Preuss *et al.*, 2020, Su *et al.*, 2022, Wuerthner *et al.*, 2022). In addition to characterizing the microbial communities, a number of these works have also investigated how environmental differences among populations influence bacteria associated with important physiological factors. For example, the presence of heavy metals in the environment influenced the relative abundance of bacteria associated with digestive functions in gut microbiotas of Mongolian toads (*Strauchbufo raddei*; Zhang *et al.*, 2016). In addition, several studies have observed a negative effect on the relative abundance of Bd inhibitory bacteria on the skin of amphibian populations experiencing disturbance from roads (Wuerthner *et al.*, 2022), agriculture (Jiménez *et al.*, 2020, Preuss *et al.*, 2020), invasive vegetation (Hernández-Gómez *et al.*, 2020a), human land-use (Assis *et al.*, 2020, Buttimer *et al.*, 2021), captivity (Bates *et al.*, 2019), and pollutants (Costa *et al.*, 2016). The body of work evaluating natural variation in microbiotas within a species' range and among populations experiencing different abiotic/biotic pressures highlight environmental filters as a strong driver shaping the distribution of bacterial symbionts across geographical space.

Included in the population category are a few studies that were also assigned to organismal, ecosystem, and biosphere groups because they sampled individuals from distinct populations of the same species. In these cases, expanding the number of populations included in the experimental work have allowed authors to make conclusions as to the generality of amphibian microbiota responses to host/environmental filters. For example, Belasen *et al.*, (2021) observed less diverse skin microbial communities on river frogs that were homozygous for the MHC IIB gene compared to heterozygotes. While river frogs collected in island habitats also exhibited less diverse microbiotas, these differences in alpha diversity between MHC IIB heterozygotes and homozygote hosts were maintained between the two habitats (Belasen *et al.*, 2021). Other host characteristics such as Bd infection status (Jani & Briggs, 2014), microhabitat use (Wuerthner *et al.*, 2022), sex (Krynak *et al.*, 2016, Hernández-Gómez *et al.*, 2018), and life history status (Kueneman *et al.*, 2014, Song *et al.*, 2021) have also been documented as consistent predictors of amphibian microbiota compositional/diversity regardless of population source. In captivity, populations can also have a lingering effect on the composition and stability of microbiotas. Several semi-natural and artificial experiments were included in the population category because they included individuals from more than one population in their study design. In these examples, a degree of population legacy has been observed in the response of individual microbiotas to influence from probiotic therapies (Davis *et al.*, 2017), captivity (Hernández-Gómez *et al.*, 2019, Passos *et al.*, 2018, Xiang *et al.*, 2018, Vaissi *et al.*, 2019), and infection with Bd (Jani &

Briggs, 2014, Bletz *et al.*, 2018, Jani & Briggs, 2018, Wilber *et al.*, 2020). Both natural and artificial experiments that consider population-variation have been helpful in identifying key host and environmental factors important to the microbial ecology of amphibian-associated microbiotas.

Genomic approaches that look at variation in host and microbiome genetics are necessary to identify key host factors influencing microbiotas and responding to environmental change (Box 4). Endemic vs. epidemic studies have shown a microbiota response to Bd infection history; however, most of these techniques do not quantify whether these altered communities differ in their ability to inhibit Bd *in vitro* or *in vivo*. As DNA sequencing becomes more accessible, utilizing technologies such as metagenomics and genomics (see Rebollar *et al.*, 2018) may allow researchers to identify 1) how host adaptive genes respond to pathogen invasion/environmental change? 2) does genetic adaptation to disease/environmental change affect how amphibian hosts interact with microorganisms in their environment or bodies? 3) is there a parallel between microbial symbiont turnover and the function of the microbial communities? An additional consideration in factors that shape microbiota assemblage is the contribution of evolutionary history which is a more cryptic contribution of environmental change. More specifically, different environmental backgrounds may lead to evolutionary responses that may also lead to modifications to host-associated immune factors related to microbial community assemblage. For example, costs associated with salt tolerance made amphibians release more cortisones which might modify the environment where microbes establish (Shidemantle *et al.*, 2021). Collectively, we need to expand our environmental factors to also consider the interaction between population legacy and environmental change.

### Community Level

Studies that evaluate the effects of environmental factors on microbiotas at the community-level address questions including: (1) How do different amphibian species within a community differ in their microbiota? (2) How does living in communities with different environmental conditions influence amphibian microbiota communities? (3) How do other members of the community (e.g., other amphibians and other taxa that function as predators, co-inhabitants, and microbes) influence a focal amphibian's microbiota? Across the community level studies, the majority focus on characterizing and comparing variation in microbiotas of different amphibian species living in the same community to understand the relative contribution of host vs. environmental factors. For example, both McKenzie *et al.*, (2012) and Bletz *et al.*, (2017b) compared the diversity and composition of the bacterial communities on the skin of cohabitating amphibians across different localities. They found that co-habiting amphibian species harbor unique skin bacterial communities indicating that in this system host-specific factors appear to more strongly regulate symbiont communities compared to environmental factors (McKenzie *et al.*, 2012, Bletz *et al.*, 2017b). In addition, a central objective in studies comparing microbiotas of co-habiting amphibians is to explore whether community interactions among amphibian hosts influences microbiota communities in a way that alters patterns of susceptibility or prevalence of pathogenic fungi (Bd or Bsal). For example, Hughey *et al.*, (2022), Rebollar *et al.*, (2019), Jiménez *et al.*, (2019), Martins *et al.*, 2022, and McKnight *et al.*, (2022) compared microbiotas of sympatric tropical/sub-tropical species and found variation in total/fungal-inhibitory bacteria richness and relative abundance was related to Bd infection probability. Alternatively, Neely *et al.*, (2022) and Kruger (2020) observed marginal or no differences in skin microbiome structure between Bd infected and un-infected frogs in temperate environments. Overall, these studies are consistent with the notion that both host and environmental factors independently and interactively influence amphibian microbiotas and ultimately host health.

Of the community-level studies, only ten evaluated how living in communities with different environmental conditions influence microbiotas. For example, Buttner *et al.*, (2021) compared the microbiota of several terrestrial salamander species across different communities in the San Francisco Bay Area, CA and found that variation in community environmental variables (percent forest cover and annual precipitation) influenced the skin microbial communities of some salamander genera more strongly than others. Similarly, Bletz *et al.*, (2017c), Ellison *et al.*, (2019a), Garcia-Recinos *et al.*, (2019), García-Sánchez *et al.*, (2022), Hill *et al.*, (2022), and Muletz-Wolz *et al.*, (2018) characterized the skin bacterial microbiome of several species of closely related salamander/frogs living in communities that differ in habitat quality or ecotype. Overall, studies that have included



taxonomy and habitat characteristics have found that phylogenetic history strongly influences the diversity and community structure of the total bacterial microbiome at higher taxonomic levels (e.g., between orders), but on lower scales (e.g., within genera and species), the effect of habitat predominates. Collectively, these studies underscore the importance of evaluating environmental by host factor interactions and support the growing consensus that environmental factors exert a strong effect on microbiome structure and composition, especially within a species.

Only three studies consider how other members of the community (other amphibians or other taxa (predators, co-inhabitants, microbes) influence amphibian microbiota. Greenspan *et al.*, (2020) used replicated bromeliad microecosystems to test how arthropod communities influence amphibian host microbiome assembly and pathogen burden. They found that arthropods influenced amphibian microbiome assembly by altering the pool of environmental bacteria, reducing host colonization by bacteria and promoting antimicrobial components of aquatic bacterial communities. Lyra *et al.*, (2018) describe differences in both bacterial microbiota alpha diversity and composition between invertebrates and tadpoles inhabiting the same habitat. Although, organisms with similar diets (e.g., snails and tadpoles) shared the highest proportion of OTUs. Finally, Weitzman *et al.*, (2018) describe strong variation in microbiome composition between sympatric amphibians and reptiles. In nature, amphibians face a diversity of inter and intra-specific interactions that may influence microbiota communities yet our understanding of when these ecological interactions influence microbiotas and the functions they perform remain limited.

### **Ecosystem Level**

Studies that look at amphibian microbiomes from the ecosystem level incorporated multiple biotic and abiotic microbial reservoirs in their microbiome surveys to understand the distribution of amphibian bacterial symbionts across hosts and the environment. At the ecosystem level, we included studies that looked at communities of amphibians, or one species, and an environmental source of microorganisms in their sampling design. Most investigations in the ecosystem category used natural observations to study the distribution of microorganisms between amphibians and abiotic environmental components (Table 1). Across all these studies, amphibians shared up to half of their microbial symbionts with the tested environmental source. In aquatic settings, substrates (e.g., water or soil) and amphibians possessed divergent communities, with the former typically possessing a low relative abundance of amphibian-associated bacteria/micro-eukaryotes (Kueneman *et al.*, 2014, Walke *et al.*, 2014, Bletz *et al.*, 2017c, Hernández-Gómez *et al.*, 2017a, Kueneman *et al.*, 2017, Bates *et al.*, 2018, Hughey *et al.*, 2019, Alexiev *et al.*, 2021, Douglas *et al.*, 2021, Martínez-Ugalde *et al.*, 2022). However, studies that looked at host/environment microbiota overlap in terrestrial systems found correlations in the composition of soil and amphibian microbiotas (Fitzpatrick & Allison, 2014, Prado-Irwin *et al.*, 2017, Bird *et al.*, 2018). These observations are evidence that there is some degree of microbial dispersal between the environment and amphibian bodies, and the level of transmission might depend on characteristics of the microhabitat amphibians use across the ecosystem.

Natural observations have also been used to assess the effect of environmental change on environmental reservoirs within amphibian habitats. For example, variation in habitat temperature and precipitation because of altitudinal or latitudinal differences among habitats have been correlated with microbiota turnover in amphibians and environmental surfaces (Albecker *et al.*, 2019, Ruthsatz *et al.*, 2020, Xu *et al.*, 2020b). Semi-natural experiments have also reported amphibian and sometimes environmental microbial community differences when comparing sites across ecosystems that differ in vegetation (Hernández-Gómez *et al.*, 2020a), pollution (Su *et al.*, 2022, Zhu *et al.*, 2022b), and human land use intensity (Hernández-Gómez *et al.*, 2017a, Barnes *et al.*, 2021). One study found richer skin microbial communities on California slender salamanders (*Batrachoseps attenuatus*) inhabiting forest patches dominated by native oak trees compared to invasive eucalyptus trees in central California (Hernández-Gómez *et al.*, 2020a). In addition, Hernández-Gómez *et al.*, (2020a) documented lower body condition indices in salamanders collected from the invasive eucalyptus forest patches indicating a negative impact of dysbiosis, environmental change, or both on host health. Despite these observations, the authors found similar numbers/composition of bacteria among the soil collected from underneath the log where the salamanders were collected from (Hernández-Gómez *et al.*, 2020a). Thus, environmental change might directly or indirectly influence

amphibian microbiotas through alterations of environmental reservoirs, degradation of host health, and/or changes in other a/biotic sources that have not yet been measured.

Because ecosystems may exhibit a non-uniform distribution of microhabitats, sympatric species of amphibians, or even individuals of the same species, may exhibit different communities with different functionalities based on what habitat they utilize. Across more than one study, terrestrial amphibians possessed higher alpha diversities and different microbial communities compared to aquatic or arboreal forms (Kueneman *et al.*, 2014, Rebollar *et al.*, 2016a, Bletz *et al.*, 2017c, Albecker *et al.*, 2019, Wuerthner *et al.*, 2022), and this pattern was mirrored when comparing the communities of biotic/abiotic reservoirs. In a reciprocal transfer experiment between pond and stream habitats Bletz *et al.*, (2016) tracked and found changes in the predicted functions of the gut and skin microbiota of salamander larvae associated with habitat shift. Interestingly, there are numerous examples where there is a correlation between microhabitat use and susceptibility to Bd, with aquatic amphibians being more resistant to the fungus than terrestrial ones (Hossack *et al.*, 2013, Mesquita *et al.*, 2017). Bd zoospores spread via the aquatic environment; thus, it is possible that continuous selective pressure from the pathogen on aquatic amphibians have led to increased immunocompetence. In fact, greater susceptibility to Chytridiomycosis has been observed in terrestrial species that interact with bodies of water less frequently (Bancroft *et al.*, 2011, Mesquita *et al.*, 2017). As a result, different exposure histories among sympatric amphibians generate an interesting phenomenon where Bd can exist both as an endemic and epidemic state within the same geographic area.

Amphibian microbiotas are not closed systems; thus, experimental approaches that consider how disturbance factors such as climate change, invasive species, pollution, captivity, and habitat change influence microbial reservoirs continue to be important. Small-scale ecosystem experiments or even artificial experiments performed in mesocosms that incorporate environmental reservoirs are imperative to measure the response of host-associated and environmental microbiotas to environmental change. Measuring the contribution of biotic and abiotic microbial reservoirs to natural amphibian microbiotas is necessary to identify sources of beneficial and pathogenic microorganisms in the environment. Identifying key environmental reservoirs might benefit the management of captive amphibian microbiotas, as substrates such as water, soil, or plants can be simply incorporated into enclosures under controlled conditions (Loudon *et al.*, 2014, Loudon *et al.*, 2016, Kenison *et al.*, 2020, Michaels & Preziosi 2020). Incorporating abiotic and biotic sources of microorganisms in captive settings might better prepare future translocates by incorporating new and functionally important bacteria into the microbiota (Loudon *et al.*, 2014, Kenison *et al.*, 2020) and/or pre-exposing them to potential pathogens in a controlled setting (Waddle *et al.*, 2021). Thus, identifying key sources of microbial symbionts in the environment might not only allow amphibian microbiome researchers to encapsulate the complexity of host-associated microbiota, but may also have important repercussions for the way captive microbiomes are managed.

### **Biosphere Level**

Studies that incorporate biosphere components into their amphibian microbiota survey design sampled across more than one ecosystem. While amphibian microbiota studies in this category are not numerous, and almost all exclusively are based on natural or semi-natural experiments (Table 1), these studies give a glimpse into the distribution of bacterial symbionts across regional, intercontinental, or sometimes global scales. At the largest scales, biosphere studies use available data from previously published work (Kueneman *et al.*, 2019, Kueneman *et al.*, 2022) or global swab sample libraries (Medina *et al.*, 2019) to evaluate the distribution of bacteria across ecosystems and different taxa. Other studies took a more regional approach and compared amphibian microbial communities between sites in two or more distinct ecosystems (Belden *et al.*, 2015, Vences *et al.*, 2016, Abarca *et al.*, 2018b, Wagener *et al.*, 2021).

Most studies observed the presence of richer communities in the skin of temperate amphibians compared to tropical ones (Belden *et al.*, 2015, Kueneman *et al.*, 2019). Differences in amphibian skin microbiota richness among habitats (e.g., aquatic, terrestrial, arboreal) varied between temperate and tropical areas as well. For example, aquatic amphibians possessed richer skin microbial communities compared to terrestrial ones in tropical systems, but the reverse has been documented in temperate systems (Kueneman *et al.*, 2019, Medina *et al.*, 2019). In contrast, gut microbiotas between tadpoles sampled in Brazil and Madagascar overlapped, suggesting conserved relationships

that might be due to diet or physiology (Vences *et al.*, 2016). Microbial turnover among the skin of amphibians inhabiting different ecosystems occurs mostly at lower taxonomic levels; however, at the phylum level most amphibian skin microbiotas were dominated first by Proteobacteria, followed by Actinobacteria and Firmicutes. Temperate and tropical communities of amphibians also differed in the relative abundance of these phyla. Two transcontinental studies observed lower representation of Proteobacteria in the microbial communities of temperate amphibians compared to tropical ones (Belden *et al.*, 2015, Kueneman *et al.*, 2019). Documented variation between temperate and tropical systems indicate that temperature and moisture are also important filters that influence the microbial ecology of amphibian skin microbiota at global scales.

Experimental studies at global scales are quite difficult to perform (Box 4). However, we encourage future researchers to continue to use the growing list of amphibian microbiota datasets and sample libraries to ask questions related to the distribution of microorganisms across global scales. One caveat that meta-analyses using datasets should take into consideration is how different laboratories, library preparation materials, and DNA sequencing instruments/runs can influence low-taxonomic turnover across samples. Ensuring that the data included in these meta-analyses originate from studies that utilize similar preparation techniques might be one way to limit the influence of variation in library preparation on sequencing bias. On the other hand, establishing standard sample collection, sequencing library preparation, and sequence handling across different laboratories might also facilitate comparisons across studies.

Taking advantage of natural/artificial large-scale events such as species range expansions, drought, or floods might also allow researchers to draw generalities on how these events influence amphibians and their microbiotas. For example, amphibians with broad latitudinal ranges present an opportunity to study how microbiota and host immunity will respond at both the northern and southern extremes of species ranges, as these are likely the areas to exhibit host species expansions/reductions in response to climate change. The effects of local filters on the assembly of amphibian microbiotas is even more evident in studies that compared invasive amphibians inside and outside of their home range. In these investigations, microbiota composition differed between invasive and native populations of Asian common toads (*Duttaphrynus melanostictus*; Santos *et al.*, 2021), cane toads (*Rhinella marina*; Abarca *et al.*, 2018b), guttural toads (*Amietophrynus gutturalis*; Wagener *et al.*, 2021), and American bullfrogs (*Lithobates catesbeianus*; Kueneman *et al.*, 2019), with the invasive species' microbiota often resembling that of resident amphibians of the invaded ecosystem (Kueneman *et al.*, 2019). In this case, studying the response of broadly distributed amphibians to environmental change might provide valuable information to predict how vulnerable and endemic species will respond.

## Conclusion

Host-associated microbiomes play an essential role in the health of organisms. Understanding how environmental factors interact with host-associated factors to shape microbiotas has critical biological, health, and conservation implications. Collectively, our review demonstrates that environmental factors can influence microbiotas through diverse mechanisms at all biological scales. Importantly, while environmental mechanisms occurring at each of the different scales can interact to shape microbiotas, the past ten years of research have mostly been characterized by targeted approaches at individual scales (65.11%). Several studies examine two biological organizational levels (27.23%) but few examine three or more levels (8.94%). Looking forward, efforts considering how environmental factors at multiple organizational levels interact to shape microbiota diversity and function are paramount. Generating opportunities for meaningful cross-disciplinary interactions and supporting infrastructure for research that spans biological scales are imperative to addressing this gap. Additionally, we note that while this review focuses on amphibian microbiota research, the insights, approaches, and areas for future directions are broadly relevant across diverse study systems. Indeed, interest in the role of environmental factors in shaping host-associated microbiomes has grown substantially and span diverse fields within biological sciences from microbiology to ecology and evolution to applied disciplines from medicine, veterinary science, and conservation biology. Despite important advances in our understanding, an important challenge that remains is the need to integrate these efforts across these siloed disciplines. Towards this end, we call for generating opportunities for

meaningful cross-disciplinary interactions and supporting infrastructure for research that spans biological scales through:

- Continued efforts that facilitate interactions across disciplines such as joint conferences or targeted symposiums that bring researchers from different disciplines together.
- Efforts at developing standardized approaches for diverse study organisms (including non-model organisms) across disciplines and across biological scales.
- Continued hierarchical approaches that simultaneously and systematically evaluate the effect of environmental factors and their interaction with host-factor to shape microbiotas including:
  - Studies that include more than one population/community/ecosystem
  - Studies that evaluate environmental conditions and systematically assess microbiota responses from organismal to biosphere levels.
- Improved data transparency and accessibility to facilitate collaborations and application of novel statistical tools (e.g. machine learning approaches that facilitate efforts to utilize data to generate predictive models for applied purposes in health or conservation).

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